Received: 20 November 2020 | Accepted: 12 June 2022

DOI: 10.1111/mms.12955

ARTICLE

Marine Mammal Science

Investigating diverse sources of variation in the amount of time Weddell seal (*Leptonychotes weddellii*) pups spend in the water during the lactation period

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Funding information

National Science Foundation, Grant/Award Numbers: ANT-1141326, ANT-1640481

Abstract

Field observations suggest that time spent in the water by Weddell seal pups during lactation varies among individuals, which could yield important developmental tradeoffs. We analyzed data from 713 pups born to 419 different mothers over 9 years to evaluate total time in the water, age at first entry, and potential sources of variation using temperature loggers attached to the rear flipper of pups. Pups first entered the water at 11–29 days of age ($M = 14.9$) and spent 4–204 hr ($M = 69.3$) in the water by 30 days of age. Age at first entry was earlier for pups with higher birth mass and mothers of above average reproductive experience. Total time in the water was related to maternal identity and greater for female pups and for pups that had higher birth mass, mothers of intermediate age, mothers that skipped reproduction in the previous year, and for pups that first entered the water at younger ages. Phenotypic traits explain observed variation in the development of a key life history behavior in the Weddell seal. Strong individual variation in time spent in metabolically costly swimming and diving might lead to variation in growth, energy stores, and survival and fitness outcomes.

KEYWORDS
Antarctica, behavior, life history strategy, locomotor development, maternal trait, offspring

1 | INTRODUCTION

Across a diverse range of species, the developmental conditions that offspring experience early in life can have lasting consequences for their survival and reproductive success (Clark & Galef, 1995; Fairbanks, 1996; Hamel et al., 2009; Lindström, 1999; Monaghan, 2008; Quéméré et al., 2018). In mammals, the nutrition that offspring receive from mothers as well as the skills and behaviors developed during the lactation period can prepare offspring for postweaning life. Just as offspring within and between cohorts can grow at different rates, behavioral development can also vary such that individuals attain varying degrees of proficiency in key skills and behaviors prior to weaning. (Fagen, 1976; Heinsohn, 1991; Martin & Bateson, 1985). The characteristics of individual offspring and their mothers as well as the environmental conditions they experience are potential sources of this variation in the behavioral development of offspring early in life and might influence the rate and degree of behavioral development attained by offspring prior to weaning.

In phocid offspring, early development involves a unique transition from life on land or ice to a life in the water, the timing of which varies among species (King, 1983). In both terrestrial and marine environments, locomotor development takes time. It requires both repeated physical activity and the physical development that occurs early in life (Martin & Bateson, 1985; Muir, 2000). The shift to swimming as the primary form of locomotion for phocid offspring also requires extensive physiological development (Donohueet al., 2000; Kanwisher & Ridgway, 1983; Noren et al., 2001; Riedman, 1990; Thorson & La Boeuf, 1994), paralleled by the development of a diverse set of skills and behaviors that increase locomotor efficiency (Kikuchi et al., 2010; Williams et al., 2000, 2004).

In most phocids, locomotor activity during the lactation period is infrequent, and entry into the water occurs after weaning (Bowen, 1991; Burns, 1997; Hooper et al., 2019; Lydersen & Kovacs, 1999). In species where pups do enter the water prior to weaning, individuals may have greater opportunity to develop important skills and behaviors in preparation for the postweaning period. However, offspring may also incur energetic costs associated with increased physical activity or thermoregulatory problems due to early entry into cold water while the blubber layer is still being developed (Blix & Steen, 1979; Noren et al., 2008; Tedman & Bryden, 1979). The offspring of capital breeding species may have more opportunities to gain experience in the water due to the close proximity of mothers throughout the lactation period, but the resources available for offspring development are limited by the amount of stored energy brought by mothers (Boness & Bowen, 1996). Trade-offs can result when the limited energy available during lactation must be distributed between competing aspects of development such as growth, activity, or thermoregulation and other maintenance, such as has been reported in neonatal and weaned gray seal (*Halichoerus grypus*) pups (Jenssen et al., 2010). Trade-offs in development can also vary among individual offspring when, among other potential factors, the allocation of energy is related to phenotypic variation in the traits of parents and offspring (Stearns, 1992). Given the potential for individual variation among phocid offspring in how they might transition to aquatic life, information on how much variation exists and the sources of this variation could provide valuable insights into the development of early swimming skills.

Weddell seals (*Leptonychotes weddellii*) differ from most other phocids in that offspring begin to enter the water during the first two weeks of life and continue to do so in the presence of attentive mothers throughout a relatively long period of dependency (Bowen, 1991; Burns 1997; Hill, 1987; Lindsey, 1937; Tedman & Bryden, 1979). Weddell seals are notable divers, and the development of these skills is critical for accessing and capturing prey as well as navigating crack systems in the sea ice to access haul-out locations (Fuiman et al., 2020; Stirling, 1969, Williams et al., 2004). Weddell seal pups are born on stable sea ice and are typically safe from predation during lactation (Lindsey, 1937; Wilson, 1907). However, pups face heightened risk of predation from orca (*Orcinus orca)* and leopard seals (*Hydrurga leptonyx*) following the annual breakup of sea ice. Entering the water early in life may be an evolutionary strategy that occurred through an increase in postweaning pup survival due to the increased efficiency of early foraging bouts and likelihood that pups avoid predation.

