Behavioural development
in southern right whale calves

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ABSTRACT: Most baleen whales migrate to low-latitude breeding grounds during winter to give birth and nurse their calves during the early stages of growth and development. While mothers invest a large amount of energy into the early development of their calves, the time allocated to important behaviours associated with maternal care (e.g. nursing) as well as the energetics related to the rapid growth of calves are important to quantify and understand to inform conservation measures. To investigate this, we conducted behavioural focal follows of southern right whale *Eubalaena australis* mother–calf pairs on a breeding ground in South Australia using unmanned aerial vehicles. Over the breeding season, we conducted behavioural focal follows of 51 mother–calf pairs for a total of 58 h across 75 d. Our observations showed that the proportion of time calves spent in nursing position and the duration of potential nursing bouts increased with increasing calf size throughout the breeding season, suggesting that calves seek to maximise energy acquisition. With increasing body size, the absolute metabolic expenditure of calves increased, underlining the importance of mothers being able to maintain low energy expenditure to ensure sufficient energy available for their calves during the nursing season. Our findings from this undisturbed population (1) demonstrate the considerable changes that calves undergo during the ~3 mo they spend on the breeding ground and (2) highlight the importance of these areas to be protected from anthropogenic disturbances that could disrupt the crucial maternal care, energy transfer and rapid early development of calves.

KEY WORDS: Baleen whale · Bioenergetics · Calf behaviour · Calf dependency · Calf development · Energy transfer · Maternal investment · Metabolic rate · Nursing · Respiration rate

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1. INTRODUCTION

All mammals begin their life dependent on the care provided by their mothers, with this care being critical for offspring survival. This maternal care includes energy transfer via milk, protection from predators and the acquisition of learning behaviours critical for survival into adulthood (Trivers 1972, Derrickson 1992, Bateson 1994). However, the degree of physical development at birth, and thus the requirement for maternal care, varies considerably between mammalian species. Most carnivorous species, for example, produce altricial offspring that are relatively poorly developed and dependent at birth (Shipman & Walker 1989). In contrast, many herbivorous species produce precocial offspring, which are born highly developed and able to perform basic locomotor tasks within minutes after birth (Sinclair et al. 2000, Testa 2002). This enables precocial offspring to move in synchrony with their

mother or group soon after birth, reducing predation risk (Derrickson 1992).

For newborn cetaceans, being well-developed and capable of surfacing independently from the mother soon after birth is imperative for survival. Similar to terrestrial herbivores, cetaceans give birth to preco-cial offspring possessing basic motor skills, which enables them to reach the surface to breathe, suckle and maintain close proximity with their mobile mother (Whitehead & Mann 2000, Szabo & Duffus 2008, Tyson et al. 2012, Videsen et al. 2017). To fur-ther ensure that newborn calves maintain close prox-imity with their mother after birth, calves are able to ride on the back of their mother (i.e. back-riding), a type of infant-carrying behaviour observed in ceta-ceans (Noren et al. 2008). This behaviour is linked to several important benefits regarding calf survival, including the calf saving energy by resting on the mother or swimming within her slipstream (Taber & Thomas 1982, Noren et al. 2008, Smultea et al. 2017). In baleen whales, calves rapidly improve locomotor skills and increase in size, reducing the cost of swim-ming (Thomas & Taber 1984, Williams 1999, Chris-tiansen et al. 2016a, Tønnesen et al. 2018). This is especially important for calves of migratory species that are born on low-latitude breeding grounds and must migrate long distances to their high-latitude feeding grounds only a few months later (Clapham 1996, Lockyer 2007, Boye et al. 2010).

The migratory pattern of several cetacean species is linked to various factors, including (1) seasonal avail-ability of resources on the feeding grounds during summer months (Tynan 1998), (2) decreased risk of predation on the breeding grounds (Corkeron & Con-nor 1999), including the possibility of using shallow-water coastal habitats as refuge from possible preda-tors (Ford & Reeves 2008, Nielsen et al. 2019), (3) reduced heat loss for calves on the warmer tropical or sub-tropical breeding grounds (Brodie 1975) and (4) skin maintenance requirements, with the warmer waters allowing skin regeneration on the breeding grounds (Durban & Pitman 2012). For baleen whales, productive high-latitude feeding grounds provide in-dividuals with abundant food resources to rapidly build up sufficient energy reserves to support them during the migration and months of fasting on the breeding grounds. This includes covering the added significant cost of lactation for females with calves during the fasting period (Lockyer 2007, Christiansen et al. 2013). Consequently, during the months spent on the breeding ground, the accumulated energy re-serves of a lactating female must sustain the daily en-ergy requirements of both herself and her rapidly growing calf (Lockyer 2007, Christiansen et al. 2018, Bejder et al. 2019). Due to the close link between the reproductive and migratory cycle in baleen whales, giving birth to precocial offspring and ensuring rapid calf growth is crucial for calf survival (Derrickson 1992, Huang et al. 2011).

Baleen whales have evolved an extreme example of maternal investment, facilitating rapid calf growth within the first 3 mo after birth (Christiansen et al. 2018) and allowing them to minimize the amount of time spent on breeding grounds before migrating back to the foraging grounds (Whitehead & Mann 2000). For example, in both humpback *Megaptera no-vaeangliae* and southern right whale *Eubalaena aus-tralis* (SRW) calves, the energy-rich milk facilitates a growth rate of ~1 m mo^{-1} in body length and an aver-age relative increase in body volume of 455% during the first 3 mo (Christiansen et al. 2016a, 2018). This substantial maternal energetic investment increases calf survival as offspring size is positively related to survival (McMahon et al. 2000), while a larger body size of the calf also reduces the mass-specific cost of transport (Williams 1999) and potentially heat loss. Specifically, a larger and more developed calf will have a better chance of surviving their first migration to the feeding grounds, as this journey requires not only sufficient energy reserves but also well-devel-oped locomotor skills to avoid predation (Pitman et al. 2015, Irvine et al. 2017). Lactating females and their calves therefore face the challenge of maximising growth and physical development within a narrow time period of 3 to 4 mo leading up to the migration back to the feeding grounds, entirely fuelled by the fi-nite lipid reserves of the mother (Lockyer 2007, Chris-tiansen et al. 2016a, 2018). Although the rapid growth of the calf will lead to benefits related to calf survival, it will also gradually increase the already high ener-getic demands of the mother, as the absolute size of the calf and hence its energy requirements (i.e. field metabolic rate, FMR) will increase with body mass, given a constant activity level. Additionally, calf activ-ity levels may increase to facilitate development of muscular myoglobin and dive capabilities (Cartwright et al. 2016), which may further intensify the energetic pressure on the mother.

The importance of the intense energy transfer be-tween baleen whale mother and calf and requirement for rapid physical development of calves have been investigated for various species using boat- and land-based observations (e.g. Taber & Thomas 1982, Thomas & Taber 1984, Payne 1986, Swartz 1986, Cartwright & Sullivan 2009, Cusano et al. 2018). From the vantage point of unmanned aerial vehicles

(UAVs), it is now possible to obtain more detailed observations of sub-surface mother–calf behaviours while minimizing disturbance and costs (Christiansen et al. 2016b, Torres et al. 2018). We used UAVs to collect video recordings of SRW calf nursing behaviour and locomotor development on a breeding ground in South Australia, which is undisturbed by human activities. Specifically, we tested 4 overarching hypotheses: (I) the level of calf dependency on its mother, measured by the proximity between mother and calf and the time spent back-riding, would decrease with increasing calf size; (II) calves would increase the frequency of surface-active behaviours and mothers would increase their speed of movement with increased calf size, via improved locomotor skills; (III) calves would increase the proportion of time spent nursing throughout the breeding season; (IV) and calf FMRs, inferred from respiration rates (Folkow & Blix 1992, Williams & Noren 2009, Christiansen et al. 2014), would increase with calf size, implying a larger consumption of energy reserves from the mother or slower growth of calves at the end of the breeding season.

