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RESEARCH ARTICLE

A novel comparison of southern sea otter (*Enhydra lutris nereis*) fur buoyancy across ontogeny

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ABSTRACT

Sea otters are extremely positively buoyant and spend most of their time resting at the water surface. It is understood that some of this buoyancy comes from the air layer that sea otters maintain in their pelage, with the lungs providing an additional source of positive buoyancy. Past studies have investigated the fur buoyant force in adult sea otters; however, little is known about the fur buoyant force in younger age classes. This study compared ontogenetic changes in the fur buoyant force of southern sea otter (*Enhydra lutris nereis*) pelage. We measured the fur buoyant force of pelt samples, scaled that to the whole animal, and calculated mass-specific fur buoyant force for six age classes: neonates (<1 month), small pups (1–2 months), large pups (3–5 months), juveniles (6 months–1 year), subadults (1–3 years) and adults (4–9 years). Each pelt sample was measured under three conditions: control, oiled and washed with Dawn® dish soap. Oiled and washed pelts had a lower fur buoyant force compared with the control pelts across all age classes. When oiled, the air layer of the pelt is ruined and no longer provides sufficient positive buoyancy. Pelts washed with Dawn® had higher variability in buoyant force compared with other conditions, and the air layer was not restored consistently. When we scaled up, we found that younger age classes were more buoyant because of their larger surface area to volume ratio. These differences in buoyancy may underlie variations in energetic costs and behavior among sea otters across development.

KEY WORDS: Buoyant force, Development, Lanugo, Oiling, Pelage, Pelt, Dawn

INTRODUCTION

The regulation of buoyancy is important for animals to effectively navigate the aquatic environment. Aquatic animals have evolved different physiological mechanisms and/or anatomical structures to regulate their buoyancy (Beck et al., 2000). For example, teleost fish have a gas-filled swim bladder, some cephalopod shells have gas-filled chambers, and sharks have hydrofoils or squalene to aid in buoyancy regulation (Alexander, 1982, 1990). In the water column, a positive buoyant force acts on animals in a vertical direction (i.e. toward the surface of the water), and this force can be generated by the animal's body volume or mass, tissue composition and respiratory systems (Williams, 2001). The buoyancy of aquatic animals can also affect locomotory strategies, such as glide duration or stroke frequency (Williams et al., 2000; Adachi et al., 2014).

Marine mammals face unique challenges in water compared with other aquatic species, as they must return to the surface to breathe (Williams, 2001). Buoyancy plays an important role in reducing energetic costs for marine mammals during swimming and diving (Castellini and Mellish, 2015). Deep-diving mammals can control their buoyancy to their advantage; for example, some marine mammals can decrease energetic costs associated with diving and overall total body volume by collapsing respiratory structures to allow for effortless, prolonged gliding during descents (Williams et al., 2000).

The physical forces that affect the buoyancy of deep-diving marine mammal species contrasts significantly with marine mammals that spend a majority of their time at the surface, like sea otters (Williams, 2001). Sea otters face unusual challenges in the aquatic environment because of their extremely dense pelage, large lung size and small body size (Cashman, 2002; Fish et al., 2002; Thometz et al., 2015; Zellmer et al., 2021). Other marine mammal species may be neutrally buoyant, and some exhale before diving (Williams, 1989; Cashman, 2002; Zellmer et al., 2021). Sea otters rarely achieve neutral buoyancy and they inhale before diving, which means otters are constantly fighting against their own buoyant force while foraging (Williams, 1989; Cashman, 2002). This positive buoyancy is generally beneficial for sea otters, as they use a majority of their time at the surface for resting and grooming (Hanson et al., 1993). Sea otter mothers also rely on this positive buoyancy to safely leave their young pups at the surface while they forage (Payne and Jameson, 1984; Thometz et al., 2015).