Most pups are thought to enter the water during lactation, where the water temperature is quite stable at −1.8°C (Littlepage, 1965). Mothers use calls and nudges to entice pups to enter the water, and closely attend pups while they are in the water at early ages (Kaufman et al., 1975; Lindsey, 1937; Sato et al., 2003; Tedman & Bryden, 1979; Thomas & Terhune, 2009). Age at first entry and total time spent in the water prior to weaning are reported to vary among pups, but levels of variation have not been quantified at a scale sufficient to understand the distribution of such traits at population levels (Hill, 1987; Lindsey, 1937; Tedman & Bryden, 1979). Because there is little evidence that pups forage prior to weaning (Burns, 1999; Burns et al., 2004), time spent in the water during lactation appears to be more important for developing swimming and diving skills than for obtaining food (Weitzner et al. 2021).

Mothers are the sole providers of parental care in Weddell seals and their energetic investment in offspring is substantial (Boness & Bowen 1996; Oftedal et al., 1987; Schulz & Bowen, 2005; Trillmich, 1996; Wheatley et al., 2006, 2008). Mothers predominately utilize a capital breeding strategy over the course of the 30–50-day lactation period (Boness & Bowen, 1996; Schulz & Bowen, 2005; Trillmich, 1996; Wheatley et al., 2008). Weddell seal mothers vary in a number of interesting traits, including age at first reproduction, parturition mass, reproductive experience, and individual quality associated with fitness, which can affect patterns of maternal care and could translate to variation in offspring development (Hadley et al., 2008; Proffitt et al., 2008b; Thomas & Terhune, 2009; Wheatley et al., 2008). Maternal features have also been linked to variation in pup birth mass (Paterson et al., 2016; Proffitt et al., 2008a), birth date (Rotella et al., 2016), and energetic allocation to pups during lactation (Macdonald et al., 2020; Paterson et al., 2016). However, possible relationships between maternal phenotype and the development of early swimming behavior in offspring are unknown, as are other sources of variation in the development of early swimming behavior. Here, we take advantage of the fact that Weddell seal mothers and their offspring can be easily captured and sampled on the sea ice (Stirling, 1969). We used iButton temperature loggers to estimate time spent in the water for a large sample of pups over 9 years (2009–2018) and evaluated diverse sources of variation in time spent in the water.

2 | METHODS AND MATERIALS

2.1 | Study site

The Erebus Bay Weddell seal population is located along the western coast of Ross Island, Antarctica, and has been intensively studied since 1968 (Stirling, 1969). Weddell seals enter Erebus Bay in the Austral spring under a thick sheet of sea ice to give birth and breed in 8–14 pupping colonies located along seasonally occurring cracks in the sea ice. The most prominent and predictable colonies form along tidal cracks, but groups also occur intermittently along cracks formed by glacial movement (Stirling, 1969). Females give birth from mid-October through November and are highly philopatric to colonies where they have previously reproduced (Cameron et al., 2007). Each year from 1982 to present, intensive efforts have been made to tag all mothers and their associated offspring in the study population with individually identifying livestock tags. Missing and broken tags have been replaced as needed to maintain individual records of age, identity, and maternal reproductive history (Cameron & Siniff, 2004).

2.2 | Data logger deployment

We programmed and water-proofed iButton (DS1922L/T) temperature loggers each year to record ambient temperatures at 6 min intervals beginning on a predetermined date during the first 4 weeks of the birthing season (October 14 to November 9). The number of iButtons programmed to start on a given day was proportional to the expected number of births per day (Rotella et al., 2016). Programmed temperature loggers were mounted on Dalton Superflexi livestock tags by pop-riveting a plastic fob to the ventral surface of the female component of the tag. Multiple layers of Plasti Dip were applied to all surfaces below the collar of the tag to achieve a smooth, watertight surface. Of the 893 loggers deployed on pups during the 9 years of study, approximately 8% of tags went unrecovered, 5% failed due to water exposure, and 4% were recovered from deceased individuals.

Each seal colony was typically visited every 24–48 hr to locate and tag newborn pups. We applied temperature logging tags to a sample of 1- to 2-day-old pups born to known-age mothers. Age at initial tagging was estimated using the state of the umbilicus and the presence of a frozen placenta at the birth site. Targeted selection was used to achieve an approximately balanced sample size of pups born to young (<8 years old), prime age (8–16 years old), and old mothers (>16 years old). For each pup in the sample, we attached a temperature tag to the interdigital webbing of the rear flippers and two identical pairs of Dalton Superflexi livestock identification tags. We weighed each pup during the initial tagging event except for one pup that was weighed 1 day later for logistical reasons (that individual's parturition mass was estimated by subtracting 1.81 kg from the recorded mass to standardize all mass measurements to the day after birth; Paterson et al., 2016). We attempted to resight and recapture each pup carrying a logger again when it was 30–40 days of age to remove the logger and recover the stored temperature data.

2.3 | Analysis of iButton temperature data

Recorded temperatures and associated time stamps (UTC + 13) were extracted from iButtons using Thermodata Viewer (Embedded Data Systems, LLC). Sea water in the area maintains a near-constant temperature of −1.8°C. The temperature loggers used in this study (iButton DS1922L/T) recorded ambient temperatures to the nearest 0.5°C. When submerged in water, individual loggers recorded consistent temperatures that closely approximated the temperature of the water and that strongly contrasted with the highly variable temperatures recorded when loggers were out of the water, which ranged from −20°C to 40°C. The difference in these patterns allowed us to analyze temperature records to determine when each tag was submerged in water. We used opportunistic sightings of instrumented pups to ground truth the temperature logger data. We compared the time of visual sighting and status of the tag (submerged/not) to the corresponding timestamp and temperature recorded by the logger. We found no discrepancies between the observed logger status and the predicted status based on recorded temperature.

