Movement patterns and activity levels are shaped by the neonatal environment in Antarctic fur seal pups

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Abstract

Tracking studies of juveniles are rare compared to those of adults and consequently, little is known about the influence of intrinsic and extrinsic factors on activity during this critical life stage. We therefore collected GPS data from birth until moult from 66 Antarctic fur seal pups in two nearby but contrasting breeding colonies. The Special Study Beach (SSB) is a high-density colony separated from the inland tussock grass habitat by a steep gully, whereas Freshwater Beach (FWB) is a low-density colony that is topographically more open. We investigated the explanatory power of multiple individual-based and environmental variables using a hidden Markov model. We found that activity was typified by central place exploration, with directed movement away from and subsequent return to a location of low activity. The probability of such directed exploration was unaffected by several factors known to influence marine mammal movement including sex, body condition and temperature. Conversely, FWB pups were more active, increased their activity with age and transitioned earlier into the tussock grass, which offers protection from predators and extreme weather. Our study illustrates the profound importance of extrinsic factors to early movement and highlights the adaptive potential of movement in the face of environmental variability.

Keywords

Activity, animal movement, fur seal, GPS, hidden Markov model (HMM), pinniped

Introduction

Movement is a defining characteristic of life, and it underpins critical components of behaviour [1] and fitness [2]. Understanding how animals adapt their movement in response to external and internal stimuli is therefore fundamental to the management and conservation of wild populations [1,3]. Rapid advancements in bio-logging technology and the increased accessibility of statistical tools for drawing meaningful inference from fine-scaled observations has led to unprecedented insights into the movement of a variety of species in their natural habitats [4,5]. Marine vertebrates in particular have benefited from such improved methodologies, exemplified by a recent analysis of more than 2,600 tracked individuals documenting extraordinary convergence in movement patterns across 50 species [6].

Despite these advancements, several authors have drawn attention to age and sex biases in the literature, with datasets of adult females being particularly over-represented [3,7]. This focus on adults is problematic because the movement and distribution of neonatal and juvenile individuals is of key importance for understanding population dynamics. For example, long-term monitoring of three albatross species has shown that high rates of juvenile mortality due to interactions with fisheries are likely driving observed declines in population size [8]. Similarly, loggerhead sea turtles occupy distinct oceanic environments as juveniles, making them more susceptible to bycatch on pelagic longlines [9].

In addition to informing conservation efforts, studies of the movement of young individuals can also provide valuable insights into the ontogeny of social and survival skills. A tracking study of European shags, for example, has shown that higher rates of juvenile mortality correlate with poor foraging proficiency [10], highlighting the importance of learning and memory for successful recruitment. Studies of several different pinniped species including Antarctic fur seals [11], New Zealand sea lions [12], Steller sea lions [13], northern fur seals [14] and grey seals [15] have also shown that sex-specific differences in foraging and diving behaviour become established early in life, implying that intrinsic factors may outweigh size-related effects associated with early sexual dimorphism on habitat choice.

These and other studies represent an important step forward in the field of movement ecology because they help to close the gap between adult movement and the ‘lost years’ of juveniles [3]. However, with few exceptions, studies of juveniles have focused on the period after nutritional independence. While this can be justified for many birds and other species where neonates are more or less stationary until weaned, in many other species movement behaviour and social interactions among conspecifics earlier in life play a key role in

development. For example, play behaviour in pre-weaned Stellar sea lions and Galápagos fur seals facilitates the development of muscle mass and hones fighting skills that are important for future foraging and reproductive success [16,17].

Antarctic fur seals (*Arctocephalus gazella*) are another pinniped species where neonatal movement may play an important role in early development. Newborn pups are regularly left unattended in dense rookeries while their mothers, who are central place foragers, intersperse short periods of nursing on land with longer foraging trips at sea [18]. Without their mothers to defend them, pups are at an increased risk of predation from predatory birds [19] and traumatic injury due to crushing by territorial males [20,21]. Furthermore, the natal coat of pups lacks the water-repellent properties of adult fur [22], which prevents them from spending prolonged time at sea, so pups can only begin to develop the efficient swimming and diving behaviour necessary for nutritional independence after they moult at around 60 days of age [23,24]. Anecdotal observations of pups venturing into shallow pools and streams shortly after birth [23] and the emergence of sex-specific differences in habitat use later in life [25] provide some insights into pup activity, but we still know surprisingly little about the intrinsic and extrinsic factors that may shape pup movement prior to moulting.

Here, we analysed hourly GPS data from 66 Antarctic fur seal pups tracked from birth until moulting (Figure 1) using a hidden Markov model. Focal individuals were selected at random from two breeding colonies, the “Special Study Beach” (SSB) and “Freshwater Beach” (FWB), which are separated by around 200 meters. Because of their close proximity, these colonies experience comparable climatic conditions and breeding females from both locations likely forage in the same area [26], which is reflected by the fact that they do not differ significantly in quality traits such as body size or condition [27]. However, the density of animals is higher at SSB than at FWB [27]. This creates a different dynamic, first because tightly packed males at SSB have little freedom to move, resulting in a more static system [28], and second because avian predators are better able to penetrate low density breeding aggregations on FWB, leading to a greater likelihood of pups being predated [27]. The two colonies also differ in their size and topology. SSB is somewhat smaller and relatively ‘closed’ as a steep gully separates the beach from the tussock grass immediately inland, while FWB is flatter and consequently more ‘open’.

We used these two colonies as a ‘natural experiment’ to investigate the influence of the early neonatal environment on fur seal movement, as well as to evaluate the relative importance of extrinsic versus intrinsic factors such as sex, age and body condition.

Furthermore, as the number of breeding individuals, foraging trip durations and pup birth weights vary appreciably from year to year depending on local food abundance [29], we replicated our study across two consecutive seasons of contrasting food availability [27]. We hypothesised that (i) intrinsic and extrinsic factors shown in previous studies to influence movement in pinnipeds, including sex [30–32], body condition [33] and ambient temperature [34–36], will also affect the movement of Antarctic fur seal neonates, (ii) activity levels and movement patterns will be influenced by density, with FWB pups being more active to avoid predation, and (iii) levels of pup activity will increase with age, as there is likely strong selection for the early development of motor skills and lean muscle mass.