2. MATERIALS AND METHODS

2.1. Study species and location

Field work was conducted at the Head of Bight (HoB) in South Australia (Fig. 1; 31° 29' S, 131° 08' E) from 13 July to 25 September 2017. HoB is a shallow (<20 m), relatively calm coastal area, where southern right whales congregate during the austral winter to mate, give birth and nurse calves before they migrate back to their Antarctic/sub-Antarctic feeding grounds during spring/summer (DSEWPaC 1999, Charlton 2017). HoB is located within the Great Australian Bight Commonwealth Marine Reserve, where vessel traffic is not permitted during the whale breeding season. Whales are present from May to November each year, with a peak in the number of mother–calf pairs between late May and early September (DSEWPaC 1999). mother–calf pairs on average (±1 SD) spend 61 ± 12 d on the breeding ground in HoB (Charlton 2017).
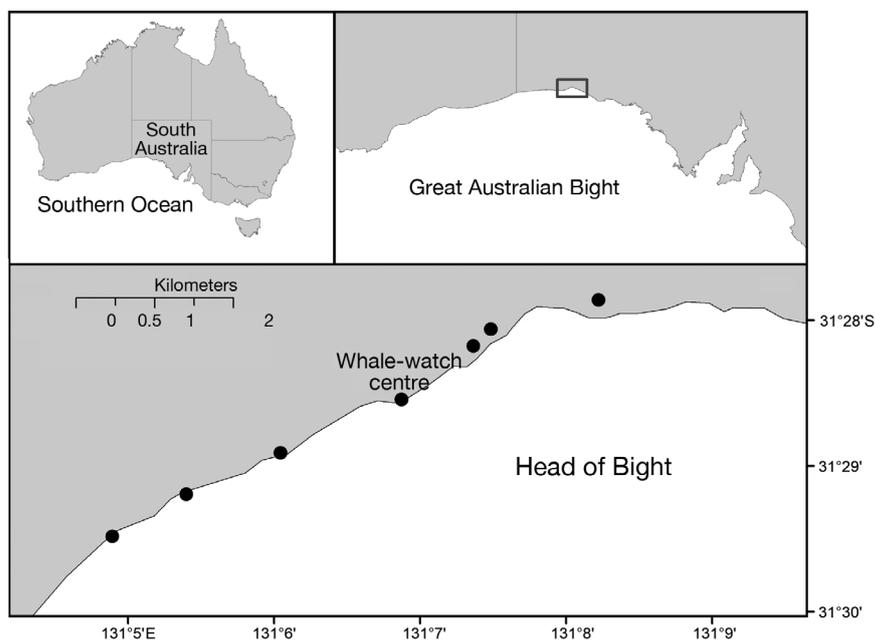

Fig. 1. Study area at the Head of Bight located along the Great Australian Bight, South Australia. Seven unmanned aerial vehicle launch sites (black dots) were used: 5 sites located along the edge of steep cliffs, another at the Whale-watch Centre (used outside of tourist visiting hours) and a site located near sea-level (beach) at the easternmost end of the study area (black dot furthest to the right)

2.2. Unmanned aerial vehicle and focal follow procedure

Behavioural focal follows (Altmann 1974) were conducted on SRW mother–calf pairs using a DJI Phantom 3 Professional UAV (diameter without propellers: 35 cm, weight: 1380 g, www.dji.com). The UAV was launched from 7 different land-based take-off sites (Fig. 1) at altitudes of 6 to 33 m above sea-level and flown above whales at a maximum distance of <2 km from the coast. Launch sites were located along a ~6 km section of coastline characterised by vertical limestone cliffs and a sandy beach (Fig. 1). The built-in DJI camera obtained video recordings with 12.4 Megapixels and had a 20 mm (35 mm format equivalent) f/2.8 lens with a 1/2.3′ complementary metal oxide semiconductor (CMOS) sensor. Focal follows of individual mother–calf pairs were performed during ≥1 consecutive flight(s). During a flight, the UAV was maintained at an altitude between 20 and 100 m above the focal mother–calf pair with the camera positioned vertically down, stabilised by a gimbal, while the UAV was rotated to face north (between 350° and 10°). The stereotyped flying ensured an optimum view of the focal mother–calf pair as well as consistent orientation of the UAV for all focal-follow video re-

cordings. The altitude of the UAV minimised potential noise disturbance by the UAV on the mother–calf pair (Christiansen et al. 2016b). When the UAV was correctly positioned above the mother–calf pair, the pilot initiated the video recording via a remote control. A live-feed of the recording was transmitted to an iPad Air tablet, which was used to maintain position of the UAV above the mother–calf pair throughout flights. SRW mothers were individually identified based on the distinct callosity pattern on their heads (Payne et al. 1983), and for consecutive flights above the same pair, the callosity pattern was used to confirm the identity of the pair. The UAV hovered above the mother–calf pair for up to 20 min for each flight, and consecutive flights above the same mother–calf pair were executed until the focal individuals moved outside of the study area or beyond the range of the UAV (>2 km), or until the end of daylight hours. Our research permit allowed us to fly for up to 3 h over the same mother–calf pair during a single day. Time intervals between consecutive flights, due to change of UAV battery, resulted in a mean (±1 SD) duration of 8 ± 3 min. UAVs were flown during good weather conditions only, i.e. wind speeds <15 knots and no precipitation. In addition to video recordings, the UAV also logged a variety of parameters during flights, e.g. UTC time, altitude (barometric and GPS) and GPS positioning (using WGS84 ellipsoid) every 100 ms.

2.3. Behavioural sampling

The focal-follow video recordings were processed in the open source software Solomon Coder (www. solomoncoder.com), where durations and occurrences of multiple pre-defined behavioural and non-behavioural variables were registered simultaneously with video playback (Table 1) (Thomas & Taber 1984, Lundquist et al. 2012, Smultea et al. 2017). Each respiration event from both the mother and the calf were also recorded. Water visibility was scored from 0 to 3, with 0 being good visibility (whales clearly visible when submerged at depth of up to 10 m) and 3 indicating poor visibility (whales only visible when surfacing). The behavioural sampling techniques used were defined as either continuous sampling (e.g. duration of behaviour) or instantaneous sampling (e.g. counts of a predefined behaviour; Table 1) (Altmann 1974).