We used code written and implemented in the R statistical computing environment (R Core Team, 2020) to analyze the temperature record from each iButton and to identify values that indicated when each tag was submerged (reference values). Time in the water was calculated by identifying sequences of at least three consecutive time steps where the recorded temperature was equal to the assigned reference value of a given tag, indicating submergence. The minimum sequence length of three consecutive time steps was conservative and precluded short forays (<18 min) from inclusion in the analysis. However, it allowed us to confidently identify periods of time when the tag was submerged, while also providing an objective criterion for comparing results across individuals. We calculated total time in the water by summing the time of all identified sequences for a given individual.

To understand changes in time spent in the water as pups aged, we calculated daily time spent in the water (daily duration) and used this information for descriptive purposes only to demonstrate underlying variability in the development of this behavior. We calculated daily duration in the same manner as total time in the water, with the exception that events beginning and ending on different days were split at midnight, such that the maximum possible daily duration was 24 hr. We summed all submersion events occurring within a 24 hr period to provide an estimate of daily time spent in the water for each individual. The data analyzed here are for those individuals whose tags provided temperature records from 11 to 30 days of age, a period during which all temperature tags were operational.

2.4 | Covariates considered

We evaluated relationships between the time a pup spent in the water and (1) fixed attributes of pups, (2) fixed and dynamic attributes of mothers, and (3) year. Offspring attributes included birth mass, age when the tag was first submerged during monitoring (age at first entry), sex, and birth date. Maternal attributes included age, age at primiparity, age-scaled relative parity (number of pups produced by a mother relative to the average number of pups produced by mothers of the same age), reproductive state in the previous year, and identity. We were primarily interested in two of these covariates, pup birth mass and maternal age, and investigated various relationships between these characteristics and time spent in the water using a suite of competitive models. Our interest in these two covariates was based on extensive evidence supporting relationships between early activity and offspring body mass (Berghänel et al., 2015; Cameron et al., 2008; Nunes et al., 2004; Théoret-Gosselin et al., 2015), and prior work conducted on this study population indicating that maternal age could act as a proxy for various metrics of maternal reproductive experience and quality (Hastings & Testa, 1998; Macdonald et al., 2020; Paterson et al., 2016). Because the time spent in the water by pups might have varied by year, we allowed the intercept of all models to be different in each year of the study (year treated as a factor).

We investigated multiple functional forms of offspring birth mass (pseudo-threshold, Franklin et al., 2000; linear, and quadratic) and predicted that heavier pups would spend more time in the water than lighter pups based on associations commonly reported between the body condition of offspring and activity early in life (Nunes et al., 1999, 2004; Sharpe et al., 2002). Heavy pups might also experience a thermoregulatory advantage in the water due to a larger thermal mass, as reported for harbor seal (*Phoca vitulina*) pups (Harding et al., 2005). We predicted that time in the water would be negatively related to age at first entry based on the idea that repeated exposure in addition to age was necessary for skill development (Fagen, 1976), and due to the constraints imposed by the 30-day monitoring period that limited data collection for individuals entering later in the lactation period (linear functional form of age at first entry in each model). Male offspring may display heightened activity levels, perhaps increasing risk early in life (Jackson et al., 1972; Taber & Dasmann, 1954) or incurring costs to growth rates (Berghänel et al., 2015). Thus, we predicted that male offspring would spend more time in the water than female offspring but that the effect would be small as this species is not highly dimorphic nor thought to be highly polygynous (Clutton-Brock, 1991; Harcourt et al., 2007). Because pups born early in the season tend to be male and have mothers of higher quality than those born after the mean birth date (Rotella et al., 2016), we predicted that pups born earlier would spend more time in the water than those born later (linear functional form of birth date).

Mothers in the population vary in several features. They typically begin reproducing at age 7–8 years old, breed intermittently thereafter, and display reproductive senescence as well as individual variation in reproductive output (Paterson et al., 2018), such that they gain experience but generally reproduce less frequently as they age. A mother's current age and prior reproductive history may provide information regarding patterns of maternal care and thus explain variation in offspring development. We evaluated several possible forms of the relationship between the age of a pup's mother and the time that a pup spent in the water using linear, quadratic, and pseudo-threshold functional forms of maternal age. We also evaluated if pups with mothers that started reproducing early in life spent more time in the water (linear functional form of maternal age at primiparity) and if mothers that produced pups more often had pups that spent more time in the water (linear relationship between time in the water and age-scaled relative parity of the mother). Mothers in the study population also vary in terms of their recent reproductive status: in the year preceding the birth of their current pup, they could have been a prebreeder (no previous pups), experienced mother (reproduced in the previous year), or skip breeder (produced a pup previously but not in the previous year). Prior reproductive experience and the ability to sustain reproduction in sequential years can be associated with patterns of maternal care (Clutton-Brock, 1984; Fleming et al., 1996; Nol & Smith, 1987). We predicted that pups born to mothers who were prebreeders in the previous year would spend less time in the water than those born to more experienced mothers due to possible relationships between the prior reproductive experience of mothers and their tendency to display maternal care behaviors associated with acquainting pups with the water. Finally, we evaluated the possibility that individual maternal effects might explain unmodeled variation in the amount of time pups spent in the water; we did this by including a random effect for maternal identity, which was informed by repeated measures on some mothers over the 9 years of study.