Methods

Field methods

This study was conducted at two breeding colonies on Bird Island, South Georgia (54°00’24.8 S, 38°03’04.1 W; Figure 2a) during the austral summers (December to March) of 2018 – 19 (hereafter referred to as 2019) and 2019 – 20 (hereafter referred to as 2020). The first of these years was among the worst on record in terms of breeding female numbers, pup birth weights and maternal foraging trip durations [27], implying that 2019 was a year of unusually low food abundance [29,37,38].

In both seasons, 25 Antarctic fur seal pups from each colony were captured two to three days after birth (December) and every ten days thereafter until they began to moult (March). Individuals were randomly selected with respect to sex and birth date during the pupping period. Capture, restraint and handling of pups followed protocols established over 36 consecutive years of the long-term monitoring and survey program of the British Antarctic Survey (BAS). Briefly, pups were captured with a slip noose or by hand and were restrained by hand. After handling, pups were returned to their mothers or released as close to their capture sites as possible. At every capture, weight and length measurements were taken, from which a scaled mass index was calculated according to Peig and Green [39]. This condition metric serves as a reliable indicator of overall fitness as it has been correlated with mortality [40] and reproductive success [41] in a variety of species.

To facilitate the tracking and recapture of focal individuals, VHF transmitters (Sirtrack core marine glue-on V2G 152A; dimensions: 40 x 20 x 10 mm body with a 200 mm antenna, weight: 16 g) were attached to the dorsal side of the neck between the shoulder blades with epoxy glue. Pups were similarly fitted with GPS loggers in waterproof ABS plastic enclosures (Perthold Engineering CatLog Gen2 GPS Loggers; dimensions: 50 x 40 x 17 mm, weight: 36 g), which recorded latitude and longitude positions every hour from birth until moulting of the pelage (Figure 1). Together, these two tags accounted for less than 1% of the mean focal pup mass at first capture (5.6 kg). Temporary bleach marks (Clairol Nice’n Easy Borne Blonde Permanent Hair Color) applied to the fur were used to identify pups. Unrecovered tags (n = 12) and bleach marks are shed naturally when the seals moult (March – April), precluding any long-term consequences for the pups.

As part of the BAS contribution to the Ecosystem Monitoring Programme of the Convention for the Conservation of Antarctic Marine Living Resources (CCAMLR), the attendance behaviour of breeding females has been monitored since 1982, with radio telemetry protocols established in 1992 to track around 25 adult females per season on FWB.

We contributed towards this ongoing effort by attaching VHF transmitters (Sirtrack core marine glue-on V2G 154C; dimensions: 65 x 28 x 13 mm body with a 250 mm antenna, weight: 42 g) to the mothers of our focal FWB pups. Adult females were captured with a noosing pole and held on a restraint board. Daily attendance was monitored using a fixed-position radio antenna (Televilt RX900) combined with visual checks of the island with a hand-held VHF receiver (AOR Ltd., AR8200). The daily absence or presence of females ashore was noted from first capture until the final measurement, when the pups either moulted or died. Mothers were fitted with cattle ear tags (Dalton Supplies, Henley on Thames, UK) in the trailing edge of each fore flipper [42] for identification.

Data analysis framework

Within our dataset, hourly GPS data were successfully collected from a total of 66 Antarctic fur seal pups (breakdown by season: n = 40 in 2019 and n = 26 in 2020; by colony: n = 32 at FWB and n = 34 at SSB). The majority of tracked individuals (n = 53, or 80%) survived until weaning. For those individuals that died, we truncated the GPS data back to the last time point that the animal was seen alive prior to analysis.

Our GPS data contained some missing locations, which in a handful of cases led to observation gaps of several hours. Most if not all missing values likely arose due to signal lapse, which occurs when the satellite connection to a GPS device is interrupted due to cloud cover, physical obstruction, etc. [43]. In an otherwise regular sequence, such missing data are manageable, but large gaps may introduce bias into the model [44]. Therefore, for observational gaps exceeding four hours, we split the individual's track into separate bursts or intervals of continuous data. Bursts that were shorter than 48 hours usually contained a considerable amount of missing observations and were therefore excluded from the analysis, corresponding to roughly 2% of the full dataset including missing locations. Overall, the tracks of 35 individuals were split into two to five bursts, while data from all other individuals (n = 31) consisted of a single burst.

Our final dataset contained 67,417 hourly observations with a median number of 1,124 observations per individual (min = 88, max = 1,916). The step lengths (in meters) between consecutive GPS locations were calculated and screened for implausible movements. We set all values larger than 400 meters/hour (corresponding to 297 observations) to be missing. This is in accordance with Jones *et al.* [25], who found that 300 meters was the maximum distance Antarctic fur seal pups younger than 50 days of age travelled.

To investigate environmental factors influencing pup movement, hourly dry bulb air temperature and wind speed measurements for Bird Island were obtained from the BAS Meteorology and Ozone Monitoring Programme, and missing values (85 observations) were linearly interpolated. The binary variables sex (with female as the reference category) and season (with 2019 as the reference category) were held constant for each individual. The continuous variables age (measured in days since initial capture, two to three days after birth) and scaled mass index (calculated every ten days) were kept constant between days and measurements. All metric variables were standardised. All analyses and visualisations for this study were implemented in R version 4.0.2 [45] using the integrated development environment RStudio [46].

Hidden Markov models

To investigate the explanatory power of environmental and individual-based variables on pup movement, we fitted a hidden Markov model (HMM) to the hourly GPS data. This time series model encompasses both the observed movement of an individual and an underlying ('hidden') state sequence, which is used to infer behavioural processes (e.g. active/ inactive) [5]. HMMs have accordingly been used to analyse animal tracking data in relation to, among others, environmental conditions [47], anthropogenic activity [48], sex [49], ontogeny [50] and individualised niches [51].

