1   Movement patterns and activity levels are shaped by the neonatal environment

2   in Antarctic fur seal pups

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19   **Abstract**

20   Tracking studies of juveniles are rare compared to those of adults and consequently, little is

21   known about the influence of intrinsic and extrinsic factors on activity during this critical life

22   stage. We therefore collected GPS data from birth until moult from 66 Antarctic fur seal pups

23   in two nearby but contrasting breeding colonies. The Special Study Beach (SSB) is a high-

24   density colony separated from the inland tussock grass habitat by a steep gully, whereas

25   Freshwater Beach (FWB) is a low-density colony that is topographically more open. We

26   investigated the explanatory power of multiple individual-based and environmental variables

27   using a hidden Markov model. We found that activity was typified by central place

28   exploration, with directed movement away from and subsequent return to a location of low

29   activity. The probability of such directed exploration was unaffected by several factors known

30   to influence marine mammal movement including sex, body condition and temperature.

31   Conversely, FWB pups were more active, increased their activity with age and transitioned

32   earlier into the tussock grass, which offers protection from predators and extreme weather.

33   Our study illustrates the profound importance of extrinsic factors to early movement and

34   highlights the adaptive potential of movement in the face of environmental variability.

35

36   **Keywords**

37   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

72   development. For example, play behaviour in pre-weaned Stellar sea lions and Galápagos

73   seals facilitates the development of muscle mass and hones fighting skills that are important

74   for future foraging and reproductive success [16,17].

75   Antarctic fur seals (*Arctocephalus gazella*) are another pinniped species where

76   neonatal movement may play an important role in early development. Newborn pups are

77   regularly left unattended in dense rookeries while their mothers, who are central place

78   foragers, intersperse short periods of nursing on land with longer foraging trips at sea [18].

79   Without their mothers to defend them, pups are at an increased risk of predation from

80   predatory birds [19] and traumatic injury due to crushing by territorial males [20,21].

81   Furthermore, the natal coat of pups lacks the water-repellent properties of adult fur [22],

82   which prevents them from spending prolonged time at sea, so pups can only begin to develop

83   the efficient swimming and diving behaviour necessary for nutritional independence after they

84   moult at around 60 days of age [23,24]. Anecdotal observations of pups venturing into

85   shallow pools and streams shortly after birth [23] and the emergence of sex-specific

86   differences in habitat use later in life [25] provide some insights into pup activity, but we still

87   know surprisingly little about the intrinsic and extrinsic factors that may shape pup movement

88   prior to moulting.

89   Here, we analysed hourly GPS data from 66 Antarctic fur seal pups tracked from birth

90   until moulting (Figure 1) using a hidden Markov model. Focal individuals were selected at

91   random from two breeding colonies, the "Special Study Beach" (SSB) and "Freshwater

92   Beach" (FWB), which are separated by around 200 meters. Because of their close proximity,

93   these colonies experience comparable climatic conditions and breeding females from both

94   locations likely forage in the same area [26], which is reflected by the fact that they do not

95   differ significantly in quality traits such as body size or condition [27]. However, the density

96   of animals is higher at SSB than at FWB [27]. This creates a different dynamic, first because

97   tightly packed males at SSB have little freedom to move, resulting in a more static system

98   [28], and second because avian predators are better able to penetrate low density breeding

99   aggregations on FWB, leading to a greater likelihood of pups being predated [27]. The two

100   colonies also differ in their size and topology. SSB is somewhat smaller and relatively

101   'closed' as a steep gully separates the beach from the tussock grass immediately inland, while

102   FWB is flatter and consequently more 'open'.

103   We used these two colonies as a 'natural experiment' to investigate the influence of

104   the early neonatal environment on fur seal movement, as well as to evaluate the relative

105   importance of extrinsic versus intrinsic factors such as sex, age and body condition.

106   Furthermore, as the number of breeding individuals, foraging trip durations and pup birth
107   weights vary appreciably from year to year depending on local food abundance [29], we
108   replicated our study across two consecutive seasons of contrasting food availability [27]. We
109   hypothesised that (i) intrinsic and extrinsic factors shown in previous studies to influence
110   movement in pinnipeds, including sex [30–32], body condition [33] and ambient temperature
111   [34–36], will also affect the movement of Antarctic fur seal neonates, (ii) activity levels and
112   movement patterns will be influenced by density, with FWB pups being more active to avoid
113   predation, and (iii) levels of pup activity will increase with age, as there is likely strong
114   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.

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

158

159   *Data analysis framework*

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

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

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

182   To investigate environmental factors influencing pup movement, hourly dry bulb air

183 temperature and wind speed measurements for Bird Island were obtained from the BAS

184 Meteorology and Ozone Monitoring Programme, and missing values (85 observations) were

185 linearly interpolated. The binary variables sex (with female as the reference category) and

186 season (with 2019 as the reference category) were held constant for each individual. The

187 continuous variables age (measured in days since initial capture, two to three days after birth)

188 and scaled mass index (calculated every ten days) were kept constant between days and

189 measurements. All metric variables were standardised. All analyses and visualisations for this

190 study were implemented in R version 4.0.2 [45] using the integrated development

191 environment RStudio [46].