2.5 | Statistical analysis

To analyze relationships between time in the water and covariates of interest, we used a nonstandard parameterization of the gamma distribution with a logarithmic link-function in a Bayesian framework. The standard parameterization of the gamma distribution assumes a constant coefficient of variation; our parameterization allowed for greater flexibility in the relationship between the mean and variance of the data. Specifically, our model supposes that the variance is proportional to $\mu^{(3-k)}$ where k is a parameter to be estimated. (Appendix S1). We centered all continuous maternal and offspring covariates by subtracting the mean and then scaled each by two standard deviations (Gelman, 2008). Coefficients for standardized regressors were assigned weakly informative normal priors ($M = 0$, precision $= 0.0001$); variances were assigned uniform priors (0, 50). Four individuals entered the water just after the ages for which data were analyzed here and were not included in the analysis.

We used the R2jags package (Su & Yajima, 2020) to fit all models for MCMC sampling in R (R Core Team, 2020). For each model, we ran three parallel chains with 30,000 samples per chain and discarded the first 1,000 samples as burn-in. The resulting posterior distribution used for inference was comprised of 87,000 samples per model. We assessed posterior convergence using graphical (Geweke diagnostic, trace plots) and analytical (Gelmin-Rubin statistic; Gelman & Rubin, 1992) outputs using functions contained in the R package ggmcmc (Fernández-i-Marín, 2016). We used graphical comparisons of observed to predicted data in the posterior distribution to conduct posterior predictive checks, and all candidate models were able to generate predicted data that were similar to the observed data.

We performed leave-one-out cross-validation using the Bayesian predictive information criterion (BPIC; Link & Sauer, 2015) to assess the predictive ability of candidate models relative to one another using the R2jags package (Su & Yajima, 2020) and parallel processing using the snowfall package (Knaus, 2015). We compared BPIC scores between the top-performing model and others in the suite using z-tests to measure the degree of difference between models (Link & Sauer, 2015; Macdonald et al., 2020).

To better understand variation in age at first entry, which was the most informative covariate in all models of total time in the water, we performed a post hoc gamma-regression analysis of potential sources of variation in this important covariate. This analysis used the methods and covariates described above on the same data set but with a pup's age at first entry into the water as the response variable.

To place regression coefficient estimates (using posterior means) into a biologically relevant context, we present predicted values for female pups born in an average year to an experienced mother with a random effect of maternal identity of zero, while varying other characteristics, e.g., birth mass. Predicted values reported in the text correspond to the mean and upper and lower bounds of a 90% highest density interval (HDI) of observed values for a given trait. We present a 90% HDI for the estimated coefficients in the model with the highest support and emphasize results for those covariates with 90% HDI values that did not include zero.

3 | RESULTS

Temperature records were available for 713 pups born over 9 years. The numbers of male and female pups monitored were nearly equal: 349 female (49%) and 364 male (51%) pups. The average birth mass was 30.2 kg (*SD* = 4.2, range: 16.8–47.2), and the average birth date was October 24 (*SD* = 5 days, range: October 12–November 6).

The data set included information from pups born to 419 different mothers. The mothers sampled across multiple years included 95, 58, 17, and 8 mothers with 2, 3, 4, and 5 pups in the sample, respectively. On average, mothers were 14.0 years old (*SD* = 5.2, range: 5–31) with a mean age at first reproduction of 8.0 years (*SD* = 1.6, range: 5–15) and a mean age-scaled parity value of 1.0 (*SD* = 0.3, range: 0.2–2.3). We collected information for 109 pups born to first-time mothers, 434 pups born to mothers who had a pup in the previous year, and 170 pups born to mothers who skipped reproduction the previous year.

Pups in the full data set spent an average of 69.3 total hours in the water (*SD* = 28.0, range: 3.7–204.2) from age 11 through 30 days of age (Figure 1). The mean daily duration across the full monitoring period was 3.5 hr (*SD* = 3.6, range = 0–24). Mean daily duration at 11 days was 0.2 hr (*SD* = 1.1, range = 0–17.9), 3.5 hr (*SD* = 3.3, range = 0–21.7) at 20 days, and 6.3 hr (*SD* = 3.7, range = 0–24) at 30 days (Figure 2). The mean number of

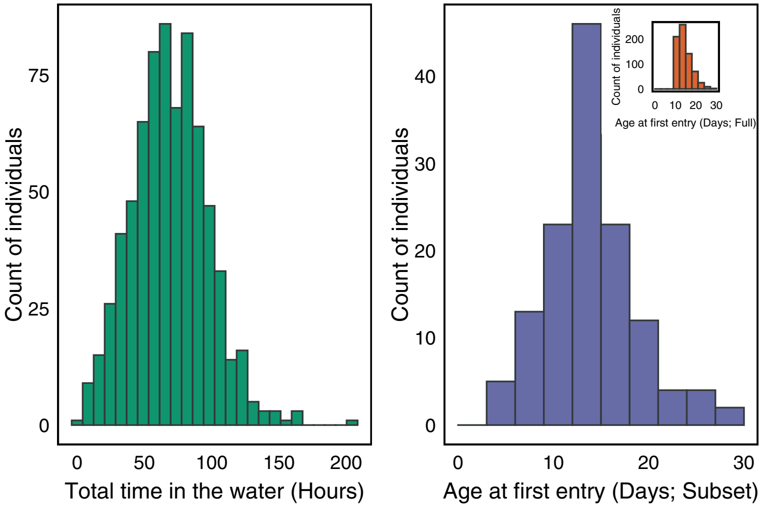

FIGURE 1 Observed variation in hours spent in the water from the full data set within the monitoring period of 11–30 days of age (left panel), age at first entry into the water for the subset of individuals for which age at first entry prior to age 11 was known (right panel), and age at first entry into the water for the full data set that did not include data prior to age 11 (inset).