To distinguish between different behavioural processes in Antarctic fur seal pups, we fitted HMMs to the hourly observed step lengths. We assumed the observation process to be the same for all individuals and modelled the step lengths using a gamma distribution, conditional on the states. Prior to building a final model, we conducted exploratory analyses on the number of states and compared univariate HMMs to bivariate HMMs additionally including the turning angle between consecutive GPS locations (see Supplementary Material S3 for more details). We restricted our final analysis to a parsimonious univariate HMM with two states as the inclusion of the turning angle as well as additional states resulted in a negligible improvement of model fit while complicating the interpretation of the underlying states [52]. To check whether the HMMs based on hourly data adequately reflect the animals' movement behaviour, we also fitted an HMM to five-minute interval GPS data collected from three fur seal pups, each between 30 – 50 days of age, for 13 – 19 days (mean = 3,965 data points). The results showed that with the coarser temporal resolution (hourly data) there was no relevant loss of information on pup activity with respect to the aims of the study (see Supplementary Material S4 for more details).

We further investigated the effects of external and internal factors – including colony, season, time of day, temperature, wind speed, sex, age and body condition – on the activity level of fur seal pups by modelling state transition probabilities as a function of the covariates using a logit link function. We allowed the effects of the covariates to differ between the two colonies by including interaction terms with the binary covariate 'colony' (FWB/SSB). To account for the periodic nature of time of day, its effect was modelled using trigonometric functions. To assess the relative importance of the covariates, we calculated the differences in AIC values between the full model and models sequentially excluding each covariate and its interaction with colony. All HMMs were fitted by numerically maximising the likelihood using *moveHMM* [44]. To further investigate model fit, we calculated pseudo-residuals and checked them for normality and autocorrelation [5]. Based on the full model, we inferred the most likely underlying state sequence using the Viterbi algorithm [5]. We also calculated the state occupancy probabilities as a function of each covariate [53], while fixing the other covariates to their respective means or reference categories.

Post-hoc analyses

The HMM decomposed the GPS data into two distinct states, which we inferred as 'inactive' and 'active' movement (see Results for more details). To determine whether additional variables that we were not able to include in the HMM explain a significant proportion of variation in activity, we built two generalised linear mixed models (GLMMs) *post-hoc*. In our first model, we included maternal attendance (0 = present ashore, 1 = absent) as the explanatory variable. As data on maternal attendance were only available for pups born on FWB, this covariate could not be included in the full HMM, which defined an interaction term between all covariates and 'colony'. In our second model, we used the survival status of each pup (0 = died, 1 = survived) as the explanatory variable. Here, we wanted to test for an association between survival status and movement without assuming the direction of causality. In both models, pup ID was included as a random effect to account for repeated measurements of individuals. The response variable was the inferred state of an individual (0 = inactive, 1 = active) at a given time point and was modelled with a binomial error distribution using *lme4* [54]. The residuals of the models were visually inspected for linearity and equality of error variances (using plots of residuals versus fits), normality (using Q – Q plots) and over or under-dispersion (by comparing the dispersion of simulated to observed residuals) using *DHARMa* [55].

Animal ethics and permits

Animal handling was carried out by the British Antarctic Survey under permits from the Government of South Georgia and the South Sandwich Islands (Wildlife and Protected Areas Ordinance (2011), RAP permit numbers 2018/024 and 2019/032). All procedures used were approved by the British Antarctic Survey Animal Welfare and Ethics Review Body (AWERB applications 2018/1050 and 2019/1058).

Results

Hourly GPS data were successfully collected from a total of 66 Antarctic fur seal pups from two nearby but contrasting breeding colonies (Figure 2a). Deployment durations ranged from 20 to 80 days (median = 51 days) for the 53 surviving pups and from 4 to 41 days (median = 15 days) for the 13 pups that died. On average, pups travelled 43.9 meters per hour. In general, pup movement showed a star-like pattern characterised by directed exploration within a relatively small area around a central location of low activity (Figure 2b). However, the spatial distribution of these 'home patches' varied by colony. Pups born at FWB remained significantly closer to their natal colony (Wilcoxon rank sum test, p = 0.002), traveling on average 87.6 meters into the tussock grass immediately inland. By contrast, pups born at SSB moved an average of 205.0 meters from their natal colony in a wider variety of directions (Figure 2c).

Hidden Markov model: Activity patterns of fur seal pups

The two states of the HMM were clearly discriminated from each other. State 1 captured smaller step lengths (mean step length = 22.5 meters) corresponding to less active movement and is hereafter referred to as the 'inactive state'. State 2 was characterised by more active behaviour covering longer distances (mean step length = 75.8 meters) and is hereafter referred to as the 'active state'. Minimal differences between the marginal distribution under the fitted model and the empirical distribution as well as the analysis of pseudo-residuals suggest that our model provides a good fit to the data (see Supplementary Material S5 for more details). Based on the Viterbi-decoded state sequences, pups spent on average 65.2% (range = 45.7 – 97.3%) of their time in the inactive state and 34.8% (2.7 – 54.3%) of their time in the active state. The pups' decoded movement patterns are summarised in Figure 2b and representative examples of individual tracks are shown in Supplementary Figure S2.

Differences in AIC values (delta AIC) between the full model and HMMs sequentially excluding each variable and its interaction term with colony are shown in Table 1. We considered variables to be relevant for modelling pup activity levels if their delta AIC values were considerably larger than zero. Based on this criterion, the covariates year, time of day and age were determined to have the strongest effects on pup activity levels via both main effects and interactions with colony (Table 1). By contrast, air temperature, wind speed, sex and body condition had little to no influence on activity levels. Pups tended to be slightly more active in the first year of the study, particularly at FWB where the probability of

occupying the active state fell from 43.8% in 2019 to 34.0% in 2020. Activity levels also showed a clear diurnal pattern, peaking in the middle of the day in both colonies (Figure 3a and b). Finally, marked differences were observed in colony-specific developmental trajectories, with animals from FWB exhibiting an almost linear increase in activity with age (Figure 3c), whereas activity levels at SSB remained more or less constant throughout ontogeny (Figure 3d). FWB pups also tended to move inland into the tussock grass earlier than pups from SSB (Figures 3e and f).