192

193 *Hidden Markov models*

194   To investigate the explanatory power of environmental and individual-based variables

195 on pup movement, we fitted a hidden Markov model (HMM) to the hourly GPS data. This

196 time series model encompasses both the observed movement of an individual and an

197 underlying ('hidden') state sequence, which is used to infer behavioural processes (e.g. active/

198 inactive) [5]. HMMs have accordingly been used to analyse animal tracking data in relation

199 to, among others, environmental conditions [47], anthropogenic activity [48], sex [49],

200 ontogeny [50] and individualised niches [51].

201   To distinguish between different behavioural processes in Antarctic fur seal pups, we

202 fitted HMMs to the hourly observed step lengths. We assumed the observation process to be

203 the same for all individuals and modelled the step lengths using a gamma distribution,

204 conditional on the states. Prior to building a final model, we conducted exploratory analyses

205 on the number of states and compared univariate HMMs to bivariate HMMs additionally

206 including the turning angle between consecutive GPS locations (see Supplementary Material

207 S3 for more details). We restricted our final analysis to a parsimonious univariate HMM with

208 two states as the inclusion of the turning angle as well as additional states resulted in a

209 negligible improvement of model fit while complicating the interpretation of the underlying

210 states [52]. To check whether the HMMs based on hourly data adequately reflect the animals'

211 movement behaviour, we also fitted an HMM to five-minute interval GPS data collected from

212 three fur seal pups, each between 30 – 50 days of age, for 13 – 19 days (mean = 3,965 data

213 points). The results showed that with the coarser temporal resolution (hourly data) there was

214 no relevant loss of information on pup activity with respect to the aims of the study (see

215 Supplementary Material S4 for more details).

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

230

231   *Post-hoc analyses*

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

249

250   *Animal ethics and permits*

251   Animal handling was carried out by the British Antarctic Survey under permits from

252   the Government of South Georgia and the South Sandwich Islands (Wildlife and Protected

253   Areas Ordinance (2011), RAP permit numbers 2018/024 and 2019/032). All procedures used

254   were approved by the British Antarctic Survey Animal Welfare and Ethics Review Body

255   (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

290 occupying the active state fell from 43.8% in 2019 to 34.0% in 2020. Activity levels also

291 showed a clear diurnal pattern, peaking in the middle of the day in both colonies (Figure 3a

292 and b). Finally, marked differences were observed in colony-specific developmental

293 trajectories, with animals from FWB exhibiting an almost linear increase in activity with age

294 (Figure 3c), whereas activity levels at SSB remained more or less constant throughout

295 ontogeny (Figure 3d). FWB pups also tended to move inland into the tussock grass earlier

296 than pups from SSB (Figures 3e and f).

297

298 *Post-hoc analyses*

299 To test additional hypotheses that could not be addressed in the HMM, we performed

300 *post-hoc* logistic regression analyses to evaluate whether the presence of the mother ashore

301 and the fate of the pup (died or survived until the end of the study) explained a significant

302 proportion of the variation in pup activity levels ('states'). As expected, pups were

303 significantly more active when their mothers were absent from Bird Island on foraging trips

304 (Figure 4a; GLMM, estimate = 0.09, *s.e.* = 0.04, *p*-value = 0.03). More interestingly, the

305 survival status of a pup was also significantly associated with activity (GLMM, estimate =

306 0.758, *s.e.* = 0.19, *p*-value < 0.001), with pups that survived until weaning spending on

307 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

342   indicative of bouts of exploration within a defined radius around a suckling location, which

343   would imply that Antarctic fur seal pups are 'central place explorers'.

344   We would expect central place exploration in fur seal pups to be adaptive given that it

345   entails energetic costs and may even make it more difficult for pups to be located by their

346   mothers when they return from foraging trips. We can envisage a number of possible

347   explanations for this behaviour. First, high levels of activity may facilitate the development of

348   the muscle mass necessary for future foraging success. Second, movement both within and

349   beyond the confines of the beach where a pup is born may increase the scope for social

350   interactions, which might be important for future mating success. Third, a transition from

351   beach habitats to the tussock grass offers protection against harsh weather conditions and may

352   reduce the risk of a pup either being crushed by a territorial male or predated.

353

354   *Results of the HMM*

355   We used an HMM framework to infer the discrete behavioural states underlying pup

356   movement and the probability of switching between these states given certain environmental

357   and individual covariates. This integrated approach to decompose behavioural patterns has

358   been applied across a wide range of species and habitats and has emerged as a powerful tool

359   for animal movement modelling [5]. In our model, we uncovered a strong influence of year,

360   whereby the probability of occupying the active state was higher in the first breading season

361   (2019), particularly for FWB pups. One possible explanation for this pattern could be that

362   inter-annual differences in movement are adaptive. The first breeding season in our study was

363   among the worst on record in terms of breeding female numbers, pup birth weights and

364   foraging trip durations [27], indicating low prey abundance and poor environmental

365   conditions [57]. Local densities at both colonies were correspondingly below average [27].