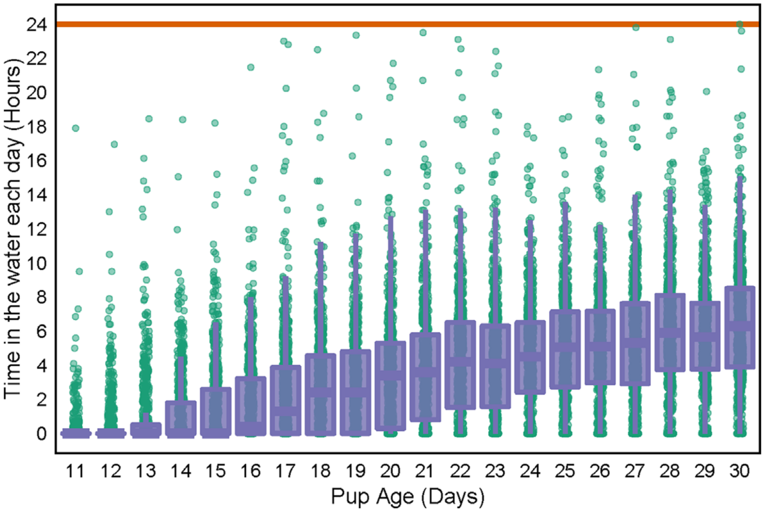

FIGURE 2 Observed variation in time spent in the water on each day in the monitoring period. The lower and upper bounds of the box correspond to the first and third quartiles (25th and 75th percentiles) of daily duration on a given day in the monitoring period. Whiskers extend to the largest or smallest value within 1.5× the interquartile range from the upper or lower bound of the box, respectively. Raw observations of daily duration are plotted in green.

individual water entries during the monitoring period was 40 (*SD* = 15.1, range = 3–101), with a mean of 2.8 entries each day (*SD* = 1.7, range = 1–22). Pups entered the water an average of 1.6 times per day at 11 days of age (*SD* = 0.9, range = 1–5, *n* = 107), 2.7 times at 20 days of age (*SD* = 1.6, range = 1–12, *n* = 543), and 3.0 times at 30 days of age (*SD* = 1.7, range = 1–13, *n* = 683). Across the entire monitoring period and all individuals, individual bouts in the water averaged 1.8 hr in duration (*SD* = 1.7, range = 0.05–28.65). Individual bouts had an average duration of 0.9 hr for 11-day-old pups (*SD* = 1.0, range = 0.07–7.2, *n* = 107), 2.3 hr for 20-day-old pups (*SD* = 1.7, range = 0.05–10.6, *n* = 543), and 3.2 hr for 30-day-old pups (*SD* = 2.5, range = 0.05–21.4, *n* = 683).

Within our full data set, 581 individuals were instrumented too late in life to provide an accurate indication of age at first water entry. We used a subset of 132 individuals (*n* = 70 females, *n* = 62 males) from six different years that were instrumented within 3 days of birth to investigate the earliest age at which pups first entered the water. The mean age at first entry for pups in this subset (14.5 days, *SD* = 4.8, range = 4.0–29; Figure 1) was similar to that estimated from the full data set (14.9 days, *SD* = 3.4, range = 11–29). However, the earliest observed entry in the subset occurred at 4 days of age, and 21.2% of pups entered the water prior to age 11 (mean age at first entry = 8 days, *SD* = 2.0 for those 28 pups).

3.1 | Model selection and assessment

All models containing covariates outperformed the intercept-only model by a clear margin (Table 1) but made very similar predictions about how time spent in the water varied as a function of the covariates (Table S1). Thus, we could not distinguish among supported functional forms but could draw inferences about predicted relationships and did so using results for the best-supported model, which contained a pseudo-threshold functional form of pup birth mass and a quadratic functional form of maternal age. Interestingly, estimated values of *k* were very similar across the four models ($k \approx 3.6$), indicating that variance in time in the water decreased as the mean increased.

Time in the water varied with several pup characteristics. Pups that were heavier at birth spent more time in the water; predicted values for time spent in the water for pups with parturition masses of 24, 30, and 37 kg (and values

TABLE 1 Results of BPIC selection process for competing models.

Model number	Functional forms	BPIC score	Delta BPIC	Model comparison	Comparison *SD*	Comparison *p*-value
1	$(\text{MA})^2$ log(BM)	−3,308.66	0.00	—	—	—
2	log(MA) $(\text{BM})^2$	−3,308.66	0.00	Model 1 & Model 2	3.66	1.0
3	log(MA) log(BM)	−3,309.37	−0.71	Model 1 & Model 3	4.23	.87
4	$(\text{MA})^2$ $(\text{BM})^2$	−3,312.90	−4.24	Model 1 & Model 4	4.61	.36
—	Null	−3,413.50	−104.84	Model 1 & Null	18.94	.00