The natal pelage of sea otter pups has been described as fluffy and especially buoyant in comparison with the adult pelage, and it is hypothesized that sea otter natal pelage is so buoyant that young pups cannot dive for the first few months of life (Thometz et al., 2015). However, the buoyancy of sea otter natal pelage has never been empirically measured. Past research compared the overall buoyancy of pups with that of adult southern sea otters (Thometz et al., 2015), but because of a lack of available data it was assumed that pup and adult pelts had similar buoyant properties, which we believe may not have accurately reflected the true buoyancy of pups. The objectives of this study were to: (1) empirically measure the buoyant force of the sea otter pelt across ontogeny, under normal conditions and after oiling, and (2) estimate the whole-animal fur buoyant force and scaled mass-specific fur buoyant force for sea otters across age classes, from pelt measurements. We predicted that sea otter pups would have the largest mass-specific fur buoyant force, as pups are assumed to be especially buoyant. We also

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predicted that sea otter pups would have the largest change in fur buoyant force when oil is applied, owing to their lower fur density compared with older age classes (Riordan et al., 2023a).

MATERIALS AND METHODS

Sample collection

In collaboration with California Department of Fish and Wildlife (CDFW), southern sea otter [*Enhydra lutris nereis* (Merriam 1904)] pelts were collected from San Luis Obispo, Monterey and Santa Cruz counties from animals that died in the wild or during rehabilitation efforts. In accordance with Section 109(h) of the US Marine Mammal Protection Act (MMPA), the US Fish and Wildlife Service's regulations implementing the MMPA at 50 CFR 18.22(a), and the US Fish and Wildlife Service's regulations implementing the US Endangered Species Act at 50 CFR 17.21(c)(3), the samples used to complete this work were collected from fresh, necropsied sea otter carcasses taken from the wild by an official or employee of CDFW in the course of their duties as an official or employee of CDFW. Only pelts considered fresh and in good condition (i.e. not matted or decayed) were used for this study. The original 24×20 cm pelt samples were collected from the back (dorsal) region of the animal. The samples were packaged in three layers of plastic food wrap, kept flat (not folded), stored in 2-gallon (≈7.57-liter) freezer bags, and kept frozen (−20°C to −16°C) until analysis in the various experiments. We analyzed a total of 37 sea otter pelt samples across six age classes: neonates (<1 month, N=9) and small pups (1–2 months, N=5) with the natal pelage, and large pups (3–5 months, N=5), juveniles (6 months–1 year, N=6), subadults (1–3 years, N=6) and adults (4–9 years, N=6) with a mature pelage type. No aged adult sea otter (10 years or greater) pelt samples were used in this study. Sea otter pelts were categorized into age classes by CDFW employees based on the well-established sea otter stranding age estimation protocols that use total body length and tooth development data as identifiers (Nicholson et al., 2020). Each pelt sample was measured under three treatment conditions: control, oiled and washed.

Fur buoyant force

We measured the buoyancy of pelts in freshwater using an apparatus similar to that described in Fish et al. (2002), in a 10-gallon (≈37.85-liter) glass tank (Fig. 1). For these measurements, we used 5×5 cm pelt pieces cut from the original pelt samples. We washed each pelt in cold running water to remove any sand or dirt. We gently dabbed the fur with paper towels to help dry the pelt samples. We then used a hair dryer (Trezero® 2200 W ceramic tourmaline blow dryer) on the cool setting to dry the pelt, as it has been found that blow drying will help restore the insulating air layer in the pelage (Williams and Davis, 1995).

The control condition consisted of a normal pelt with the air layer present. To ensure the pelt did not float upon submersion, we adhered the pelt to a round glass plate (13 cm diameter) using sealant (Loctite® clear silicone waterproof sealant, Westlake, OH, USA) and then flattened the pelt using a smooth plastic tube (12.7×3.81 cm, length×diameter) as a roller to remove any air bubbles between the pelt and the glass plate. After the control trial, we applied 10 ml of Scott Well unrefined crude oil (Texas Raw Crude©, Midland, TX, USA) at 25°C to the pelt using a syringe, and gently massaged the oil into the fur for 30 s, similar to the grooming movements performed by a sea otter, ensuring the oil was evenly distributed across the pelt sample. We measured the buoyancy of the oiled pelt using the same methodology. We collected and properly disposed of all crude oil hazardous waste using PPE (gloves, goggles, facial coverings). Once an oiled trial was completed (∼5–10 min), we washed the pelt using Dawn® dishwashing detergent (Dawn® Ultra Dishwashing Liquid, Proctor & Gamble, Cincinnati, OH, USA). We applied 0.5–1 ml of Dawn® to the oiled pelt using a syringe, and we gently massaged small amounts of the detergent into the pelt. We then used cold running water to remove the detergent, and repeated adding 0.5–1 ml of Dawn®, followed by rinsing, until the pelt was fully clean. Washed pelts were considered clean when no oil or soap residue was visible and the water coming off the pelt was clear. We conducted additional visual inspections of the pelt after the pelt was patted dry with paper towels, to ensure all oil and soap was removed before blow-drying the pelt. We recorded the time spent washing and the total amount of Dawn® needed to fully wash the pelt. Before measuring buoyancy after washing with Dawn®, we attempted to restore the air layer via blow drying, and then we reattached each pelt sample with sealant.