366   Given a greater risk of predation at low density [27], pups might increase their activity to

367   avoid harassment, pecking injuries and predation by generalist seabirds, such as southern and

368   northern giant petrels [58]. Alternatively, higher levels of activity could be a consequence of

369   increased stress hormone levels. As mothers spent more time at sea foraging in 2019, pups

370   were subjected to longer periods of food deprivation. Such extended bouts of starvation in

371   pinniped pups have been associated with an increase in glucocorticoids [59], which are known

372   to increase activity levels in some species [60]. Understanding the interrelationships among

373   prolonged fasting, glucocorticoids levels and activity in fur seal pups may help to shed further

374   light on individual responses to environmental challenges.

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

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

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

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

409 lacked the water-repellent fur of adults and were thus poorly protected from the elements [22].

410 Reduced activity [34] and huddling behaviour [36] have been documented in pinniped

411 neonates as effective thermoregulatory behaviours to withstand the respectively hottest and

412 coldest daily temperatures, so we anticipated a reduction in pup activity under marginal

413 weather conditions. However, large variation in temperature was not observed on Bird Island

414 (2019 mean temperature = 3.7°C ± s.d. 1.3; 2020 mean temperature = 3.9°C ± s.d. 1.4).

415 Consequently, behavioural adjustments in activity for effective thermoregulation may not

416 have been necessary in the specific context of our study. Alternatively, other climatic

417 variables that we could not account for, such as precipitation or humidity, may have a

418 disproportionate influence on activity levels. Future studies involving the direct observation

419 of focal individuals under diverse climatic conditions would shed further light on this topic.

420   The HMM also showed that pup activity levels were largely unaffected by body

421 condition. This was unexpected because Antarctic fur seal pups rely on their mother's milk

422 for nutrition before moulting their pelage and must tolerate bouts of starvation lasting up to 11

423 days while their mothers forage at sea [18]. As a result, pup growth is known to decline with

424 prolonged maternal absence [62], implying that fewer resources should be available for

425 movement. Taken at face value, the lack of a relationship between body condition and

426 movement may suggest that the short-term benefits of high activity, such as muscle mass

427 development and increased social interaction, may outweigh the costs associated with

428 diverting resources from growth. This would be in line with a previous study that similarly

429 found that Galápagos fur seal pups maintained high activity levels throughout bouts of

430 starvation [17]. However, it is also possible that an effect of body condition could not be

431 detected in our study because our model assumed that condition was constant between

432 successive measurements, whereas in practice it will vary to some extent from day to day.

433   Despite a number of studies having shown that sex-specific differences in activity,

434 habitat use, foraging and diving behaviour are established early in life in several pinniped

435 species [12–16,63], including Antarctic fur seals [25], our HMM did not uncover any obvious

436 sex differences in activity. This is probably a consequence of the timeframe of our study.

437 Jones et al. [25], for example, were only able to detect sex-specific differences in habitat use

438 in Antarctic fur seal pups older than 41 days. Given that we focused on the time window from

439 birth until moulting at around 60 days of age, the results of the two studies are consistent and

440 lend support to the notion that sex-specific movement patterns take several weeks to become

441 established.

442

443   *Results of the* post-hoc *analysis*

444   Finally, *post-hoc* analysis showed that pups were significantly less active when their

445   mother was ashore, suggesting that pup activity is correlated to some extent with maternal

446   foraging behaviour. This association is most likely a reflection of the upmost importance of

447   milk consumption for pup survival and development. A mother may spend as little as 24

448   hours and on average only 2 days ashore during each nursing bout [61], so pups must

449   maximise nutrient update during this time. Moreover, adult female fur seals frequently display

450   aggressive behaviour towards foreign pups [20], potentially limiting a pup's opportunity for

451   social interactions when the mother is present [17].

452   We also found that pups that died tended to be less active. In our dataset, cause of

453   death was assigned to all but one pup as either starvation ($n = 5$) or predation ($n = 6$), closely

454   related determinants given that smaller, weaker pups may be more likely to be predated. One

455   possible explanation for the reduced activity of pups that died could therefore be related to

456   poor body condition. While this would appear to contradict the lack of an overall association

457   between activity and condition in the HMM, it is possible that activity may decline only after

458   body condition falls below a critical threshold [17], an effect we may not have captured due to

459   the small number ($n = 13$) and early occurrence (median $= 15$ days) of mortalities in our

460   dataset. Alternatively, causality could flow in the other direction, with less active pups being

461   more likely to be predated. This would be more in line with our HMM results as well as with

462   the hypothesis that increased activity is related to predator-avoidance behaviour.

463

464   *Conclusions*

465   We document the movement behaviour and activity levels of Antarctic fur seal pups

466   between birth and moulting in relation to a multitude of extrinsic and intrinsic explanatory

467   variables. Our findings suggest that during this early life stage, pup activity is mainly shaped

468   by extrinsic factors including year, time of day and colony of birth. In contrast to a previous

469   study of activity later in life [25], we found little effect of intrinsic factors such as body

470   condition and sex. Our study therefore highlights the importance of external influences during

471   this critical phase of life when pups are at their greatest risk of predation and have not yet

472   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.