Note. Model selection results indicating the functional forms tested in each model (MA = maternal age, PM = birth mass), BPIC score, and results of *z*-tests of difference in BPIC score between the top model and others. Candidate models did not differ in structure other than in the combination of functional forms applied to pup birth mass and maternal age. The top-performing model, which included a logarithmic form of birth mass and quadratic form of maternal age, had the following structure: $\mu_{i,j,t} = \text{Year}_j + \beta_1\log(\text{birth.mass}_i) + \beta_2\text{mom.age}_i + \beta_3(\text{mom.age}_i)^2 + \beta_4\text{first.entry}_i + \beta_5\text{birth.date}_i + \beta_6\text{pup.sex}_i + \beta_7\text{age.primiparity}_i + \beta_8\text{relative.parity}_i + \beta_9\text{repro.status}_i = \text{Prebreeder} + \beta_{10}\text{repro.status}_i = \text{Skipbreeder} + \text{mom.id}_t$, where $\mu_{i,j,t}$ corresponds to the estimated mean time in the water for an observation on pup i, born in year j, to a mother with identity t.

for remaining covariates set to reference values) were 65.7 hr (90% HDI = 60.7–70.5), 70.5 hr (66.5–74.2), and 75.6 hr (70.4–80.4), respectively. Pups that first entered the water at later ages also spent less total time in the water. Pups with ages at first entry of 11, 15, or 20 days are predicted to spend 85.7 hr (80.6–91.2), 70.0 hr (66.2–73.8), or 54.3 hr (49.7–58.5) in the water, respectively. Opposite to our a priori predictions, we found that, on average, female pups were predicted to spend several hours more in the water than males from 11 to 30 days of age (Figure 3; predicted means: females = 70.5 hr [66.7–74.4]; males = 66.2 hr [62.7–69.7]). We did not find evidence that the amount of time a pup spent in the water was related to its birth date (estimated coefficient = −0.01 [−0.072, 0.053]).

Our modeling results provided evidence that several maternal characteristics were associated with variation in the time pups spent in the water. Based on a quadratic functional form of maternal age, pups with 6-, 14-, and 21-year-old mothers are predicted to spend 65.5 hr (58.2–73.0), 70.5 hr (66.6–74.3), and 66.34 hr (62.1–70.8) in the water, respectively, between 11 and 30 days of age (Figure 4).

In contrast with our a priori predictions regarding maternal breeding experience, pups born to primiparous mothers and those born to mothers that gave birth in the previous year spent similar amounts of time in the water, whereas pups born to mothers who skipped reproduction the previous year spent more time in the water (69.0 hr [60.9–77.9], 70.5 hr [66.7–74.4], and 76.1 hr [71.5–81.0] in the water, for experienced, prebreeder, and skip-breeder mothers, respectively). We did not find evidence that maternal age at primiparity or age-scaled relative parity were related to the amount of time that a pup spent in the water (coefficients associated with each covariate had 90% HDI's that widely overlapped 0). Estimated random effects of individual mothers indicated that pups which shared all covariate values except the identity of their mother differed by a few hours in time spent in the water (Figure S1). We found that time in the water was similar across all 9 years of study (*M* = 71.3 [68.0–74.7]), with only one candidate model identifying a year with predicted time in the water that differed from the average (2018; *M* = 63.2 [57.4–69.1]; Table S1).

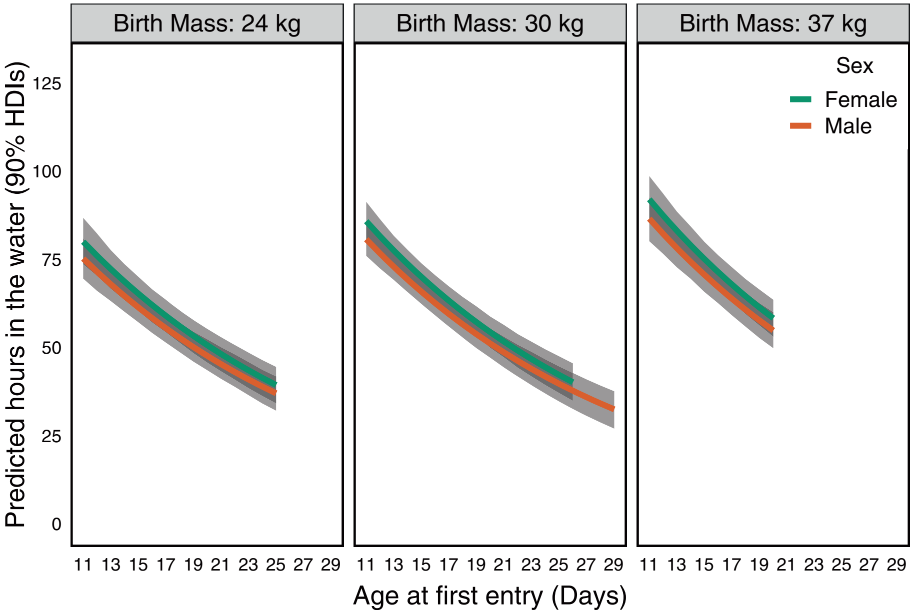

FIGURE 3 Predicted hours spent in the water across observed values of pup birth mass, sex, and age at first entry into the water from 11 to 30 days of age. Predictions have been limited to ranges of birth mass, sex, and age at first entry consistent with the data.