2.4. mother–calf proximity

From the focal follow video recordings, still frames were extracted at 5 s intervals to evaluate the proximity between mothers and calves. A 5 s interval was selected to increase the probability of capturing image frames with both the mother and

Table 1. Southern right whale *Eubalaena australis* behavioural ethogram defined in mother–calf focal follow UAV video recordings, with continuous and instantaneous behavioural events recorded

Behaviour	Definition	Sampling technique
Apparent nursing	Calf dived next to the mother's mammary gland area and stayed submerged with its head continually in the region of the mammary gland. The calf was facing in the same direction as the mother, while its tail was visible below or next to tail of mother throughout the dive, and the body of both mother and calf were horizontal or near-horizontal (Smultea et al. 2017, Videsen et al. 2017).	Continuous
Back-riding by calf	Calf positioned with its rostrum or body on top of mother between her rostrum and tail stock. Mother can be either at surface or submerged slightly (Smultea et al. 2017).	Continuous
Mother rolling	Body turns 180° or 360° along its longitudinal axis. The roll of the mother is continuous, as she typically rolls 180° and remains motionless upside-down at the surface with her pectoral fins out of the water for several seconds.	Continuous
Calf rolling	Body turns 360° along its longitudinal axis. The roll of the calf is marked as an instantaneous event because of the very short duration (~1 s).	Instantaneous
Breaching	Rostrum or up to ~2/3 of body pushed out of the water, producing white-water as the whale hits the surface of the water.	Instantaneous
Tail slapping	The tail and/or the tail stock is raised out of the water after which it is moved, generally with force, onto the surface of the water, generating white-water.	Instantaneous
Pectoral fin slapping	Either of the pectoral fins are raised out of the water after which it is moved, generally with force, onto the surface of the water, generating white-water.	Instantaneous

calf visible. In a custom-made script in MATLAB R2015b (The MathWorks), the position of the tip of the rostrum and the blowhole were extracted as pixel coordinates (x,y). Only frames where both the rostrum and the blowhole were clearly visible for both animals were used. In the event that either the mother or calf was clearly visible with a straight body, a third coordinate was extracted: the notch of the fluke. From these pixel coordinates, the relative distance from the tip of the rostrum to the blowhole (i.e. rostrum-blowhole length in pixels, RBL) and the distance from the tip of the rostrum to the notch of the fluke (i.e. total length in pixels, TL) were estimated. The proportion of RBL in relation to TL was then used to locate the centre of the whales (50% of TL). To infer the centre of the whales for still-frames, where the notch of the fluke was not visible, the relationship between TL and RBL (both obtained from still-frames on the same day) was used. Circular areas with a diameter equal to the length (in pixels) of the mother or calf were then centred on the mother and the calf at 50% of their TL, respectively. If the 2 circles overlapped in an image, we classified the pair as being in close proximity during that time (i.e. an indicator for the possibility of physical contact). Conversely, if the circles did not overlap, the mother and calf were classified as not being in close proximity with each other (i.e. a lower chance of visual or physical contact).

2.5. Maternal speed of movement

As the UAV was maintained directly above the focal mother during a focal follow, the horizontal distance travelled by the UAV could be used as a proxy for the distance travelled by the mother–calf pair. The GPS position of the UAV was used to estimate the average speed of movement of the mother during each focal follow. This was done by calculating the distance travelled using the *pathdist*() function from the Antarctic Mapping Tools (Greene et al. 2017) in MATLAB R2015b. This assumes the global WGS84 ellipsoid and is consistent with the GPS coordinates recorded by the UAV. As the mother–calf pairs moved ~500 m, on average, during a focal follow, it was not deemed necessary to use an ellipsoid developed specifically for the Australian geography. The speed of movement of the mother was then calculated by dividing the distance travelled by the duration of a given video recording.

2.6. Calf size and calculated body mass

Vertical aerial photographs of the focal mother–calf pair were obtained with a DJI Inspire 1 Pro quadcopter UAV (56 cm diameter, 3.4 kg, www.dji.com). The UAV was equipped with a range finder and a 16 megapixel DJI Zenmuse X5 camera with an Olympus M.Zuiko 25 mm f1.8 lens and a polarized filter. This allowed for precise altitude measurements and images of high resolution, which was not achievable from the stills obtained from the videos. Photogrammetric methods were used to extract the length in pixels of mothers, measured from tip of rostrum to the notch of the fluke, following the protocol of Christiansen et al. (2018). Photogrammetry was only conducted when both the notch of the fluke and rostrum were clearly visible in the frame of the photos and the body axis of the whale was straight. The pixel measurements were converted to distance measurements by calculating the length of the whales in metres in the camera sensor, based on their relative length in the photograph knowing the image resolution. Finally, the measurement was scaled to actual length, in metres, using the height of the UAV and focal length of the camera lens (see Christiansen et al. 2018). The absolute calf body lengths (in metres) were calculated from the relative body length of the calf obtained from the pixel measurements of TL (proportional to the measured length of their mother). From the calculated lengths of the calves, body weight (kg) was calculated from the weight–length relationship developed for North Atlantic right whales *Eubalaena glacialis*: body mass = $4.1 \times 10^{-5} + \text{length}^{2.8}$ (Fortune et al. 2012).

2.7. Statistical analyses

All statistical analyses were performed in R v.3.4.3 (R Core Team 2017). Whale behaviours (Table 1) were pooled for each individual mother–calf pair across flights and days and aggregated either as (1) the proportion of time a pair was observed performing or engaged in a given behaviour (i.e. for continuous behaviours: the sum of the behavioural durations by animals divided by the total duration of observation) or (2) the rate of occurrence of a given behaviour (i.e. for instantaneous events: the frequency of the behaviour divided by the total duration of the observation). The proportion of time was a suitable format to capture continuous behaviours, while the rate of occurrences was used for instantaneous events (Table 1). However, both approaches controlled for

Hypotheses
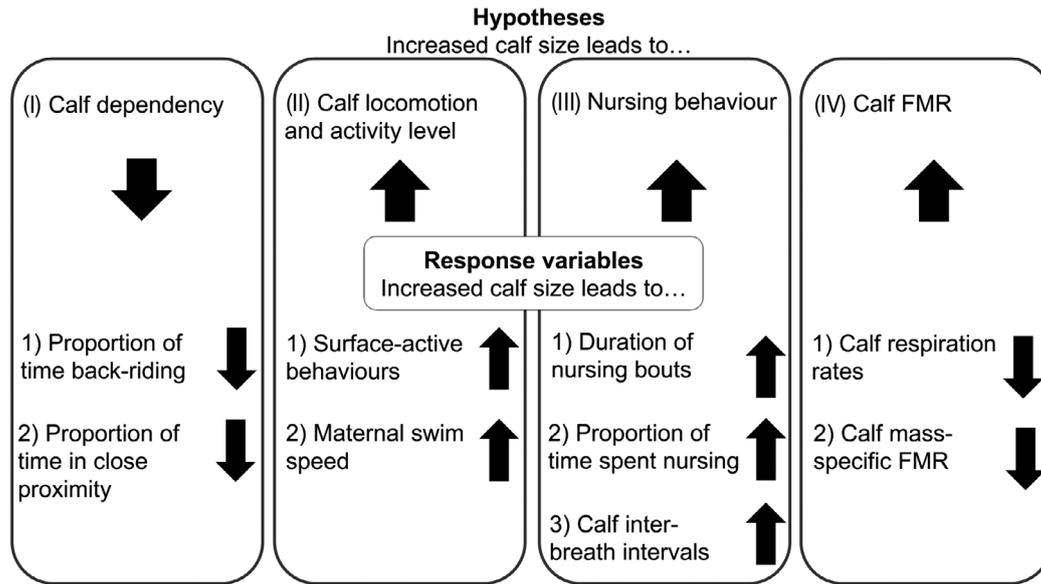Increased calf size leads to…

Fig. 2. A conceptual diagram showing the 4 overarching hypotheses and the response variables from the related statistical analyses. Downward facing arrows indicate a decrease, and upward facing arrows indicate an increase. FMR: field metabolic rate. See Table 2 for model analyses

variations in the duration of focal follows. Prior to analyses, data were explored for potential influential points and outliers by calculating leverage and Cook's distance, respectively, and based on this, no points were removed. To analyse the data, several models were created (Fig. 2, Table 2), including linear mixed effects models (LMMs) and generalised linear mixed effects models (GLMMs) created in the *lme4* package to fit random effects and, in the case of the GLMMs, non-normally distributed response variables (Bates et al. 2015). To analyse proportional response variables with random effects and a high occurrence of zero and one values, generalised additive mixed models (GAMMs) were created in the *gamlss*

package (Stasinopoulos & Rigby 2007). All models included the calculated calf body mass (BM_C; in kg) as a fixed effect and the mother–calf ID and Julian Day as random effects to account for pseudoreplication (Table 2). Model selection was based on Akaike's information criterion (AIC) (Burnham et al. 2011). To assess model fit of LMMs and GLMMs from the *lme4* package, marginal R^2 (R^2_m) and conditional R^2 (R^2_c) were obtained using the *MuMIn* package (Barto 2018), where R^2_m is the variance explained by the fixed effects, and R^2_c is the variance explained by both the fixed and random effects, i.e. the entire model (Nakagawa & Schielzeth 2013). The p-values and *F*-statistics were obtained using the *lmerTest*