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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671 **Tables**

672 Table 1: Differences in AIC values (ΔAIC) between the full model and HMMs sequentially

673 excluding each variable and its interaction term with colony.

674

Covariate	Exclude	AIC	ΔAIC	
all		592365		675 676
sex	Interaction with colony	592368.9	3.9	677
	all terms	592366.3	1.3	678
age	interaction with colony	592443.7	78.7	679
	all terms	592534.6	169.6	680
body condition	interaction with colony	592370.4	5.4	681
	all terms	592386.5	21.5	682
time of day	interaction with colony	592377.7	12.7	683
	all terms	592535.4	170.4	684
season	interaction with colony	592408.9	43.9	685
	all terms	592418.4	53.4	686
temperature	interaction with colony	592367.5	2.5	687
	all terms	592367.8	2.8	688
wind speed	interaction with colony	592362.1	-2.9	689
	all terms	592360.1	-4.9	690
colony	all terms	592557.5	192.5	691 692

693

694 **Figures**

695 Figure 1: VHF monitoring and GPS tracking. (a) VHF transmitters for pups (top) and mothers

696 (bottom) were temporarily attached to the dorsal side of the neck between the shoulder blades

697 with epoxy glue. GPS loggers in waterproof ABS plastic enclosures were similarly fitted to

698 pups. Tag specifications: Sirtrack core marine glue-on V2G 152A, 40 x 20 x 10 mm body

699 with 200 mm antenna, weight 16 g; Sirtrack core marine glue-on V2G 154C, 65 x 28 x 13

700 mm body with 250 mm antenna, weight 42 g; Perthold Engineering CatLog Gen2 GPS

701 Loggers, 50 x 40 x 17 mm, weight 36 g. (b) Antarctic fur seal mother-pup pair. VHF

702 transmitters are visible on both individuals, while the pup has additionally been fitted with a

703 GPS logger and given a temporary bleach mark for identification. Unrecovered tags and

704 bleach marks shed naturally with the pelage moult during March to April, precluding any

705 long-term consequences for the animals. Photo credit: Claire Stainfield.

706

707 Figure 2: Movement patterns of Antarctic fur seal pups on Bird Island, South Georgia (see

708 inset). (a) Location of the two fur seal breeding colonies from which pups were tagged with

709 GPS loggers. Freshwater Beach (FWB) and Special Study Beach (SSB) are separated by

710 approximately 200 meters. (b) Decoded states from the HMM showing the inferred activity

711 patterns of 66 pups throughout ontogeny. Pups tended to exhibit star-like movement patterns,

712 with directed movement away from and subsequent return to a central location of low activity.

713 (c) GPS locations recorded throughout ontogeny for 32 pups born on FWB and 34 pups born

714 on SSB. Animals from FWB stayed relatively close to their colony of birth, whereas SSB

715 pups often moved farther inland. To aid visibility, each panel is a magnified view of Bird

716 Island (longitude range = -38.060: -38.045, latitude range= -54.014: -54.005) and

717 consequently, some decoded states and GPS points recorded outside this frame are not visible.

718 For a complete map of the entire island showing all recorded states and positions, see

719 Supplementary Material Figure S1. For representative examples of individual GPS tracks,

720 including one pup from each breeding colony and season, see Supplementary Material Figure

721 S2.

722

723 Figure 3: (a–d) Mean probability (± 95% confidence interval) of being in an 'active'

724 behavioural state as a function of the covariates included in the HMM. Probabilities were

725 calculated for each covariate and state by fixing the other covariates to their respective means

726 or reference categories. Confidence intervals for the probabilities were obtained based on

727 Monte Carlo simulation from the estimators' approximate distribution as implied by

728   maximum likelihood theory. (a, b) Pups from both breeding colonies exhibit diurnal

729   movement patterns characterised by a higher probability of being active during the day. (c, d)

730   The probability of being in an active state gradually increased from birth to nutritional

731   independence for FWB pups, while SSB pups showed similar levels of activity throughout

732   ontogeny. (e, f) FWB pups moved away from their colony of birth and inland into the tussock

733   grass behind the beach habitat earlier, whereas pups at SSB tended to transition to the tussock

734   grass later in ontogeny.

735

736   Figure 4: Results of post-hoc analyses. (a) Pups were less active when their mothers were

737   present on the island; (b) Pups that died spent less time overall in the active state. Sample

738   sizes (n), GLMM slope estimates and p-values are provided.

739 **Supplementary material**

740

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

742

743 Figure S2: Representative examples of individual GPS tracks, including one pup from each

744 breeding colony and season.