Post-hoc analyses

To test additional hypotheses that could not be addressed in the HMM, we performed *post-hoc* logistic regression analyses to evaluate whether the presence of the mother ashore and the fate of the pup (died or survived until the end of the study) explained a significant proportion of the variation in pup activity levels (‘states’). As expected, pups were significantly more active when their mothers were absent from Bird Island on foraging trips (Figure 4a; GLMM, estimate = 0.09, *s.e.* = 0.04, *p*-value = 0.03). More interestingly, the survival status of a pup was also significantly associated with activity (GLMM, estimate = 0.758, *s.e.* = 0.19, *p*-value < 0.001), with pups that survived until weaning spending on average 34% more time in the active state (Figure 4b).

Discussion

We collected and analysed hourly GPS data from Antarctic fur seal pups tracked from birth until moulting in order to investigate the drivers of movement patterns and activity levels during this critical life stage. We found that pup movement was characterised by a star-like pattern, with individuals repeatedly returning to a central location of low activity after bouts of directed exploration. The HMM showed that the probability of such active movement was highest during the day and was mainly influenced by season, colony of birth and age. Our findings provide fresh insights into the movement patterns of pinnipeds prior to nutritional independence and highlight the importance of the life-history stage and the neonatal environment on behaviour.

Movement in fur seal pups

A recent study of movement in Antarctic fur seal pups found evidence for sex-specific differences in habitat use prior to nutritional independence and the onset of overt sexual size dimorphism. Specifically, male pups were found to exhibit more risk prone behaviour with increasing age, traveling further at sea and spending more time in exposed beach habitats [25]. While this study highlighted the importance of an intrinsic factor, sex, on neonatal movement, the contributions of other factors, both intrinsic and extrinsic, remained largely unexplored. We therefore used HMMs to conduct a formal analysis incorporating multiple environmental and individual-based variables including the time of day, air temperature, wind speed, age, body condition and sex. Rather than focusing on animals from a single colony, our study design incorporated variation in both density and terrain by tracking pups from two contrasting breeding colonies, while replication across two consecutive seasons also allowed us to account for inter-annual variation in food availability.

Our hourly GPS data revealed a distinct pattern of terrestrial pup movement that has not been reported in previous studies. Specifically, we documented a star-like pattern characterised by directed movement away from and subsequent return to a location of low activity. This appears to be a genuine behavioural pattern rather than an artefact of our temporal scale of sampling, as GPS locations collected every five minutes from a subset of individuals revealed a very similar picture (Supplementary Material Figure S4). Star-like movement patterns are typified by central place foragers, which make round trips between a central location and a foraging patch [56]. However, as fur seal pups are entirely reliant on their mothers for food until they moult, repeated movements away from a central location are unlikely to have anything to do with resource acquisition. Instead, our results appear to be

indicative of bouts of exploration within a defined radius around a suckling location, which would imply that Antarctic fur seal pups are ‘central place explorers’.

We would expect central place exploration in fur seal pups to be adaptive given that it entails energetic costs and may even make it more difficult for pups to be located by their mothers when they return from foraging trips. We can envisage a number of possible explanations for this behaviour. First, high levels of activity may facilitate the development of the muscle mass necessary for future foraging success. Second, movement both within and beyond the confines of the beach where a pup is born may increase the scope for social interactions, which might be important for future mating success. Third, a transition from beach habitats to the tussock grass offers protection against harsh weather conditions and may reduce the risk of a pup either being crushed by a territorial male or predated.

Results of the HMM

We used an HMM framework to infer the discrete behavioural states underlying pup movement and the probability of switching between these states given certain environmental and individual covariates. This integrated approach to decompose behavioural patterns has been applied across a wide range of species and habitats and has emerged as a powerful tool for animal movement modelling [5]. In our model, we uncovered a strong influence of year, whereby the probability of occupying the active state was higher in the first breading season (2019), particularly for FWB pups. One possible explanation for this pattern could be that inter-annual differences in movement are adaptive. The first breeding season in our study was among the worst on record in terms of breeding female numbers, pup birth weights and foraging trip durations [27], indicating low prey abundance and poor environmental conditions [57]. Local densities at both colonies were correspondingly below average [27]. Given a greater risk of predation at low density [27], pups might increase their activity to avoid harassment, pecking injuries and predation by generalist seabirds, such as southern and northern giant petrels [58]. Alternatively, higher levels of activity could be a consequence of increased stress hormone levels. As mothers spent more time at sea foraging in 2019, pups were subjected to longer periods of food deprivation. Such extended bouts of starvation in pinniped pups have been associated with an increase in glucocorticoids [59], which are known to increase activity levels in some species [60]. Understanding the interrelationships among prolonged fasting, glucocorticoids levels and activity in fur seal pups may help to shed further light on individual responses to environmental challenges.

Another clear extrinsic determinant was the time of day, with activity levels peaking just before solar noon. This observation is in line with a previous study of Galápagos fur seal pups [17], but otherwise very little is known in general about diurnal patterns of activity among fur seals while ashore. Daily meter-resolution location data from densely packed territory holding males reveal negligible movements from day to day [28], implying that these animals remain more or less stationary. By contrast, telemetry studies on adult female fur seals correlate nocturnal foraging behaviour with diel variation in the time of arrival and departure from the breeding colony [61]. Consequently, it is unclear to what extent our results can be extrapolated across the life history, especially given the likelihood of an ontogenetic shift in times of peak activity as pups transition from a reliance on milk to nutritional independence.

The HMM also revealed an increase in pup activity with age, but only for pups born at FWB. One explanation for this colony-specific difference could be that FWB pups are able to express their full behavioural repertoire throughout the course of ontogeny, becoming more active as they grow, whereas pups born on SSB are constrained by the high density of conspecifics. In particular, pups that traverse tightly packed harems on SSB run a higher risk of being crushed by a territorial male or bitten by a breeding female [20,21]. Alternatively, we recently found that FWB pups are more likely to be predated by generalist seabirds [27]. This might translate into an increase of predator-avoidance activity as pups mature, which would help to explain why activity no longer increases after around 40 days of age, when the majority of individuals have transitioned to the more sheltered tussock grass [25].