During treatment conditions, we weighed each sample twice: once when dry (in air) and once when submerged (in water). We measured mass of the pelage in air (m_{af}) to the nearest 0.01 g using an electronic balance (Ohaus® Electronic Balance SPX222, Parsippany, NJ, USA). We measured pelage mass in water (m_{wf}) by submerging the secured pelt on a glass plate. The submerged glass plate rested on a 3-D printed holder that hung from the scale, which rested on a plexiglass sheet covering half the tank (Fig. 1). We attached a 100-g ballast weight to the bottom of the holder to provide sufficient negative buoyancy to fully submerge the sample. This process was repeated on the same pelt for all three treatment conditions. After the Dawn® trials, we cut down the hairs using sharp, haircutting shears, and we then used facial razors to shave the hairs as close to the skin as possible. We recorded the time spent shaving the pelts.

To calculate the pelt buoyant force (F_{b}; N) of the air layer in the fur (Fish et al., 2002), we used the mass with the fur intact in air (m_{af}) and in water (m_{wf}) for all three treatment conditions, as well as the mass with the fur shaved in air (m_{as}) and in water (m_{ws}), according to the equation:

$$F_{\mathrm{b}} = \boldsymbol{g}(m_{\mathrm{af}} - m_{\mathrm{wf}} - m_{\mathrm{as}} - m_{\mathrm{ws}}), \tag{1}$$

where $\boldsymbol{g}$ is gravitational acceleration (9.8 m s^{-2}), m_{af} is pelage mass (kg) in air, m_{wf} is pelage mass (kg) in water, m_{as} is skin mass (kg) in air with hair removed and m_{ws} is skin mass in water with hair removed.

Scaled fur buoyant force

To scale up F_{b} to the whole animal, we estimated the whole-animal fur buoyant force (F_{wa}; N) using the following equation:

$$F_{\mathrm{wa}} = \frac{F_{\mathrm{b}}}{A_{\mathrm{p}}} \cdot S, \tag{2}$$

where F_{b} is pelt buoyant force (N), S is estimated total body surface area (m^2) and A_{p} is pelt sample area (m^2). To estimate S for each sea otter sample, we used the following equation:

$$S = 0.087 \cdot M_{\mathrm{b}}^{0.67}, \tag{3}$$

where 0.087 is the area constant determined in Costa and Kooyman (1982), M_{b} is body mass (kg) and 0.67 is the constant for the 2/3 rule of surface area to volume scaling. We used M_{b} for the individual animals from which the pelts were collected. To calculate the scaled mass-specific fur buoyant force (F_{ms}; N kg^{-1}), we divided