Table 2. Summary of the statistical models used for the analyses. LMM: linear mixed model; GAMM: generalised additive mixed model; GLMM: generalised linear mixed model; BM_C: calf body mass; (1|variable): random effect. The response variables were all for the calf, apart from maternal speed of movement, where the response was on the speed of movement of the mother to represent mother–calf swim speed

Model	Response ~ Fixed effect + (1| Random effect)	Error distribution	Link function
GLMM	Proportion of time back-riding ~ BM_C + (1|mother–calf ID) + (1|Julian day)	Binomial	Logit
GAMM	Proportion of time in close proximity ~ BM_C + (1|mother–calf ID) + (1|Julian day)	One-inflated beta	Logit
GLMM	Surface-active behaviours (1/0) ~ BM_C + (1|mother–calf ID) + (1|Julian day)	Binomial	Logit
LMM	Log10(maternal speed of movement (m s^{-1})) ~ BM_C + (1|mother–calf ID) + (1|Julian day)	Gaussian	Identity
GLMM	Proportion of time nursing ~ BM_C + (1|mother–calf ID) + (1|Julian day)	Binomial	Logit
GLMM	Nursing bout duration (min) ~ BM_C + (1|mother–calf ID) + (1|Julian day)	Gamma	Log
GLMM	Inter-breath-interval (min) ~ BM_C + (1|mother–calf ID) + (1|Julian day) [a]	Gamma	Log
LMM	Respiration rate (breaths min^{-1}) ~ BM_C + (1|mother–calf ID) + (1|Julian day) [a]	Gaussian	Identity
LMM	Field metabolic rate (J d^{-1}) ~ BM_C + (1|mother–calf ID) + (1|Julian day)	Gaussian	Identity

[a]Separate models were created for both mother and calf response variables

package (Kuznetsova et al. 2017). The dispersion was evaluated for each model. To ensure that model assumptions were met, we performed model validation tests. Homogeneity of variances was investigated using scatterplots of residual versus fitted values, and the normality of residuals was investigated in quantile-quantile plots.

2.7.1. Calf independence

Two variables were used to test the hypothesis that the level of calf dependency on its mother, measured by the proximity between mother and calf and the time spent back-riding, would decrease with increasing calf size: (1) the proportion of time calves spent back-riding and (2) the proportion of time mother–calf pairs spent in close proximity. The proportion of time spent back-riding was investigated in relation to the calculated body mass (from here on referred to as 'calf body mass') of calves using a GLMM (Table 2). To investigate the proportion of time that mother–calf pairs spent in close contact, a GAMM with a one-inflated beta distribution was used (Table 2), as this model and distribution can handle proportion data that is highly skewed towards values of exactly one.

2.7.2. Calf locomotion, activity level and maternal speed of movement

To test the hypothesis that calves would increase the frequency of surface-active behaviours and mothers would increase their speed of movement with increased calf size, via improved locomotor skills, we investigated (1) if surface-active behaviours are more likely to occur with increasing calf body mass and (2) if maternal speed of movement increased with calf body mass. A GLMM was used to test if the presence of surface-active behaviours increased with increasing calf body mass (Table 2). An LMM was used to test if the average speed of movement of mothers increased with increasing calf body mass. Maternal swim speed was log-transformed to comply with model assumptions (Table 2).

2.7.3. Nursing behaviour

To test the hypothesis that calves would increase the proportion of time spent nursing with increased size, we investigated (1) the duration of a nursing bout and (2) the proportion of time spent nursing.

Further, the calves' inter-breath-interval (IBI) was calculated by dividing the duration of a focal follow with the number of breaths recorded during that focal follow. The IBI was used to compare the calf breath-hold ability with their nursing bout durations. The mothers' IBI was also calculated to investigate their relative energy expenditure as the size of their calves increased through the breeding season. A GLMM was used to test if the proportion of time spent nursing was independent of the calf body mass (Table 2). Furthermore, the nursing bout duration relative to calf body mass was investigated, using a GLMM (Table 2). Finally, the effect of calf body mass on the IBI of mothers and calves was tested using separately fitted GLMMs (one model for mothers and one for calves; Table 2).

2.7.4. Respiration rate and field metabolic rate

Calf respiration rates (i.e. number of respirations divided by the duration of an entire focal follow) was calculated for each calf and used to test the hypothesis that calf FMR would increase with calf size. This was conducted by fitting an LMM to the relationship between the mean respiration rate (hereafter 'respiration rate') of calves and individual calf body mass (Table 2). Second, the effect of calf growth and development on the relative energy expenditure (inferred from respiration rates) of mothers was tested by fitting an LMM to the respiration rate of mothers as a function of the body mass of individual calves (Table 2). Third, the calf respiration rates were used to estimate calf FMRs to investigate the relationship between calf body mass and calf FMR.

To estimate FMR, the rate of oxygen consumption, V_{O_2} (l min^{-1}), was first estimated from published bioenergetic models (Folkow & Blix 1992, Christiansen et al. 2014):

$$V_{O_2} = E_{O_2} \cdot V_T \cdot F_{O_2air} \cdot f_R \tag{1}$$

where E_{O_2} represents the average oxygen extraction coefficient of 45%, i.e. the amount of oxygen extracted from the air during each breath (Folkow & Blix 1992), V_T represents the volume of the lungs in litres that fill with air during each breath (i.e. tidal volume), F_{O_2air} is the proportion of oxygen in inspired air (0.21), and f_R is the observed respiration rate (breaths min^{-1}). Total lung capacity (TLC) was estimated using the relationship TLC = 0.1 × mass (kg)$^{0.96}$, and V_T was assumed to be 60% of TLC (Piscitelli et al. 2013). Calf FMR was then calculated by multiplying V_{O_2} with a calorific coefficient (20.2 kJ

$l\,O_2^{-1}$, energy per litre of oxygen). This value is based on the approximation for an animal with a diet consisting mainly of protein and fat (Hlastala & Berger 2001). An LMM was used to test the relationship between calf FMR and calf body mass (Table 2).

2.8. Ethical note

All research was carried out under a permit from Murdoch University Animal Ethics Committee (O2819/16), a research permit from the South Australian Department of Environment, Water and Natural Resources (M26501-3) and a Marine Parks permit (MO00082-4-R). UAV operations were carried out under an RPA Operator's Certificate (CASA.ReOC.0075) and 2 UAV Operator Certificates (Christiansen and Sprogis), in accordance with regulations by the Australian Civil Aviation Safety Authority (CASA). The noise impact of similar sized UAVs on baleen whales when flying at altitudes >10 m is below that of ambient noise levels in similar shallow, near-shore areas of Western Australia (Christiansen et al. 2016b).