In addition to pups from FWB increasing their activity over time, we also found that they tended to move earlier into the tussock grass than pups from SSB. While this earlier transition could simply be a consequence of increased activity, it might also be adaptive for FWB pups to move inland as quickly as possible given the higher risk of predation at low density [27]. In other words, pups may move into the more sheltered tussock grass earlier in life to avoid predatory seabirds and might thereafter display a higher propensity for active movement to offset reduced social interactions in the dense vegetation. However, differences in the topography of the two colonies might also influence the timing of this transition, as a steep gully separates the beach at SSB from the tussock grass, while FWB offers a more gradual transition between the two habitats. To disentangle the effects of density and topography would require a larger study embracing a greater diversity of breeding colonies.

Contrary to our initial expectations, the HMM found little to no effect of air temperature and wind speed on pup activity. This is surprising given that the pups in our study

lacked the water-repellent fur of adults and were thus poorly protected from the elements [22]. Reduced activity [34] and huddling behaviour [36] have been documented in pinniped neonates as effective thermoregulatory behaviours to withstand the respectively hottest and coldest daily temperatures, so we anticipated a reduction in pup activity under marginal weather conditions. However, large variation in temperature was not observed on Bird Island (2019 mean temperature = 3.7°C ± *s.d.* 1.3; 2020 mean temperature = 3.9°C ± *s.d.* 1.4). Consequently, behavioural adjustments in activity for effective thermoregulation may not have been necessary in the specific context of our study. Alternatively, other climatic variables that we could not account for, such as precipitation or humidity, may have a disproportionate influence on activity levels. Future studies involving the direct observation of focal individuals under diverse climatic conditions would shed further light on this topic.

The HMM also showed that pup activity levels were largely unaffected by body condition. This was unexpected because Antarctic fur seal pups rely on their mother's milk for nutrition before moulting their pelage and must tolerate bouts of starvation lasting up to 11 days while their mothers forage at sea [18]. As a result, pup growth is known to decline with prolonged maternal absence [62], implying that fewer resources should be available for movement. Taken at face value, the lack of a relationship between body condition and movement may suggest that the short-term benefits of high activity, such as muscle mass development and increased social interaction, may outweigh the costs associated with diverting resources from growth. This would be in line with a previous study that similarly found that Galápagos fur seal pups maintained high activity levels throughout bouts of starvation [17]. However, it is also possible that an effect of body condition could not be detected in our study because our model assumed that condition was constant between successive measurements, whereas in practice it will vary to some extent from day to day.

Despite a number of studies having shown that sex-specific differences in activity, habitat use, foraging and diving behaviour are established early in life in several pinniped species [12–16,63], including Antarctic fur seals [25], our HMM did not uncover any obvious sex differences in activity. This is probably a consequence of the timeframe of our study. Jones *et al.* [25], for example, were only able to detect sex-specific differences in habitat use in Antarctic fur seal pups older than 41 days. Given that we focused on the time window from birth until moulting at around 60 days of age, the results of the two studies are consistent and lend support to the notion that sex-specific movement patterns take several weeks to become established.

Results of the post-hoc *analysis*

Finally, *post-hoc* analysis showed that pups were significantly less active when their mother was ashore, suggesting that pup activity is correlated to some extent with maternal foraging behaviour. This association is most likely a reflection of the upmost importance of milk consumption for pup survival and development. A mother may spend as little as 24 hours and on average only 2 days ashore during each nursing bout [61], so pups must maximise nutrient update during this time. Moreover, adult female fur seals frequently display aggressive behaviour towards foreign pups [20], potentially limiting a pup's opportunity for social interactions when the mother is present [17].

We also found that pups that died tended to be less active. In our dataset, cause of death was assigned to all but one pup as either starvation (n = 5) or predation (n = 6), closely related determinants given that smaller, weaker pups may be more likely to be predated. One possible explanation for the reduced activity of pups that died could therefore be related to poor body condition. While this would appear to contradict the lack of an overall association between activity and condition in the HMM, it is possible that activity may decline only after body condition falls below a critical threshold [17], an effect we may not have captured due to the small number (n = 13) and early occurrence (median = 15 days) of mortalities in our dataset. Alternatively, causality could flow in the other direction, with less active pups being more likely to be predated. This would be more in line with our HMM results as well as with the hypothesis that increased activity is related to predator-avoidance behaviour.

Conclusions

We document the movement behaviour and activity levels of Antarctic fur seal pups between birth and moulting in relation to a multitude of extrinsic and intrinsic explanatory variables. Our findings suggest that during this early life stage, pup activity is mainly shaped by extrinsic factors including year, time of day and colony of birth. In contrast to a previous study of activity later in life [25], we found little effect of intrinsic factors such as body condition and sex. Our study therefore highlights the importance of external influences during this critical phase of life when pups are at their greatest risk of predation and have not yet developed their water-repellent adult coat.

Data Availability Statement

Raw data will be uploaded to the Dryad Digital Repository upon acceptance of this manuscript. R code is available as a R Markdown file and included in the Supplementary material.

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Author contributions

RN, CS, CF-C and CT collected the data. SM and TA built the HMM models. JIH, RL and JF conceived of the study and contributed funding and materials. All of the authors commented on and approved the final manuscript.

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Tables

Table 1: Differences in AIC values (ΔAIC) between the full model and HMMs sequentially excluding each variable and its interaction term with colony.

Covariate	Exclude	AIC	ΔAIC
all		592365	
sex	Interaction with colony	592368.9	3.9
	all terms	592366.3	1.3
age	interaction with colony	592443.7	78.7
	all terms	592534.6	169.6
body condition	interaction with colony	592370.4	5.4
	all terms	592386.5	21.5
time of day	interaction with colony	592377.7	12.7
	all terms	592535.4	170.4
season	interaction with colony	592408.9	43.9
	all terms	592418.4	53.4
temperature	interaction with colony	592367.5	2.5
	all terms	592367.8	2.8
wind speed	interaction with colony	592362.1	-2.9
	all terms	592360.1	-4.9
colony	all terms	592557.5	192.5

Figures

Figure 1: VHF monitoring and GPS tracking. (a) VHF transmitters for pups (top) and mothers (bottom) were temporarily attached to the dorsal side of the neck between the shoulder blades with epoxy glue. GPS loggers in waterproof ABS plastic enclosures were similarly fitted to pups. Tag specifications: Sirtrack core marine glue-on V2G 152A, 40 x 20 x 10 mm body with 200 mm antenna, weight 16 g; Sirtrack core marine glue-on V2G 154C, 65 x 28 x 13 mm body with 250 mm antenna, weight 42 g; Perthold Engineering CatLog Gen2 GPS Loggers, 50 x 40 x 17 mm, weight 36 g. (b) Antarctic fur seal mother-pup pair. VHF transmitters are visible on both individuals, while the pup has additionally been fitted with a GPS logger and given a temporary bleach mark for identification. Unrecovered tags and bleach marks shed naturally with the pelage moult during March to April, precluding any long-term consequences for the animals. Photo credit: Claire Stainfield.