745

746 Figure S3: The number of states in an HMM must be specified before running the model and

747 only models with a biologically meaningful numbers of states should be tested. We expected

748 Antarctic fur seal pup movement to include a resting state (short step-lengths), an active state

749 (long step-lengths with more directed movement) and potentially a local exploration state

750 (moderate step-lengths with high degrees of turning). Thus, we evaluated HMMs with two

751 and three movement states, respectively. We also compared univariate HMMs to bivariate

752 HMMs that included the turning angle between consecutive GPS locations. The marginal

753 distribution under the fitted model and the empirical distribution is shown. In the 3-state

754 HMM, the states' distributions of both the step length and especially the turning angle

755 overlapped greatly and did not allow us to adequately distinguish the active from the local

756 exploration state. The distribution of the turning angle in the 2-state bivariate HMM was the

757 same for both states and therefore did not add any information to the model. Overall, neither

758 the additional state (three rather than two) nor the inclusion of the turning angle resulted in a

759 significant improvement of model fit. We therefore restricted our final analysis to a

760 parsimonious univariate HMM with two states.

761

762 Figure S4: HMMs fitted to 5-minute interval GPS data collected from three fur seal pups,

763 each between 30 – 50 days of age, for 13 – 19 days (mean = 3,965 data points). We evaluated

764 HMMs with two and three movement states. With respect to the aims of our study, there is no

765 relevant loss of information on pup activity by using the coarser temporal resolution (hourly
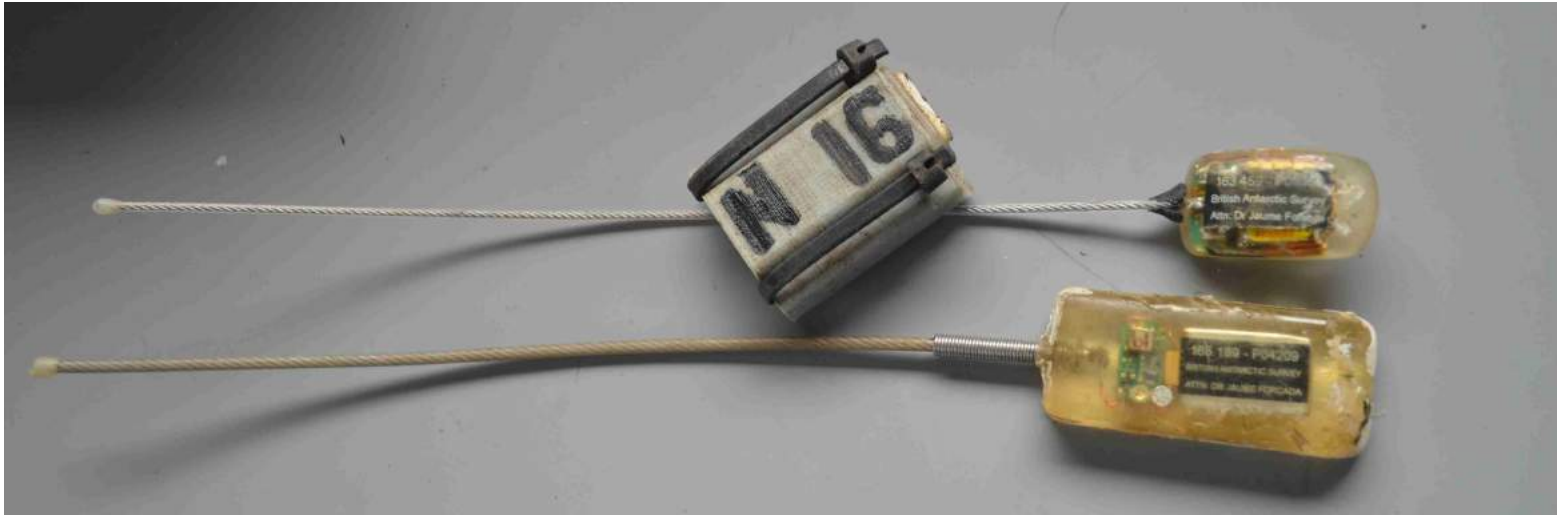
766 data).