3. RESULTS

3.1. Data collection and morphometric measurements

Fieldwork was conducted from 13 July to 25 September 2017. Out of the 75 d, 34 d (45%) had suitable weather conditions for flying the UAV. A total of 58 h and 46 min of behavioural focal follows were conducted, collected during 283 flights over 51 individual mother–calf pairs of southern right whales, amounting to 104 focal follows. Individual flights ranged in duration from 5 to 20 min (mean ± SD: 13 ± 3.0 min). The total focal follow observation time of each mother–calf pair ranged from 5 to 216 min (72 ± 23 min), and 23 (45%) of these mother–calf pairs were observed on >1 d during the field season (1.9 ± 1.2 d observed). Across the season, the length of the calves ranged from 4.3 to 8.6 m (mean ± SD: 6.5 ± 1.2 m). The mean ± SD body lengths of mothers were 14 ± 0.70 m (range: 13–16 m). From these measurements, the predicted body mass of calves ranged from 940 to 7900 kg (mean ± SD: 3800 ± 1400 kg).

3.2. Calf independence

Back-riding was observed for a total of 3 h (5.1%) for the total observational period of 58 h and 46 min and was observed in 43% of focal follows and for 41 individual calves. The proportion of time individual calves were observed back-riding was 0.051 ± 0.063 (mean ± SD, N = 104). The proportion of time spent back-riding decreased 0.0079 ± 0.0054 t^{-1} increase of calf body mass (Fig. 3; GLMM: $F_{1,102} = 8.9$, p = 0.0042, $R^2_m = 0.035$, $R^2_c = 0.18$), ranging between a proportion of 0 and 0.24 of the time across all calf body sizes. Individual mother–calf pairs were in close proximity during a mean (±1 SD) proportion of 0.92 ± 0.1 of the time (interquartile range: 0.92–1.0, median: 0.99, N = 95). The proportion of time mother–calf pairs spent in
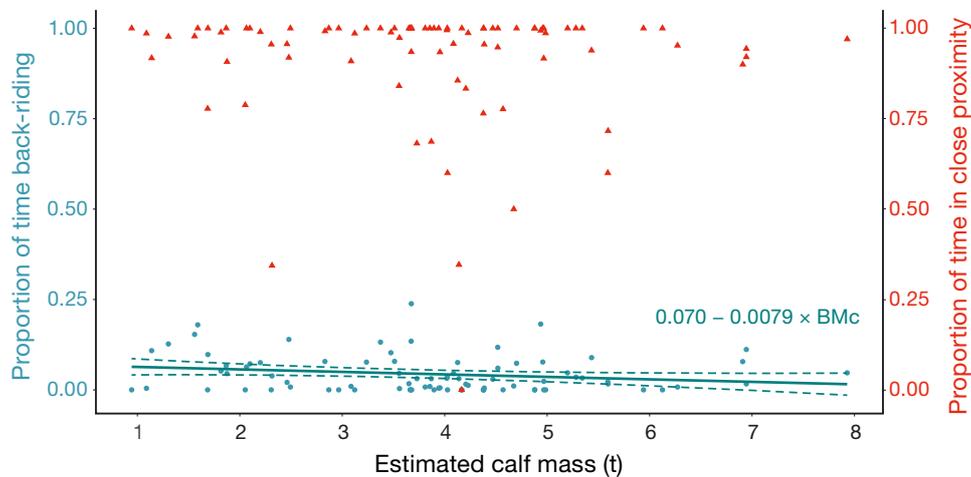

Fig. 3. Proportion of time southern right whale *Eubalaena australis* calves were observed back-riding as a function of their calculated body mass (BM_C; metric tons) (blue points). The solid blue line represents the fitted values of the GLMM (GLMM: $F_{1,102} = 8.9$, p = 0.0042, $R^2_m = 0.035$, $R^2_c = 0.18$, N = 104), with dashed blue lines representing 95% confidence interval. The red points represent the proportion of time mother–calf pairs were in close proximity, which was unaffected by calf body mass (GAM: $F_{1,93} = 1.2$, p = 0.29, $R^2 = 0.013$) (N = 95)

contact was independent of calf body mass (Fig. 3; GAM: $F_{1,93} = 1.2$, p = 0.29, $R^2 = 0.013$).

3.3. Calf locomotion, activity level and maternal speed of movement

Calf surface-active behaviours were observed in 31 of the individual calves, with a mean (±1 SD) rate of 9.0 ± 24 occurrences h^{-1}. For 2 focal follows, the number of surface-active behavioural events reached 107 and 218 during a 40 and 100 min observation, respectively. The most frequently observed surface-active behaviour was tail slapping, which, on average, was performed 3.6 ± 19 times h^{-1}. Breaching was the least frequent surface-active behaviour, performed only 1.6 ± 9.7 times h^{-1}. There was no significant relationship between the presence of surface-active behaviours and calf body mass (Fig. 4; GLMM: $F_{1,102} = 2.6$, p = 0.12, $R^2_m = 0.035$, $R^2_c = 0.16$). The estimated speed of movement of mothers ranged between 0.18 and 2.3 m s^{-1} with a mean of 0.64 ± 0.37 m s^{-1}, and 96% of the speed estimates were <1.5 m s^{-1}. The maternal speed of movement significantly decreased at an exponential rate of 0.048 ± 0.016 m s^{-1} t^{-1} increase in calf body mass (Fig. 5; LMM: $F_{1,66} = 7.42$, p = 0.011, $R^2_m = 0.11$, $R^2_c = 0.46$).

3.4. Nursing behaviour

Nursing was observed for 40 individual calves (78%). Calves spent a proportion of 0.10 ± 0.14 (mean ± SD; N = 104) of their time in nursing position, with the proportion of time in nursing position signifi-

Fig. 5. Maternal speed of movement (m s^{-1}; base-10 log-transformed) of southern right whale *Eubalaena australis* mothers as a function of calculated calf body mass (BM_C; t). The solid blue line indicates the best fitting LMM (LMM: $F_{1,66} = 7.42$, p = 0.011, $R^2_m = 0.11$, $R^2_c = 0.46$), with the dashed lines representing the 95% confidence interval (N = 68)

cantly increasing by 0.022 ± 0.0097 t^{-1} increase in calf body mass (Fig. 6; GLMM: $F_{1,102} = 9.1$, p = 0.0027, $R^2_m = 0.027$, $R^2_m = 0.25$). The mean duration of a nursing bout was 0.95 ± 0.64 min (N = 70), and the nursing bout duration significantly increased at a rate of 0.085 ± 0.021 min t^{-1} increase in calf body mass (Fig. 7a; GLMM: $F_{1,68} = 10.7$, p = 0.0090, $R^2 = 0.50$). The average IBI was 0.64 ± 0.35 and 2.5 ± 0.85 min (N = 104) for calves and mothers, respectively, and increased by 0.066 ± 0.010 and 0.045 ± 0.0090 min t^{-1} increase in calf body mass for calves and mothers, respectively (Fig. 7b; $GLMM_{calf}$: $F_{1,102} = 43.6$, p < 0.001, $R^2 = 0.70$; $GLMM_{mum}$: $F_{1,102} = 11.5$, p = 0.0051, $R^2 = 0.38$).
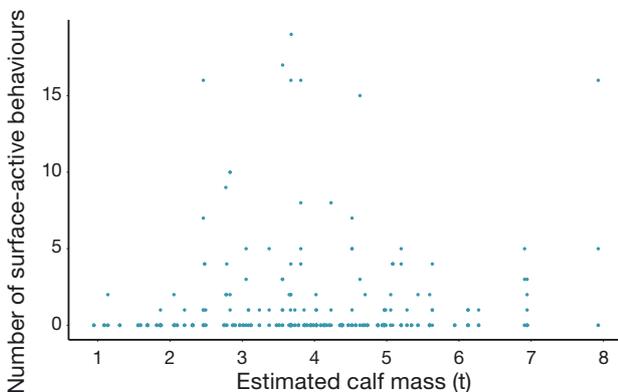