Figure 2: Movement patterns of Antarctic fur seal pups on Bird Island, South Georgia (see inset). (a) Location of the two fur seal breeding colonies from which pups were tagged with GPS loggers. Freshwater Beach (FWB) and Special Study Beach (SSB) are separated by approximately 200 meters. (b) Decoded states from the HMM showing the inferred activity patterns of 66 pups throughout ontogeny. Pups tended to exhibit star-like movement patterns, with directed movement away from and subsequent return to a central location of low activity. (c) GPS locations recorded throughout ontogeny for 32 pups born on FWB and 34 pups born on SSB. Animals from FWB stayed relatively close to their colony of birth, whereas SSB pups often moved farther inland. To aid visibility, each panel is a magnified view of Bird Island (longitude range = -38.060: -38.045, latitude range= -54.014: -54.005) and consequently, some decoded states and GPS points recorded outside this frame are not visible. For a complete map of the entire island showing all recorded states and positions, see Supplementary Material Figure S1. For representative examples of individual GPS tracks, including one pup from each breading colony and season, see Supplementary Material Figure S2.

Figure 3: (a–d) Mean probability (± 95% confidence interval) of being in an ‘active’ behavioural state as a function of the covariates included in the HMM. Probabilities were calculated for each covariate and state by fixing the other covariates to their respective means or reference categories. Confidence intervals for the probabilities were obtained based on Monte Carlo simulation from the estimators’ approximate distribution as implied by

maximum likelihood theory. (a, b) Pups from both breeding colonies exhibit diurnal movement patterns characterised by a higher probability of being active during the day. (c, d) The probability of being in an active state gradually increased from birth to nutritional independence for FWB pups, while SSB pups showed similar levels of activity throughout ontogeny. (e, f) FWB pups moved away from their colony of birth and inland into the tussock grass behind the beach habitat earlier, whereas pups at SSB tended to transition to the tussock grass later in ontogeny.

Figure 4: Results of post-hoc analyses. (a) Pups were less active when their mothers were present on the island; (b) Pups that died spent less time overall in the active state. Sample sizes (*n*), GLMM slope estimates and *p*-values are provided.

Supplementary material

Figure S1: Map of Bird Island, South Georgia, showing all recorded GPS positions and states.

Figure S2: Representative examples of individual GPS tracks, including one pup from each breading colony and season.

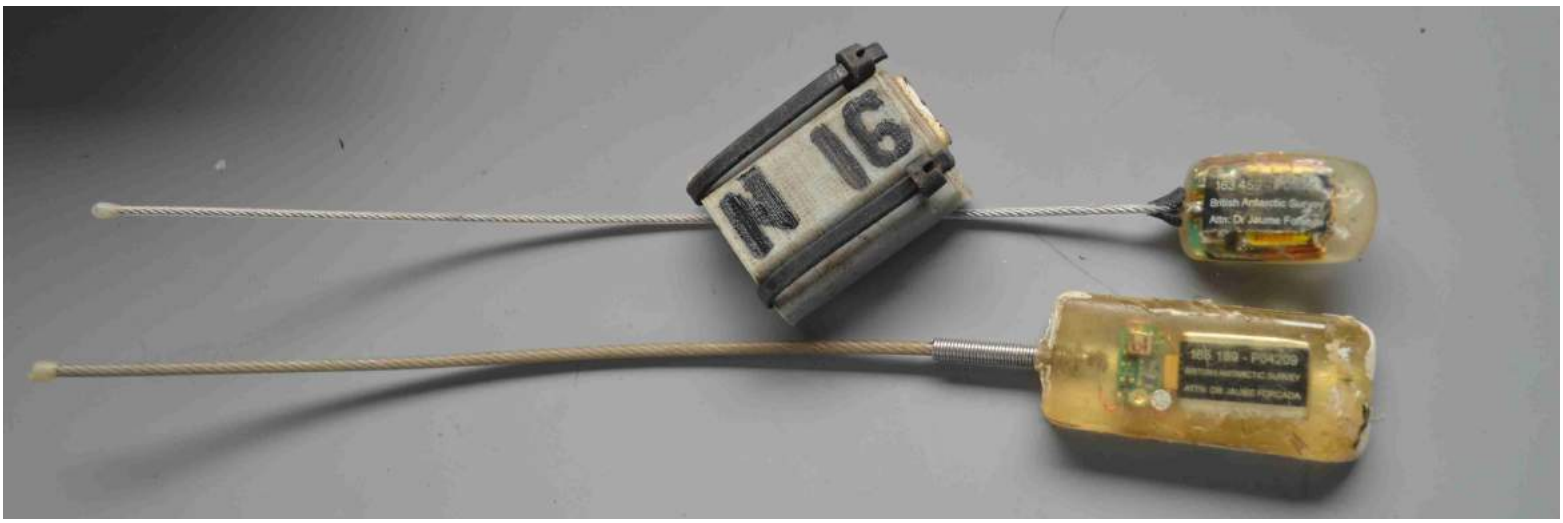
Figure S3: The number of states in an HMM must be specified before running the model and only models with a biologically meaningful numbers of states should be tested. We expected Antarctic fur seal pup movement to include a resting state (short step-lengths), an active state (long step-lengths with more directed movement) and potentially a local exploration state (moderate step-lengths with high degrees of turning). Thus, we evaluated HMMs with two and three movement states, respectively. We also compared univariate HMMs to bivariate HMMs that included the turning angle between consecutive GPS locations. The marginal distribution under the fitted model and the empirical distribution is shown. In the 3-state HMM, the states' distributions of both the step length and especially the turning angle overlapped greatly and did not allow us to adequately distinguish the active from the local exploration state. The distribution of the turning angle in the 2-state bivariate HMM was the same for both states and therefore did not add any information to the model. Overall, neither the additional state (three rather than two) nor the inclusion of the turning angle resulted in a significant improvement of model fit. We therefore restricted our final analysis to a parsimonious univariate HMM with two states.