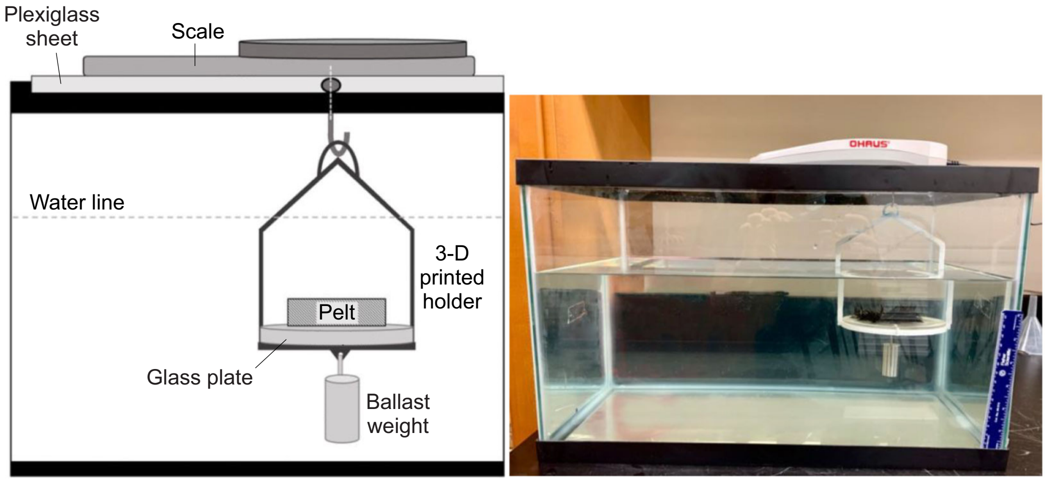

Fig. 1. The fur buoyancy apparatus. Diagram of the apparatus setup for a submerged southern sea otter (*Enhydra lutris nereis*) pelt (left), and photo of the buoyancy system with an oiled pelt *in situ* (right). Methods adapted from Fish et al. (2002).

whole-animal buoyant force by the body mass, using the following equation:

$$F_{ms} = \frac{F_{wa}}{M_b}. \quad (4)$$

Statistical analyses

All analyses (Supplementary Materials and Methods) were performed in R version 4.2.0 (https://www.r-project.org/). A P-value ≤0.05 was considered significant for all analyses. We compared pelt buoyant force, whole-animal fur buoyant force and scaled mass-specific fur buoyant force (Dataset 1) using linear mixed-effects models from the lmerTest package in R (Kuznetsova et al., 2017). Each model included treatment condition (control, oiled, washed) and age class as main effects, along with all possible interactions, and sea otter sample ID as a random effect. To make pairwise comparisons, we computed estimated marginal means for treatment and age class combinations in our models using the emmeans package in R (Lenth, 2018). We compared differences across age classes in the amount of Dawn® needed to clean each pelt, and the amount of cleaning time and shaving time after the fur crude oil treatments (Dataset 1), using a one-way ANOVA followed by a Tukey's honestly significant difference test. To investigate the correlation between sea otter hair density and buoyancy (Dataset 1), we ran linear regression models for pelt buoyant force, whole-animal fur buoyant force and mass-specific fur buoyant force. Hair density values were from a previous study on the same pelt samples (Riordan et al., 2023a).

RESULTS

Fur buoyant force

There was no significant difference in pelt buoyant force (F_b) across age classes ($F_{5,31}$=2.14, P=0.060; Table 1, Fig. 2), and no significant interaction between age class and condition ($F_{10,62}$=1.89, P=0.063). The mean F_b for all age classes was 0.311±0.083 N for control pelts, 0.145±0.031 N for oiled pelts and 0.197±0.078 N for washed pelts. There was a significant difference in F_b across conditions ($F_{2,62}$=64.95, P<0.001; Fig. 2). F_b was significantly higher in the control condition compared with oiled pelts (P<0.001) and washed pelts (P<0.001). Washed pelts had significantly higher F_b than oiled pelts (P=0.003). There was no significant difference in the amount of Dawn® required to clean the sea otter pelt samples ($F_{5,31}$=2.041, P=0.1), the amount of time spent cleaning the pelts ($F_{5,31}$=1.063, P=0.4) or the amount of time spent shaving the pelts ($F_{5,31}$=1.762, P=0.15) across all age classes (Table 2).

Scaled-up fur buoyant force

There was a significant interaction between age class and condition for whole-animal fur buoyant force (F_{wa}) ($F_{10,62}$=4.31, P<0.001; Fig. 3), and there was a significant difference in sea otter F_{wa} across age classes ($F_{5,31}$=15.14, P<0.001) and conditions ($F_{2,62}$=42.38, P<0.001). Across all age classes, F_{wa} was highest in the control condition, lowest for oiled pelts and intermediate for washed pelts (P<0.0001 for all comparisons; Table 1, Fig. 3). F_{wa} was significantly higher for adults in the control condition compared with all other age classes and conditions (P<0.0001–0.0360). With the exception of the adults, there was no significant difference in F_{wa} between the control and washed condition across age

Table 1. Average southern sea otter (*Enhydra lutris nereis*) body mass (M_b; kg), pelt buoyant force (F_b; N), whole-animal fur buoyant force (F_{wa}; N) and mass-specific fur buoyant force (F_{ms}; N kg^{-1}) across age classes and conditions