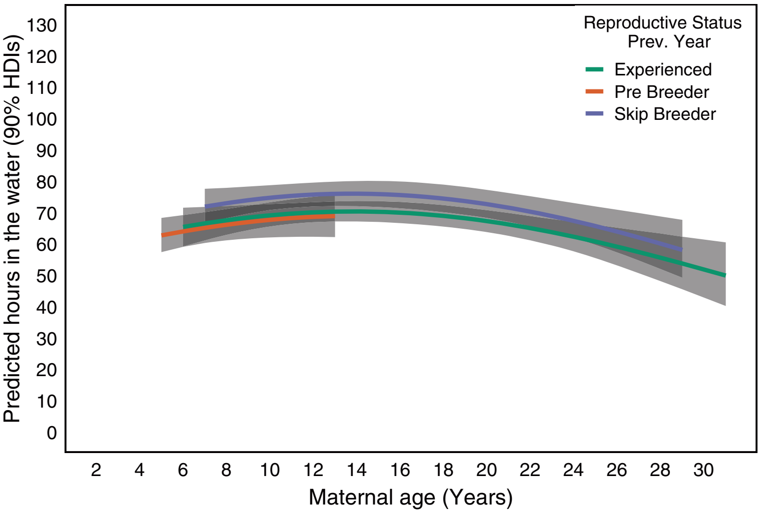

FIGURE 4 Predicted hours spent in the water across observed values of maternal age and reproductive status the previous year from 11 to 30 days of age. Predictions have been limited to ranges of maternal age and reproductive status consistent with the data.

Regarding sources of variation in the age at which a pup first entered the water, we identified several modest sources of variation (Figure S2). Heavier pups are predicted to enter the water earlier: pups weighing 37, 30, or 24 kg at birth are predicted to enter the water for the first time at 13.7 days of age (13.3–14.1), 14.4 days of age (14.1–14.9), and 15.3 days of age (14.8–16.0), respectively. Age at first entry to the water was negatively related to the age-scaled relative parity of the mother. We found evidence that mothers with higher relative parity values produced pups that entered the water at slightly younger ages: predicted ages of first entry for pups born to mothers with relative parity values of 0.6 (a value near the low end of observed values), 1.0 (an average value), and 1.8 (a value near the high end of observed values) are 15.0 days of age (14.3–15.6), 14.4 days of age (14.1–14.8), and 13.6 days of age (12.9–14.2), respectively. We did not find evidence that pup sex, pup birth date, maternal age, age at primiparity, or a mother's reproductive status were related to when a pup first entered the water (all had estimated coefficients with 90% HDI's that substantially overlapped zero). Age at first entry into the water was fairly consistent among pups born to the same mother and differed by about 2 days for a female with a random effect at the low end of the distribution compared to a mother at the upper end. We found that all 9 years had similar average ages at first entry (average = 14.5 days of age [14.1–14.9]) with the most extreme years having averages that were just 1 day earlier (2010: $M = 13.3$ days of age [12.7–13.9]) or later (2016: $M = 15.8$ days of age [15.1–16.5]).

4 | DISCUSSION

We report novel and notable levels of variation in time spent in the water and age at first entry in Weddell seal pups and provide information on the characteristics of pups and their mothers associated with this variation. Age at first entry was the most influential covariate in our analysis of total time spent in the water. Once a pup entered the water, we found that it generally continued to do so and typically increased the amount of time per day that it spent in the water (Figure S3). This pattern was similar whether pups entered for the first time early or late in the period of maternal care; we did not find evidence of compensation for delayed entry during the monitoring period. This result complements the findings of previous studies that reported improvement in swimming skills with age in Weddell seal pups (Burns, 1999; Kooyman et al., 1983) but provides new insight by highlighting the importance of experience and repeated exposure in addition to age.

We found no evidence of interannual variation in total time in the water and little influence on age at first entry. Earlier work on this species reported an average age at first water entry of approximately 14 days (Lindsey, 1937; Tedman & Bryden, 1979), indicating that age at first entry in this species has remained remarkably consistent through time. The consistency in age at first entry observed across individuals in our study, as well as in previous work, implies the presence of stabilizing selection pressures on this trait. If so, entering too early or too late in life could have substantial consequences for pup survival. The inability of young pups to exit the water is a source of mortality in the predator-free environment of the breeding colonies (Thomas & Terhune, 1983), though pup survival throughout lactation is quite high (Proffitt et al., 2010). On the other hand, pups that entered late in our monitoring period and spent less time in the water may be more susceptible to predation or starvation risk early in the postweaning period than members of their cohort with more experience in the water. Due to long recruitment times (Hadley et al., 2006) and low juvenile survival rates (Proffitt et al., 2008a), investigating linkages between time spent in the water during lactation and postweaning survival rates is a challenge, but such work would provide interesting insight into the long-term consequences of this behavior.

The consistency in age at first entry also indicates that physiological development could limit early entry into the water. Weddell seals are born with little to no blubber, and instead rely on a thick coat of lanugo as their primary source of thermoregulation. Lanugo is an excellent insulator when dry but loses its capacity to trap air and heat when wet (Pearson et al., 2019; Ray & Smith, 1968). For this reason, it is generally assumed that the offspring of ice-breeding seals do not enter the water before acquiring enough blubber for insulation (Castellini & Mellish, 2015), and our results suggest that insulation might reach critical mass for efficient water entry by ~14 days of age when many first enter the water. Though further investigation into the rate and variation associated with early blubber deposition in Weddell seals would be welcome, it appears that subcutaneous fat layers increase linearly from near zero at birth to approximately 4 cm by 4 weeks old, and that blubber deposition mirrors increases in body mass during the first 4 weeks of life (Elsner et al., 1977). Pearson et al. (2018) report that the proportion of blubber in pups increases from 25% to 38% of mass between birth and 3 weeks of age and that pups are able to maintain internal body temperatures when submerged by 5 weeks of age. However, our data show that pups regularly spend time in the water by 2 weeks of age despite the energetic cost that is likely when entering cold water with partially developed blubber. A recent study on this population documents the presence of an energy tradeoff associated with this behavior and suggests that spending time in the water may provide advantages to developing pups that outweigh the energy costs (Pearson et al., 2022).