767

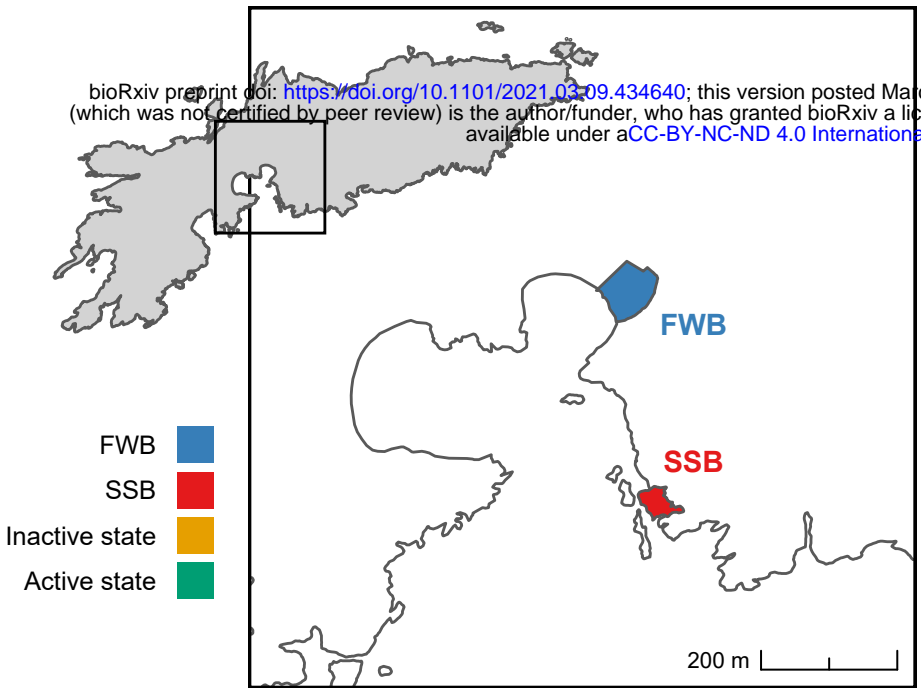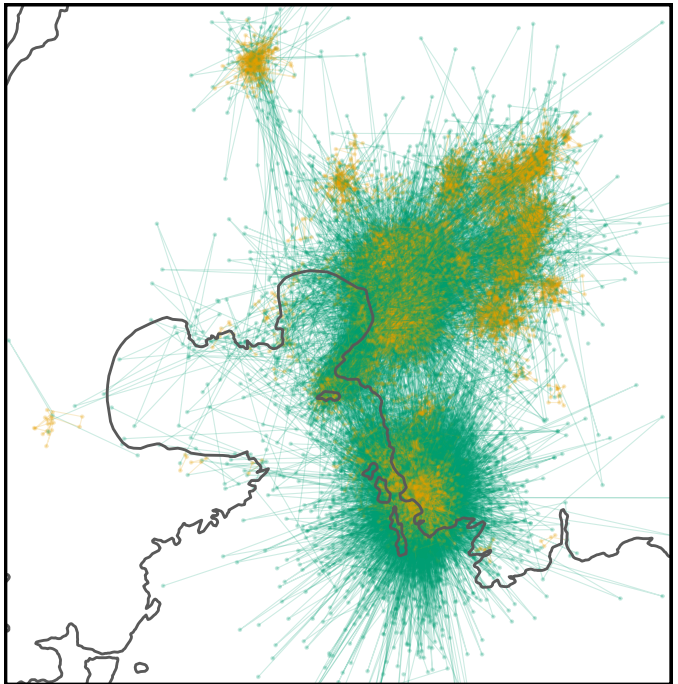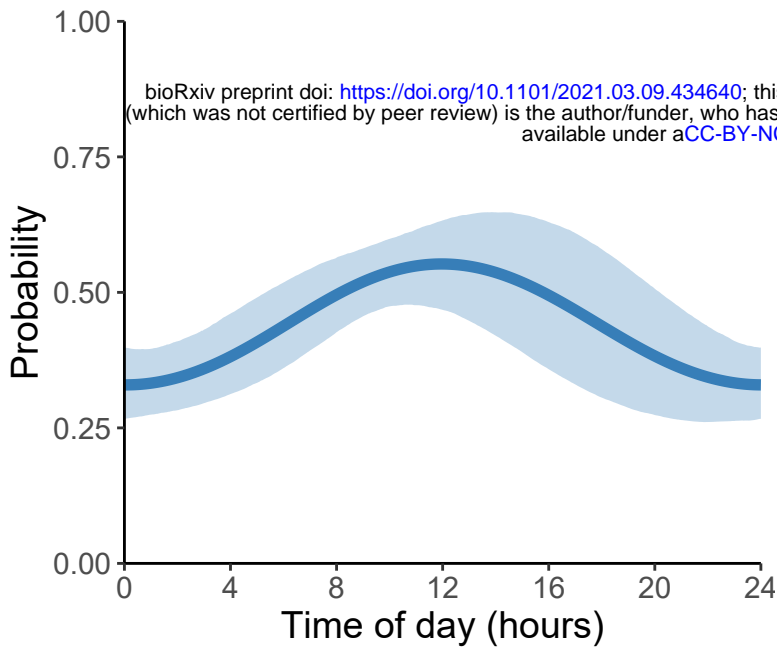768 Figure S5: Pseudo-residuals of the final HMM.