			F_b (N)			F_{wa} (N)			F_{ms} (N kg^{-1})		
Age class	N	M_b (kg)	Control	Oiled	Washed	Control	Oiled	Washed	Control	Oiled	Washed
Neonate	9	2.37±1.22	0.24±0.08	0.14±0.03	0.17±0.11	15.12±8.20	8.55±3.72	10.88±8.82	6.40±1.93	3.87±0.92	4.56±2.75
Small pup	5	3.81±0.91	0.37±0.09	0.15±0.04	0.27±0.08	31.30±8.84	12.61±4.31	22.45±4.72	8.40±2.42	3.35±0.90	6.18±2.24
Large pup	5	5.38±1.78	0.29±0.06	0.16±0.05	0.17±0.05	30.95±8.85	17.36±8.20	17.60±7.04	6.00±1.46	3.16±0.69	3.40±1.01
Juvenile	6	6.45±2.39	0.36±0.36	0.14±0.01	0.25±0.10	42.87±9.72	16.44±4.42	31.12±15.64	7.03±1.68	2.64±0.41	4.82±2.04
Subadult	6	12.02±3.09	0.29±0.14	0.14±0.03	0.19±0.09	55.71±33.86	25.34±6.39	35.35±19.74	4.44±1.87	2.13±0.41	2.88±1.45
Adult	6	21.60±4.83	0.31±0.08	0.15±0.03	0.13±0.03	84.67±27.30	28.10±10.90	35.02±8.37	3.96±0.95	1.90±0.32	1.68±0.46

Values (means±1 s.d.) are provided for samples used in fur buoyancy trials. N represents the number of individual pelt samples for each age class.

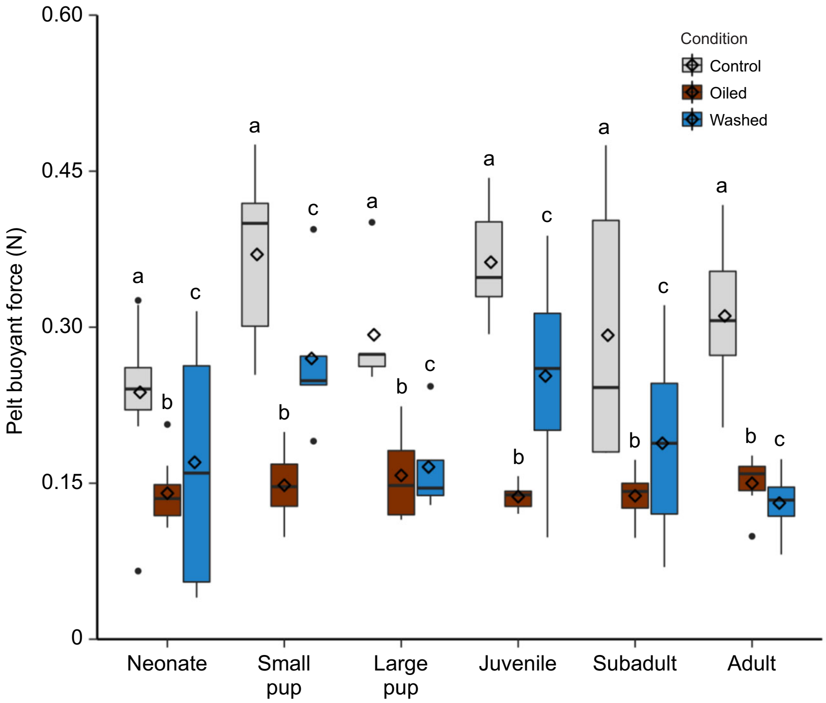

Fig. 2. Pelt buoyant force of southern sea otter pelts. The pelt buoyant force (F_b; N) of southern sea otter (*E. lutris nereis*) pelt samples across ontogeny, including neonates (<1 month, *N*=9), small pups (1–2 months, *N*=5), large pups (3–5 months, *N*=5), juveniles (6 months–1 year, *N*=6), subadults (1–3 years, *N*=6) and adults (4–9 years, *N*=6), and by pelage condition: control (gray), after oiling with crude oil (brown) and washed with Dawn® (blue). The horizontal line within each box indicates the median value and the box boundaries indicate the upper and lower interquartile range. Vertical lines indicate minimum and maximum values within 1.5 times the interquartile range. Individual points are outlier values >1.5 and <3 times the interquartile range. Diamonds within boxplots indicate the mean values for each age class. Different letters above the boxes indicate statistically significant findings among condition means. There were no significant differences in F_b across age classes within a condition ($F_{10,62}$=1.89, *P*=0.063). Across all age classes, F_b was significantly higher for the control pelts than for pelts washed with Dawn® (*P*<0.001), which in turn was significantly higher than F_b after oiling (*P*=0.003).

classes (*P*=0.1652–1.0000). There was no significant difference in F_{wa} across age classes in the washed condition (*P*=0.0700–1.0000).