Fig. 4. Number of calf surface-active behaviours as a function of their calculated body mass (BM_C; t) (GLMM: $F_{1,102} = 2.6$, p = 0.12, $R^2_m = 0.035$, $R^2_c = 0.16$). The 2 data points with 107 and 218 occurrences of surface-active behaviour have been omitted from the figure to better show the trend of the remaining data points
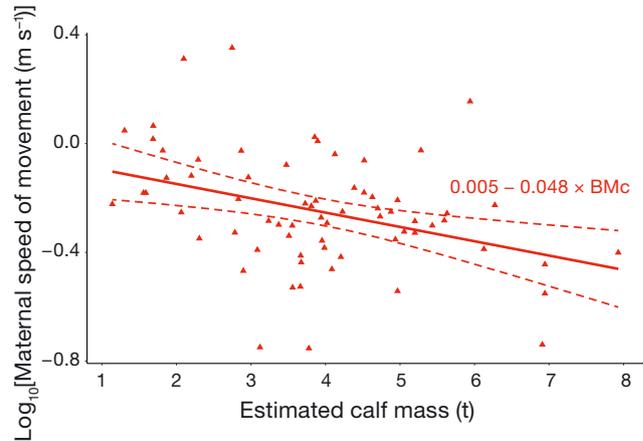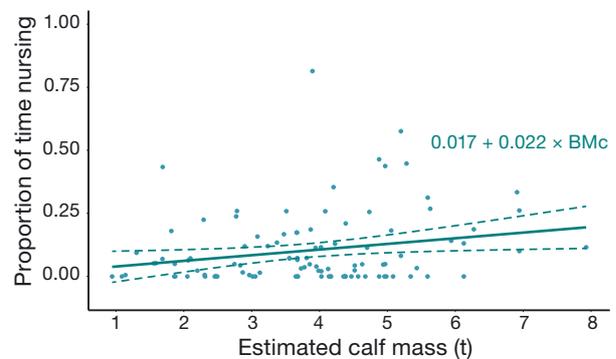

Fig. 6. The proportion of time spent nursing as a function of calculated calf body mass (t) in southern right whale *Eubalaena australis* calves. Solid blue line indicates the best fitting GLMM (GLMM: $F_{1,102} = 9.1$, p = 0.0027, $R^2_m = 0.027$, $R^2_c = 0.25$), and the dashed blue lines represent 95% confidence intervals (N = 104)
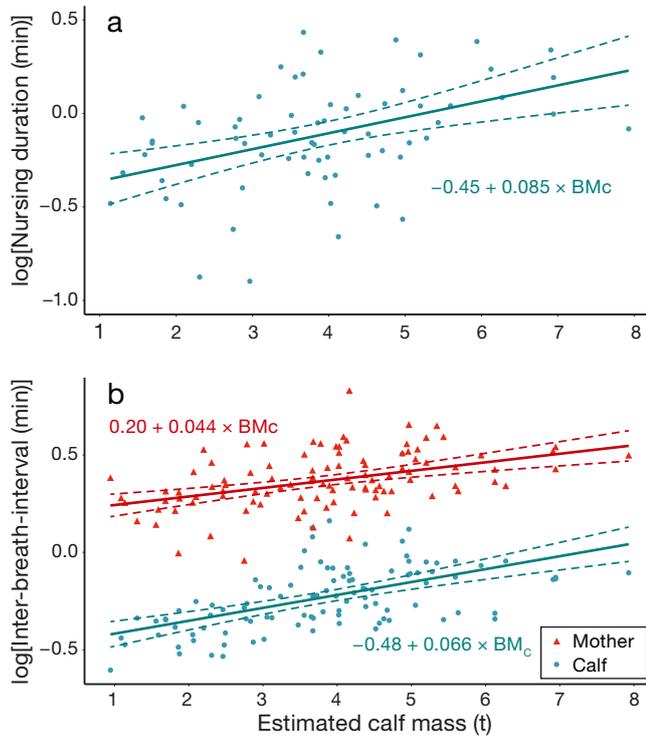
Fig. 7. (a) The apparent nursing bout duration (min; base-10 log-transformed) as a function of calculated calf body mass (BM$_c$, t) with the best fitting GLMM (solid line) (GLMM: $F_{1,68}$ = 10.7, p = 0.0090, R^2 = 0.50) and the 95% confidence intervals (dashed lines) (N = 70). (b) Calf (blue) and mother (red) inter-breath-intervals (IBI; base-10 log-transformed) as a function of calculated calf body mass (BM$_{C,}$ t) with the best fitting GLMM (solid lines) (GLMM$_{calf}$: $F_{1,102}$ = 43.6, p = 5.4 × 10^{-5}, R^2 = 0.70; GLMM$_{mum}$: $F_{1,102}$ = 11.5, p = 0.0051, R^2 = 0.38) and the 95% confidence intervals (dashed lines) (N = 104)

3.5. Respiration rate and field metabolic rate

Lactating females had a respiration rate of 0.46 ± 0.15 breaths min^{-1} across the breeding season. The respiration rate for calves was 1.8 ± 0.65 breaths min^{-1} (range: 0.31–4 breaths min^{-1}). The respiration rate significantly decreased with 0.34 ± 0.038 and 0.049 ± 0.010 breaths min^{-1} t^{-1} increase in calf body mass for calves and mothers, respectively (Fig. 8; LMM$_{calf}$: $F_{1,102}$ = 62.7, p < 0.001, R^2_m = 0.42, R^2_c = 0.85; LMM$_{mum}$: $F_{1,102}$ = 20.8, p < 0.001, R^2_m = 0.22, R^2_c = 0.32). The mean estimated FMR of calves was 730 ± 230 MJ d^{-1} and ranged from 400 to 1000 MJ d^{-1} at the calculated weights from 940 to 7900 kg, which represents a 250% increase in FMR during the breeding season. The FMR values significantly increased with increasing body mass of calves (LMM: $F_{1,102}$ = 14.9, p = 0.0031, R^2_m = 0.17, R^2_c = 0.85) with FMR scaling to the power of 0.47 of body mass.
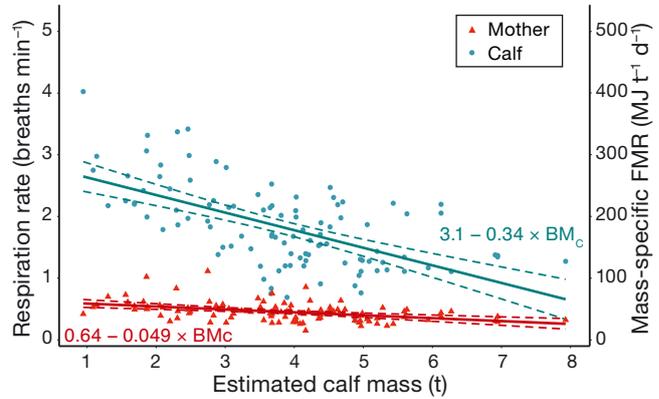