769

770 R Markdown

a

b
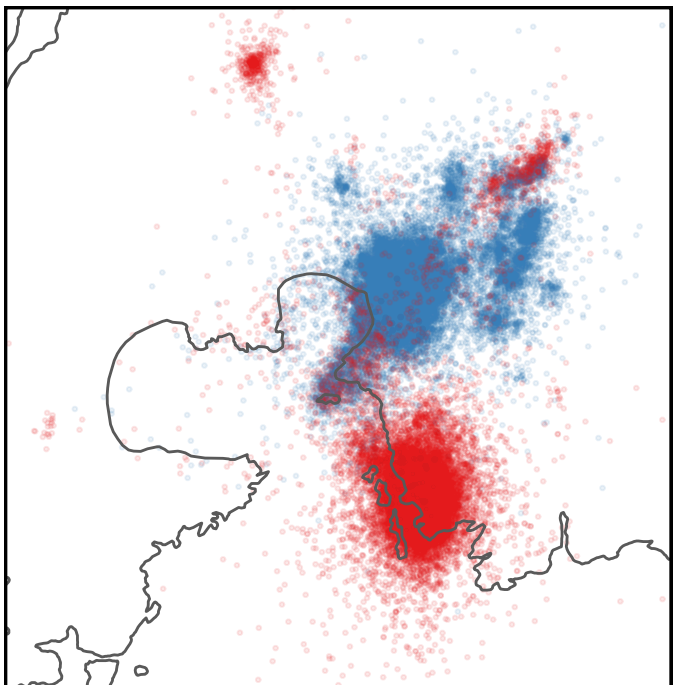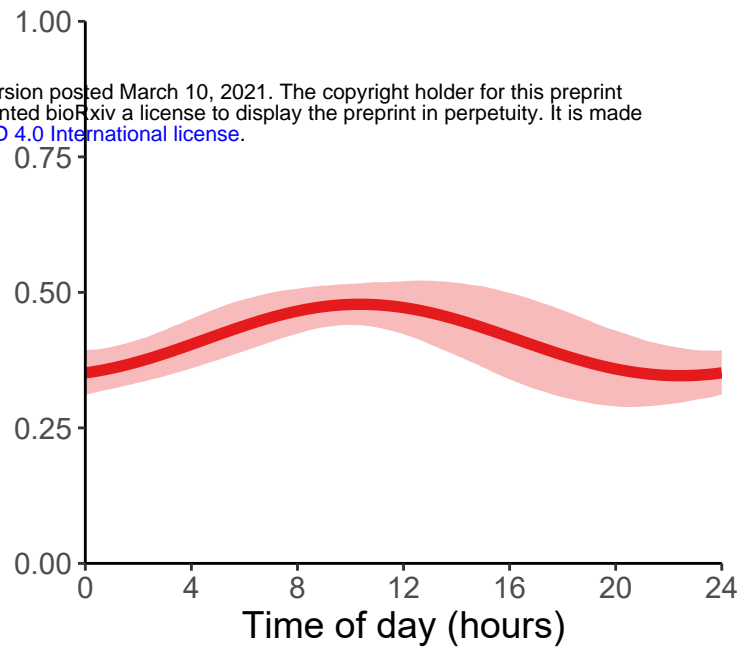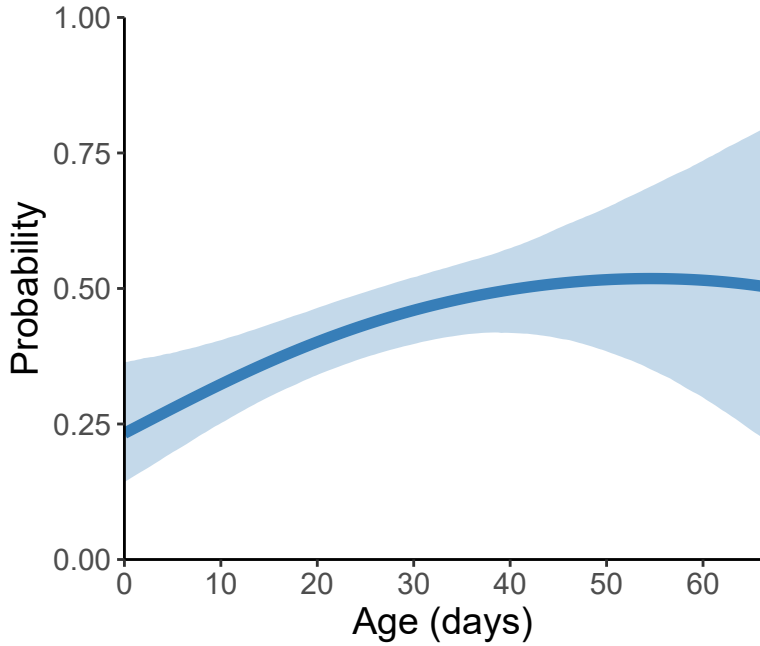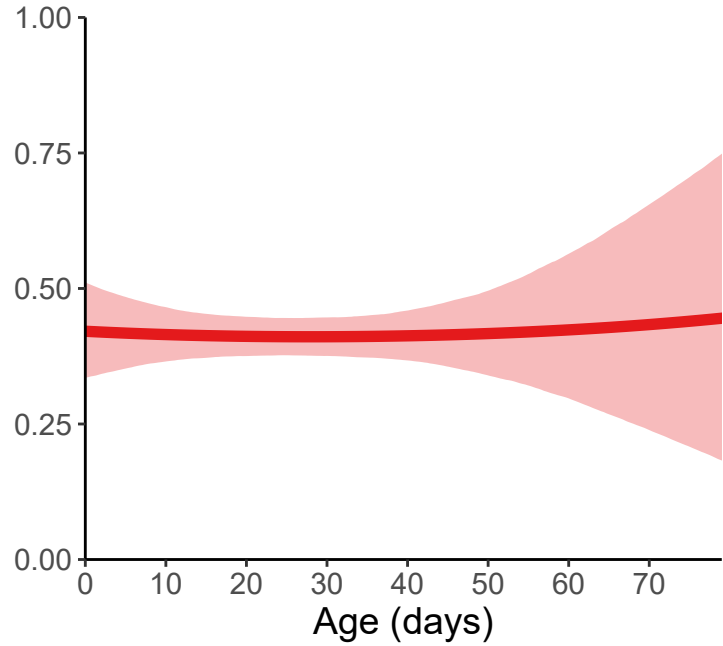