There was a significant difference for the scaled mass-specific fur buoyant force (F_{ms}) across age classes ($F_{5,31}$=6.66, *P*<0.001) and for all conditions ($F_{2,62}$=59.00, *P*<0.001; Fig. 4), but there was no significant interaction between age class and condition ($F_{10,62}$=1.77, *P* =0.086; Fig. 4). F_{ms} was highest in the control condition, lowest for the oiled condition and intermediate in the washed condition for all age classes (*P*<0.0001–0.0018). For age classes overall, F_{ms} was significantly higher for neonates (*P*=0.0059), small pups (*P*=0.0005) and juveniles (*P*=0.0212) compared with adults. Additionally, F_{ms} was significantly higher for small pups compared with subadults (*P*=0.0052).

Hair density versus whole-animal fur buoyant force

There was no significant relationship between hair density and pelt buoyant force ($F_{1,35}$=2.732, r^2=0.0459, *P*=0.1073), according to the equation F_b=0.00006101(hair density)–25.06. Also, there was no relationship between hair density and mass-specific fur buoyant force ($F_{1,35}$=3.656, r^2=0. 06,871, *P*=0.0641; Fig. 5), according to the equation F_{ms}=−0.001638(hair density)+7.43065. However, there was a significant positive relationship between hair density and whole-animal fur buoyant force ($F_{1,35}$=54.32, r^2=0.5969, *P*<0.0001), according to the equation F_{wa}=0.05533(hair density)+6.47382 (Fig. 5).

Table 2. Amount of Dawn® (ml) required to remove crude oil from the pelts, the amount of time (min) needed to wash the pelts and the amount of time (min) it took to shave southern sea otter (*E. lutris nereis*) pelts across age classes

Age class	*N*	Amount of Dawn® (ml)	Clean time (min)	Shave time (min)
Neonate	9	8.72±4.06	8.28±2.74	52.33±32.40
Small pup	5	11.40±2.61	8.20±0.84	58.00±20.49
Large pup	5	9.60±1.52	7.70±0.84	65.00±32.02
Juvenile	6	8.33±1.03	6.17±1.13	44.17±12.81
Subadult	6	12.50±3.94	8.50±2.88	85.83±33.53
Adult	6	11.67±2.66	8.08±1.80	79.17±36.93

Values (means±1 s.d.) are provided for samples used in fur buoyancy trials. *N* represents the number of individual pelt samples for each age class.

DISCUSSION

Our control condition pelt buoyant force (F_b) findings are consistent with previous research on adult sea otter pelts (Fish et al., 2002) (Table 1). We originally predicted we would see differences in pelt buoyancy between the natal pelage (neonates, small pups, some large pups) and the adult pelage (all other age classes) (Riordan et al., 2023a). However, we found no differences in F_b across ontogeny for our sea otter pelt samples (Table 1, Fig. 2), likely because the pelt samples were similarly sized and trapped a similar amount of air within the fur. However, we did observe differences across age classes when we scaled the buoyant force up to the whole animal (F_{wa}) and accounted for body size (F_{ms}). Whole-animal fur buoyant force increased with age (Fig. 3), because larger animals have more pelage overall and therefore more trapped air to provide buoyancy. Indeed, we saw a positive relationship between whole-animal fur buoyant force and hair density (Fig. 5), which increases with age in sea otters (Riordan et al., 2023a).