Figure S4: HMMs fitted to 5-minute interval GPS data collected from three fur seal pups, each between 30 – 50 days of age, for 13 – 19 days (mean = 3,965 data points). We evaluated HMMs with two and three movement states. With respect to the aims of our study, there is no relevant loss of information on pup activity by using the coarser temporal resolution (hourly data).

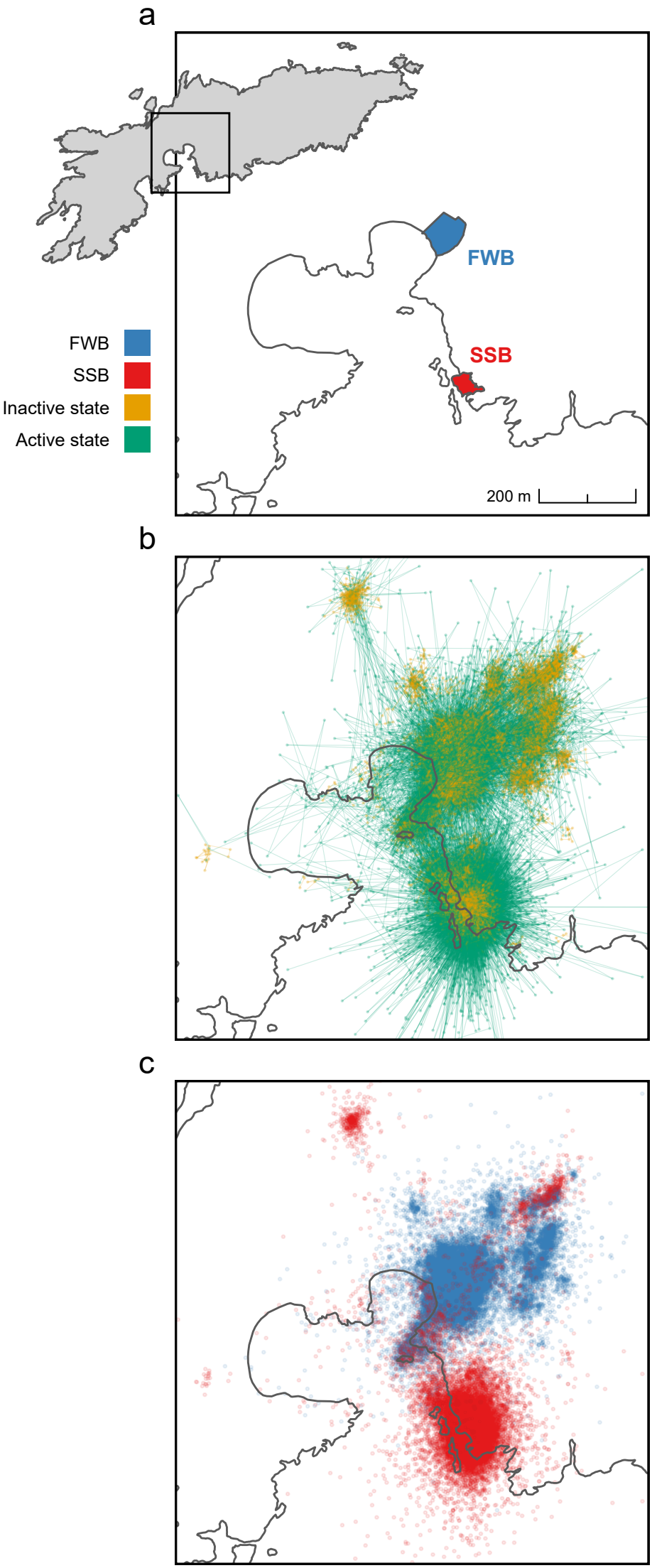
Figure S5: Pseudo-residuals of the final HMM.