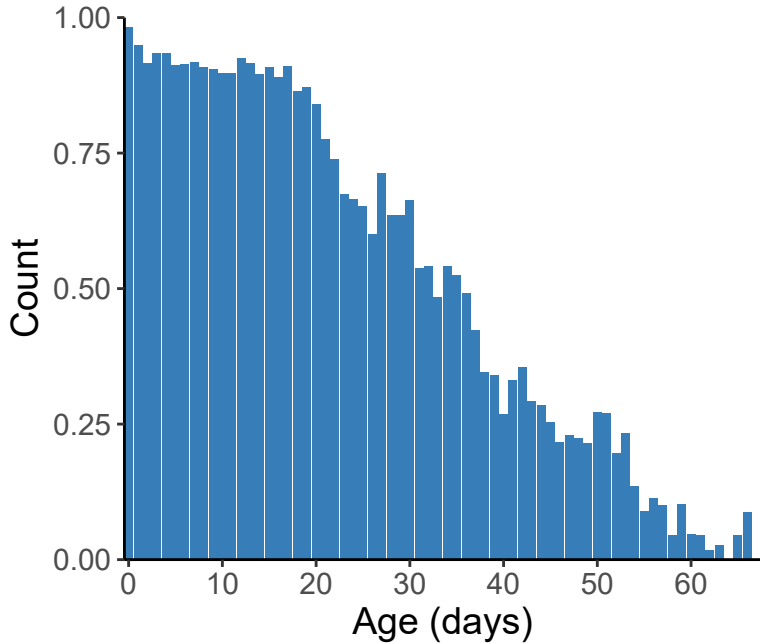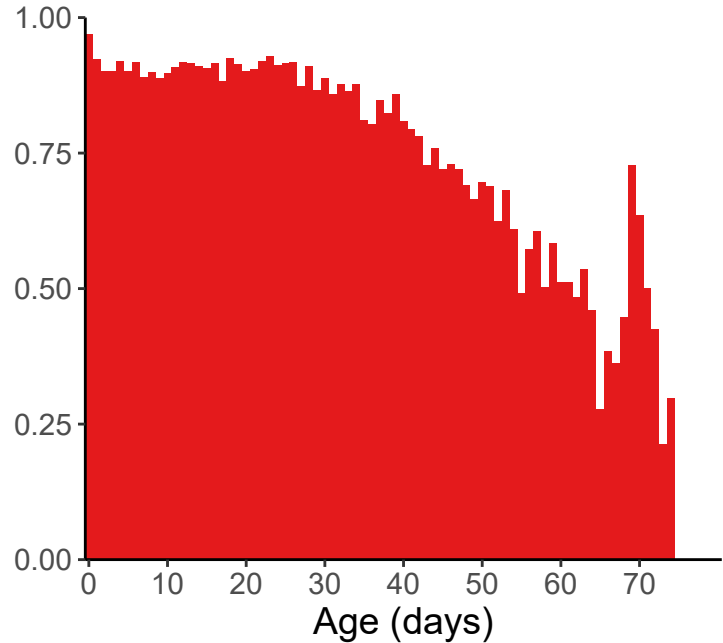
a
$n = 24$, estimate = -0.091, $p = 0.032$
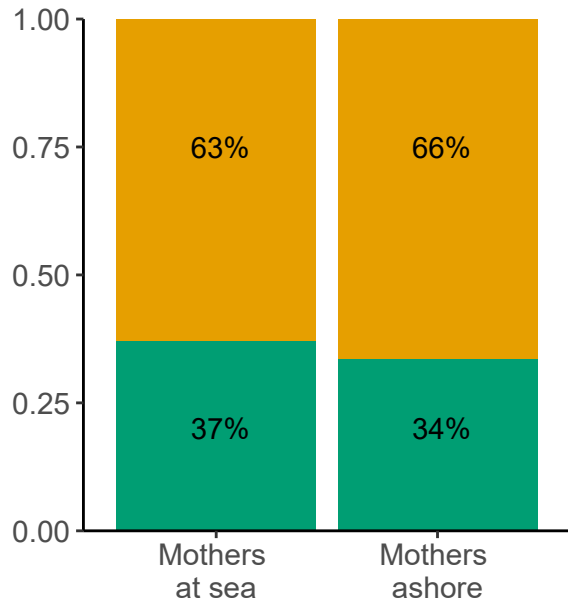
b
$n = 66$, estimate = -0.758, $p < 0.001$