Fig. 8. Respiration rate (breaths min^{-1}) as a function of the calculated body mass for southern right whale calves (BM$_C$, t). The solid blue line is the best fitting LMM ($F_{1,102}$ = 62.7, p = 5.5 × 10^{-10}, R^2_m = 0.42, R^2_c = 0.85) for calf respiration rate as a function of calf body mass with the 95% confidence interval (blue dashed lines). The solid red line is the best fitting LMM ($F_{1,102}$ = 20.8, p = 4.4 × 10^{-5}, R^2_m = 0.22, R^2_c = 0.32) for maternal respiration rate as a function of the calf body mass with the 95% confidence interval (red dashed lines). The right y-axis shows the mass-specific metabolic rate for calves (MJ t^{-1} d^{-1}) corresponding to respiration rate (N = 104)

4. DISCUSSION

While recent studies have quantified the rapid growth in size of baleen whale calves during the first months after birth (Christiansen et al. 2016a, 2018), the interplay between calf growth and behaviour, locomotion, nursing and energetics has received less attention. Here, we sought to overcome the limitations of observing mother–calf *Eubalaena australis* behaviours and interactions from land and boat-based platforms by using a UAV to perform behavioural focal follows (Torres et al. 2018). Our findings are based on a detailed behavioural data set that span 2.5 mo of the early development of SRW calves. This early development takes place on the breeding grounds and is the most energetically demanding phase of the reproductive cycle of female baleen whales (Lockyer 2007, Christiansen et al. 2016a, 2018). We provide insights into the behavioural development of SRW calves and demonstrate the substantial changes that calves undergo during the first months of life, in terms of independence, locomotion, activity level, breath hold ability and energy expenditure. While we found significant relationships of body mass on all these variables, the low R^2 values of some models highlight that other variables are also influential and future research should aim to identify these. Further, our findings highlight the importance of sufficient maternal

energy reserves to support early calf development during this critical period. Finally, our data represents to our knowledge the behaviour of a healthy, undisturbed SRW population that is showing strong recovery from whaling (Bannister 2017) and hence can potentially be used as a baseline for right whale behavioural studies in other parts of the world, including the critically endangered North Atlantic right whale (Pace et al. 2017).

4.1. Calf independence

Rapid development in offspring independence has been proposed as an advantage of giving birth to precocial offspring (Derrickson 1992). In mammals that produce well-developed offspring, independence is coupled with a decrease in maternal care behaviours (Bateson 1994), such as back-riding by calves in cetaceans (Derrickson 1992, Noren et al. 2008). We find that back-riding composed ~5% of the total observation time in SRW mother–calf pairs. Previous studies on cetacean calves have reported a significant decrease in the time spent back-riding with increasing calf maturity and increased locomotor proficiency (Taber & Thomas 1982, Mann & Smuts 1999, Smultea et al. 2017). This is consistent with our finding that SRW calves decreased their time spent back-riding by 9% during the 2.5 mo of observations. This suggests that calves rapidly increase locomotor independence during the period spent on the breeding ground. The higher proportion of time spent back-riding in the youngest calves suggests that mothers perhaps require calmer waters for the less-mobile calves. Back-riding assists the growth and development of locomotor skills of the calves without increased energetic costs of manoeuvring, and it helps calves staying afloat when breathing due to low buoyancy of lean calves right after birth (Brodie 1975, Christiansen et al. 2018). However, along the south coast of Australia, SRW mothers often venture close to shore, bringing calves close to or into the surf zone (Nielsen et al. 2019). Hence, in the potentially more energetically demanding surf zone, back-riding may allow calves to rest at the surface.

Mother–calf pairs remained close to each other, with either visual or tactile contact possible, for >90% of the time. This high cohesion was independent of calf body mass. Maintaining close proximity has the advantages of access to milk, saving on energetic costs of locomotion, protection from predators (e.g. sharks and killer whales *Orcinus orca*), and a decreased need for loud and frequent acoustic com-munication that might attract eavesdropping predators (Norris & Prescott 1961, Videsen et al. 2017, Nielsen et al. 2019). On the HoB breeding ground, the water became increasingly turbid as the afternoon wind speed increased towards the end of the breeding season. It is therefore unlikely that mother–calf pairs were able to maintain visual contact beyond just a few tens of meters from each other. Instead, it is likely that SRWs use acoustic communication to reunite following a separation. However, acoustic communication between a mother and her calf has the drawback of potential predators eavesdropping and locating the pair. By maintaining a close proximity to each other, the need for acoustic communication can be minimised, as documented for humpback whales *Megaptera novaeangliae* (Videsen et al. 2017). In support of this, Nielsen et al. (2019) found that SRW mother–calf pairs on a breeding ground along the southwestern coast of Australia use infrequent and low-amplitude acoustic signals, while near to the surf zone. This combination of the production of infrequent, low-amplitude acoustic signals and a noisy habitat decreases the risk of detection from predators, which may be the underlying cause for mothers bringing calves into the surf zone on the breeding grounds and retaining close proximity to calves.

4.2. Calf activity level and locomotion

In many mammalian species, observations of offspring attempting to perform adult-like behaviours, including fighting and interacting with conspecifics, have been classified as 'play' (Spinka et al. 2001). These types of behaviours may be important for offspring development in the period leading up to weaning and independence (Spinka et al. 2001). Specifically, these behaviours are linked to the development of stamina, coordination and crucial skills related to survival (Barber 1991). Although play is energetically demanding, it likely increases fitness, as the offspring prepares for future unexpected events (Barber 1991). Similarly, surface-active behaviours displayed by calves (e.g. tail and pectoral fin slapping, breaching and rolling) have been identified as 'play' and are considered important in the development of survival skills, including predator defence, socialising, foraging or reproduction (Thomas & Taber 1984, Mann & Smuts 1999). Contrary to the findings of Thomas & Taber (1984), we show that the rate of surface-active behaviours remains low throughout the breeding season for calves and, interestingly, that

there is no significant increase in these activities with calf size. The low overall occurrence of surface-active behaviours minimizes energy expenditure, allowing more of the energy from the mother to be allocated towards growth (Lockyer 2007). Further, it also allows the mother–calf pair to remain inconspicuous to predators. In addition, surface-active behaviours may be related to particular times of the day or to weather conditions (Kavanagh et al. 2017). Thus, because UAV observations were only performed during day-light hours at wind speeds <15 knots with zero pre-cipitation, our findings may be biased towards be-haviours more frequently performed in calmer, quieter weather conditions.

We show that SRW mothers decreased their swim speed with increasing calf size. This is consistent with previous studies of various cetacean species (Thomas & Taber 1984, Mann & Smuts 1999). For example, SRW mother–calf pairs in Península Valdés, Argen-tina, employed a constant speed of travel when calves were newborn but decreased this travelling behaviour as calves grew larger (Thomas & Taber 1984). The au-thors suggest that continuous travel may be important for newborns that have relatively low buoyancy at birth and therefore may need the lift generated by for-ward-motion to maintain position for breathing and suckling. Further, it has been suggested that constant travel at an early age may facilitate the development of muscles used for swimming in preparation for mi-gration back to the feeding grounds (Thomas & Taber 1984). At the slowest measured speeds, it is likely that whales were drifting with the current with no locomo-tive costs, thus lowering their energy expenditure. This is supported by observations from the UAV, in that resting or slow travelling whales had an average speed of 0.64 m s^{-1} (i.e. 2.3 km h^{-1}) that can easily be explained by currents only. This is similar to right whale mother–calf pairs in South Africa (0.3 and 0.5 m s^{-1}, respectively) (Mate et al. 2011).