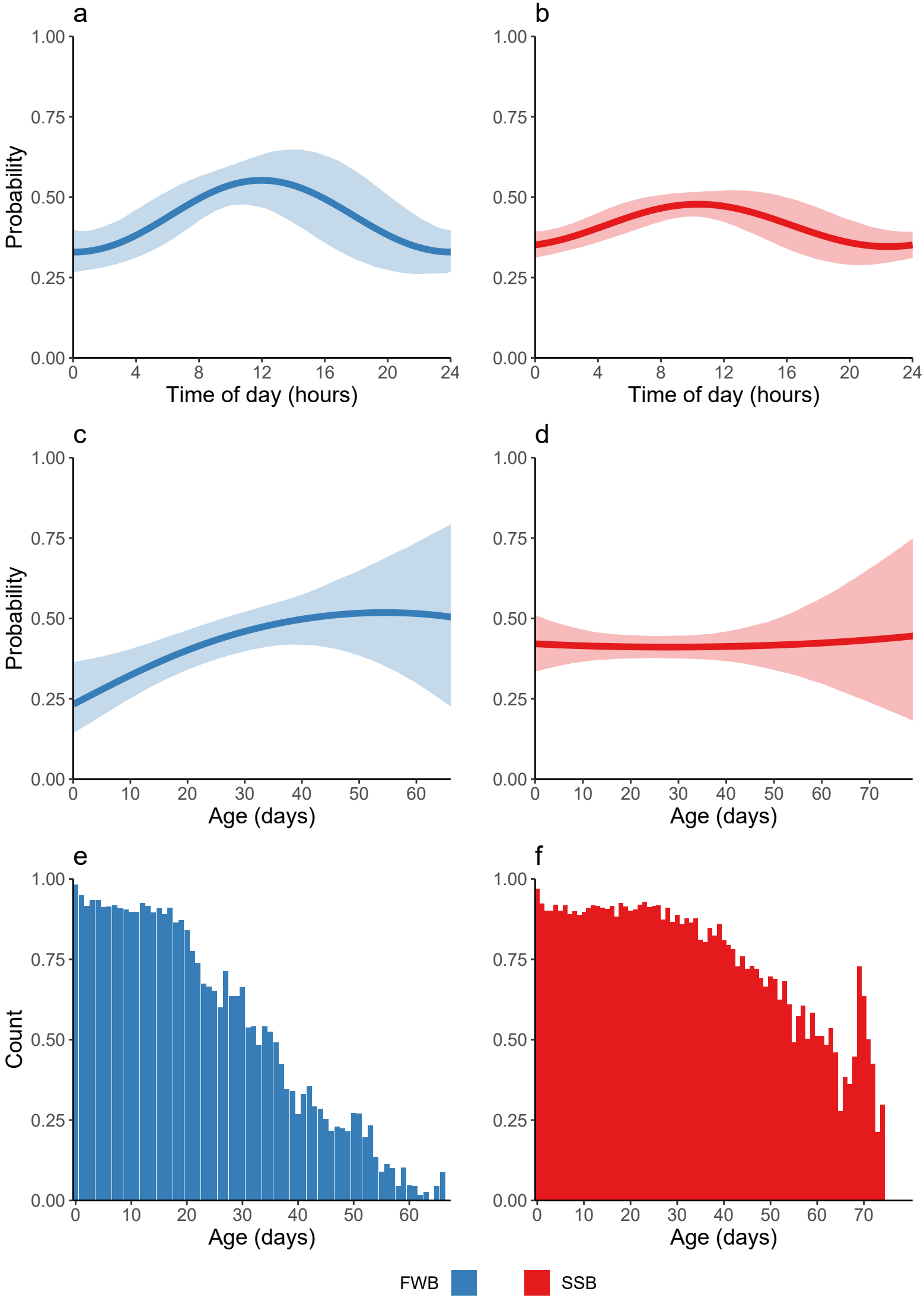
R Markdown

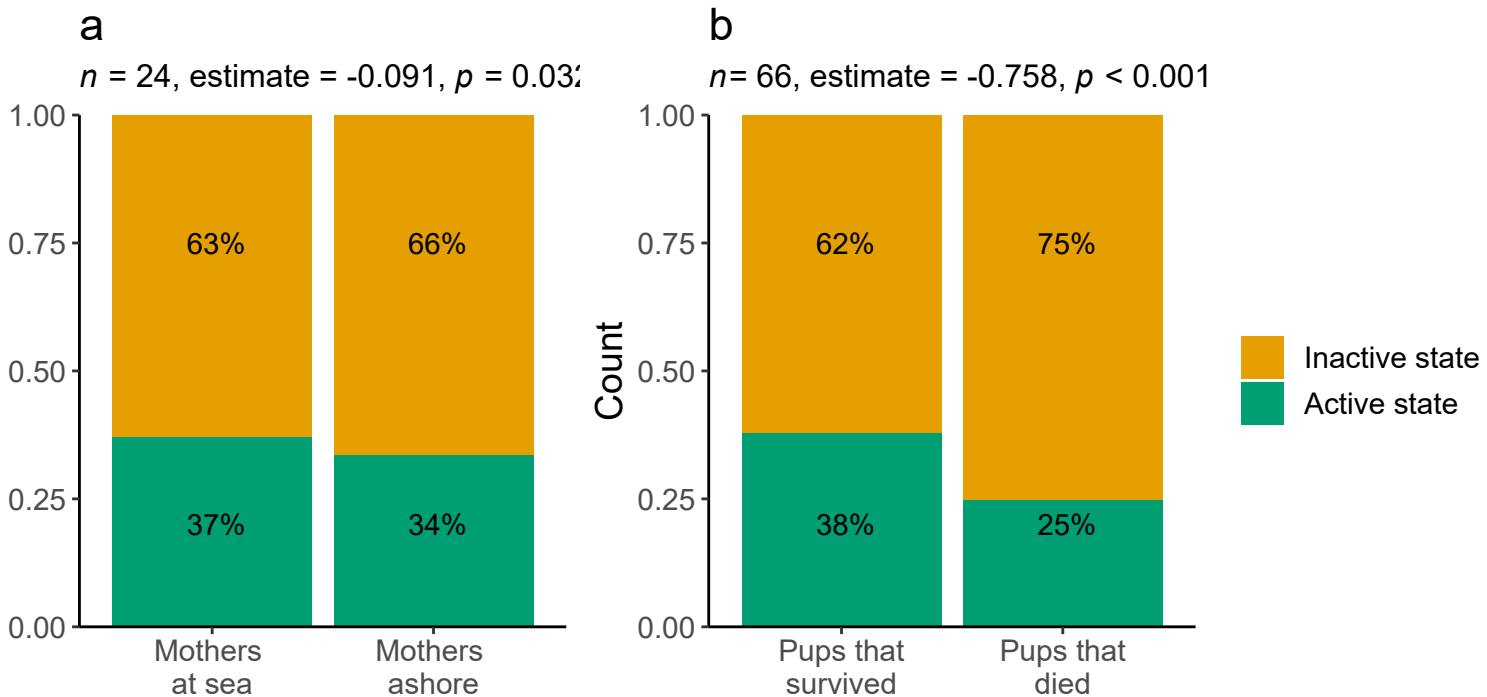
a



b


a
FWB
SSB
Inactive state
Active state
FWB
SSB
200 m
b
c


a
b
c
d
e
f
Probability
Count
Time of day (hours)
Age (days)
1.00
0.75
0.50
0.25
0.00
0
4
8
12
16
20
24
10
30
40
50
60
70
FWB
SSB


a
n = 24, estimate = -0.091, p = 0.03
1.00
0.75
0.50
0.25
0.00
63%
66%
37%
34%
Mothers at sea
Mothers ashore
b
n= 66, estimate = -0.758, p < 0.001
Count
62%
75%
38%
25%
Pups that survived
Pups that died
Inactive state
Active state