From this perspective, our finding that pups born heavier spent more time in the water from 11 to 30 days of age and tended to enter earlier than did those that were born lighter, is likely due to patterns of blubber deposition and subsequent increases in insulation. This would suggest that better body condition, rather than larger muscle mass, enables some pups to enter earlier and spend more time in the water than others. Pups that are born heavier may also experience more efficient heat retention while in the water due to a lower surface area to volume ratio (Pearson et al., 2014). Further, pups born heavier tend to wean at heavier weights in this population (Paterson et al., 2016), which indicates that a pup's prenatal energy reserves could serve as an index of the reserves available to be allocated to postnatal activity in the water. We add to a large body of work across a wide range of mammal species linking the body condition of offspring to their physical activity early in life (Barber, 1991; Brownlee, 1954; Burghardt, 2005; Fagen, 1981; Goszczyński, 1986; Müller-Schwarze, 1968; Nunes et al., 1999; Sharpe et al., 2002), including Weddell seals in this study population (Burns, 1999; Kooyman et al., 1983).

A recent study of maternal allocation patterns conducted on pups in our study population found no evidence of a difference in maternal allocation based on the sex of offspring (Macdonald et al., 2020), and no evidence has been found to support a sex-difference in offspring mass at parturition (Paterson et al., 2016) or weaning (Macdonald et al., 2020) that could explain the slight difference in locomotor activity observed between male and female pups. However, in other large mammals, male offspring tend to have higher energy requirements than their female counterparts (Clutton-Brock et al., 1985). In northern elephant seals (*Mirounga angustirostris*), males and females were found to utilize different metabolic fasting strategies that may be associated with later reproductive success (Kelso et al., 2012). If Weddell seals exhibit similar patterns of sex-specific energy allocation, male pups may spend less time in the water to compensate for higher developmental costs and reach a weaning weight similar to that of females on average. Or, as was recently found for gray seals (Carter et al., 2020), the early sex differences we found may be indicative of adult behavioral differences associated with dispersal or colony attendance (Brusa et al., 2021).

Our finding that time in the water was maximized for pups born to middle-aged mothers corresponds well with results of previous work on this population reporting that body mass and various demographic features peak in middle-aged mothers (Paterson et al., 2016; Proffitt et al., 2007; Rotella et al., 2016). Mothers that skipped reproduction in the previous year tend to produce pups that are heavier at birth (Paterson et al., 2016), and such pups may spend more time in the water due to the thermoregulatory and/or energy advantages these prenatal resources provide. Work on this population also indicates that the potential advantages experienced by pups born to mothers that skipped reproduction the previous year could be extended into the postnatal period, as pups born to these mothers are expected to wean at higher weights (Macdonald et al., 2020). Our follow-up analysis of age at first entry provided evidence that pups born to mothers with above-average age-scaled relative parity tended to enter the water earlier in life. Paterson et al. (2016) reported a strong, positive relationship between age-scaled relative parity and the post-parturition mass of pups in this study population, which suggests possible linkages between reproductive experience, patterns of maternal allocation, and pup behavior. Future work on the topic could improve our understanding of the specific mechanisms involved now that such differences are in evidence.

We document extensive variation in time spent in the water and age at first entry into the water in the first 30 days of life in Weddell seals. Our results provide new information regarding relationships between phenotypic characteristics and the development of key behaviors in Weddell seal offspring and indicate that additional factors not investigated here, such as the behavioral heterogeneity of individual pups, may also be involved. Further, our results indicate that individuals vary in how much time they spend in metabolically costly swimming and diving, which could lead to individual variation in growth, energy stores, and development of swimming and diving skills that could have important survival and fitness consequences.

ACKNOWLEDGMENTS

We thank the many field technicians and previous graduate students who collected data for this work. This project was supported by the National Science Foundation, Division of Polar Programs under grant numbers ANT 1141326 and ANT 1640481 to J.J.R., R.A.G., and Donald B. Siniff and prior NSF Grants to R.A.G., J.J.R., D. B. Siniff, and J. Ward Testa. Logistical support for fieldwork was provided by Lockheed Martin, Raytheon Polar Services Company, Antarctic Support Associates, the United States Navy and Air Force, Petroleum Helicopters Incorporated, and Air Center Helicopters Incorporated. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Shane M. Petch: Conceptualization; investigation; methodology; software; validation; visualization. **Jay J. Rotella:** Conceptualization; investigation; methodology; software; supervision; validation. **William A. Link:** Software. **J. Terrill Paterson:** Software. **Robert A. Garrott:** Conceptualization; investigation; methodology; supervision; validation.

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How to cite this article: Petch, S. M., Rotella, J. J., Link, W. A., Paterson, J. T., & Garrott, R. A. (2022). Investigating diverse sources of variation in the amount of time Weddell seal (*Leptonychotes weddellii*) pups spend in the water during the lactation period. *Marine Mammal Science*, 1–16. https://doi.org/10.1111/mms.12955