4.3. Nursing behaviour

Calves must maximise their growth during the brief time they spend on the HoB breeding grounds. They therefore need to acquire large amounts of the energy-dense milk from their mothers. A rapid development of calf breath-holding capabilities en-ables them to perform prolonged dives, thereby al-lowing them to significantly increase time spent nursing (Fig. 7) (Thomas & Taber 1984, Cartwright & Sullivan 2009, Cartwright et al. 2016). Consistent with this, we demonstrate a gradual increase in the duration of potential nursing bouts with increasing calf size, allowing larger calves to suckle for longer periods of time. The similarity between the increased breath-hold ability and the duration of nursing bouts of calves with increasing size (Fig. 7) indicates that calves utilise their increased abilities to maximise the time spent submerged in nursing position. Further, we found that the overall proportion of time spent in nursing position increased with calf size. It is likely that an increase in time spent nursing appears towards the end of individual mother–calf pairs' res-idency at HoB, exemplifying a strategy towards max-imising growth and accumulation of energy reserves before the onset of their migration to the feeding grounds (Thomas & Taber 1984). Alternatively, it may reflect a decrease in the mothers' milk produc-tion availability as she may not be able to sustain a constant production of milk throughout the breeding season (Oftedal 1997), causing the calves to spend more time acquiring milk or stimulating the mother to deliver milk. However, the constant rate of decline of body condition in lactating SRW females (Chris-tiansen et al. 2018) indicates that the energy output in milk is either similarly constant or increasing, given the apparent decrease in activity of the lactat-ing females (Figs. 5 & 8). To support this, in other capital breeding marine mammals, milk production peaks toward the end of the nursing period (Lyder-sen & Hammill 1993, Mellish et al. 1999).

We found that potential nursing comprised, on av-erage, ~10% of the time for calves. On the breeding ground off Península Valdés, Argentina, SRW calves spend ~5% of the time in nursing position independ-ent of size (Thomas & Taber 1984), whereas hump-back whale calves in Western Australia are in a suck-ling position for ~20% of the time (Videsen et al. 2017). These differences may be due to differences between populations, species, habitat and/or the ob-servational methods used. The method in the Thomas & Taber (1984) study consisted of cliff-based observa-tions with telescopes or binoculars, whereas the pres-ent study benefits from a higher degree of detail due to technological advancements of UAVs, i.e. being able to observe behaviours through the water from an aerial vantage point and at closer distances. For the humpback whales, Videsen et al. (2017) inferred suck-ling rates from multi-sensor acoustic tags that re-mained on the calves for ~7 h. An advantage of the tag method is that it provides insight into behaviours re-gardless of the time of day and weather conditions, which was a limitation for the UAV method. However, with that noted, the UAV method is less costly, logisti-cally viable and minimally invasive.

The nursing bout duration of 0.9 min (54 s) recorded here closely coincides with results from underwater observation of suckling time in humpback whales off Maui, Hawaii collected with underwater observation of 0.5 min (Zoidis & Lomac-Macnair 2017). However, the apparent nursing observed with a UAV when calves dive down and remain in the mammary area of mothers cannot be verified as direct milk transfer (Whitehead & Mann 2000), and consequently, we may overestimate the actual suckling time. Calves regularly press their rostrum against the mammary area of the mother, presumably to initiate milk transfer (Johnson et al. 2010, Zoidis & Lomac-Macnair 2017). From an aerial perspective, this behaviour appears as nursing, due to the similar position of the calf: stationary with its head under the mammary gland area of the mother. However, short dives of <10 s, similar in execution to nursing dives, were performed regularly in between longer duration nursing dives of calves at HoB, often with calves switching between the lateral sides of the mother. These dives may function to induce milk transfer through the use of tactile cues (Johnson et al. 2010). The use of such cues performed by the calf to facilitate milk delivery has been proposed for humpback whales, where mechanical rather than acoustic cues were prevalent during nursing dives (Videsen et al. 2017). However, more data from underwater video recordings or from on-animal acoustic and motion-sensing tags are needed to address this question further.

4.4. Respiration rate and field metabolic rate

Although we found a significant decrease in SRW calf respiration rate with size, their 4.5-fold increase in absolute body mass during the first 3 mo of their lives (Christiansen et al. 2018) resulted in a substantial estimated increase of 250% in calf FMR during this same time period. However, such FMR extrapolations assume that the lung volume of calves increases at the same rate as calf mass, which may not be the case since a substantial part of the increase in calf mass is likely to be fat tissue (Christiansen et al. 2018). Christiansen et al. (2018) showed that the body volume of lactating SRW females at HoB decreased at a constant rate of $0.126 \text{ m}^3 \text{ d}^{-1}$, while calves increased in body volume at an average rate of $\sim 0.08 \text{ m}^3 \text{ d}^{-1}$. The exponential increasing FMR of the growing calves is hence mismatched by the constant rate of decline in maternal body volume on the breeding ground. To maintain a constant energy expenditure

during the nursing period, the fasting mothers may be able to offset the increasing energetic expenditure of lactation by lowering their own daily metabolic demands across the breeding season, as seen in other capital breeding marine mammals (Mellish et al. 2000). This notion is supported by the observed decrease in respiration rate (Fig. 8) and swim speed of the mothers (Fig. 5) throughout the breeding season. Further, the composition of the milk may change during the breeding season as observed in other species of marine mammals that are fasting during the nursing period, such as elephant seals *Mirounga* sp. and humpback whales, where the fat content increases and water content decreases during the nursing period (Riedman 1990, Oftedal 1997). Such a shift in lipid composition may be a way for the lactating female to conserve water and increase the efficiency of nursing, allowing a short and intense lactation period (Riedman 1990), while it may also reflect the development of the offspring's ability to digest more fat-heavy food (Berta et al. 2006).

As the body condition of lactating females decreases during the breeding season, it may affect the timing of the migration towards the feeding grounds. Future research should address whether it is the body condition of the mother or the size of the calf that triggers the migration back towards the feeding grounds, and whether mothers of better body condition would be able to nurse their calves for a longer period on the breeding grounds, hence producing bigger calves that are more likely to survive the migration to the feeding grounds. The question also remains how much of the limited energy of lactating females is allocated to development of calf locomotor skills compared to calf growth.

4.5. Conclusions

Despite the limited time that SRWs spend on their breeding ground, fasting, lactating females transfer an enormous amount of energy to their calves (Christiansen et al. 2018). To facilitate the high energy transfer, a substantial part of the daily time budget of mothers is devoted to milk delivery. Here, we show that SRW calves are in nursing position ~10% of the time and that this proportion increased with calf size. Increased time spent nursing may reflect an increased energy expenditure of calves as they grow larger. The high proportion of time spent nursing emphasises the vulnerability of SRW mother–calf pairs to disturbances in the environment that could either disrupt crucial energy transfer between a mother and calf or increase

the daily energy expenditure for either of them. A way for calves to decrease their energy expenditure is by remaining close to the mother. We show that calves are within an adult body length (<14 m) to its mother for >90% of the time. However, the estimated fixed rate of volume loss by the lactating females are mismatched by an increasing rate of FMR of the growing calf. Thus, to maintain the documented calf growth rates, lactating females may reduce their maintenance metabolism. This notion is supported by the decreased ventilation rate of mothers during the breeding season. The apparent necessity of a lactating female to maintain low energy expenditure during the breeding season highlights the importance of protecting the breeding habitats to minimise human disturbance, e.g. boat-based whale-watching, shipping, fishing and oil and gas development. A similar result of maintaining a low energy expenditure was documented for lactating humpback whales on a breeding ground in Western Australia (Bejder et al. 2019). Such disturbances would potentially increase the energy expenditure of both mother and calves and/or decrease the amount of time nursing can occur and hence the amount of energy available to allocate to calf growth, which may ultimately lead to a lower chance of survival (Christiansen et al. 2014). Nursing areas are therefore important for the healthy growth not only of the calves but also for the population.

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