The relative amount of buoyancy provided by fur decreases as body size increases (Fish et al., 2002). Mass-specific positive buoyant forces of neonate sea otters were previously estimated to be twice that of the adults (Cashman, 2002; Thometz et al., 2015). Our scaled mass-specific findings are consistent with those estimates, and these results demonstrate the importance of a larger surface area to volume ratio in neonates and small pups, as it allows them to generate more buoyant force relative to their smaller body mass (Fig. 4). A pup must float on its own at the water's surface when its mother embarks on short foraging bouts; this is when the buoyancy of a pup becomes especially important (Payne and Jameson, 1984; Thometz et al., 2015). Pups begin attempting to dive at around 5 weeks of age, but the pups are not successful in diving until

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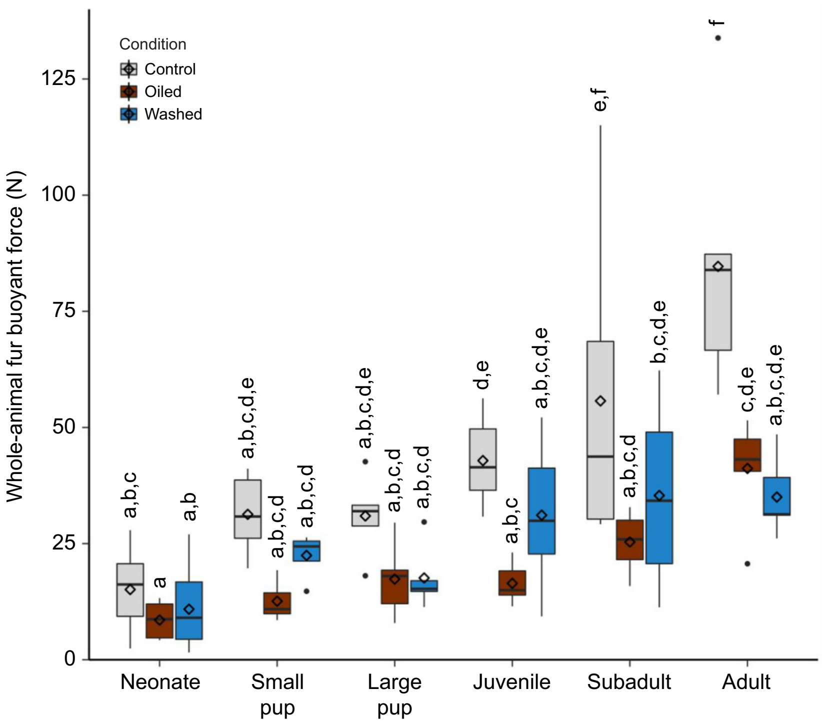

Fig. 3. Whole-animal fur buoyant force for southern sea otters. The whole-animal fur buoyant force (F_{wa}; N) for southern sea otter (*E. lutris nereis*) pelts across ontogeny, including neonates (<1 month, *N*=9), small pups (1–2 months, *N*=5), large pups (3–5 months, *N*=5), juveniles (6 months–1 year, *N*=6), subadults (1–3 years, *N*=6) and adults (4–9 years, *N*=6), and by pelage condition: control (gray), after oiling with crude oil (brown) and washed with Dawn® (blue). The horizontal line within each box indicates the median value and the box boundaries indicate the upper and lower interquartile range. Vertical lines indicate minimum and maximum values within 1.5 times the interquartile range. Individual points are outlier values >1.5 and <3 times the interquartile range. Diamonds within boxplots indicate the mean values for each age class. Different letters above the bars indicate statistically significant findings among means. F_{wa} was generally reduced in the oiled condition compared with the control condition across age classes (*P*<0.0001). F_{wa} values in the washed condition were not consistent across age classes because of the successful or unsuccessful reintroduction of the air layer (*P*=0.0700–1.0000).

around 10 weeks of age (Hanson et al., 1993). The trade-off with the high relative buoyancy seen in young sea otter pups is that they cannot dive yet, but they can float very well at the surface.

In animals that have an air layer in the fur, the pelage is more susceptible to fouling and water infiltration (Costa and Kooyman, 1982; Webb and King, 1984; Kruuk and Balharry, 1990; Loughlin, 2013; Fish, 2000). If the air layer becomes disturbed from oiling, the fur loses its buoyant properties (Fig. 2). Past studies have investigated the effects of oiling on adult sea otter thermal function (Costa and Kooyman, 1982; Williams et al., 1988; Dunkin, 2001; Riordan et al., 2023b), but no previous study has researched the effect of oiling on sea otter buoyancy and made direct comparisons across ontogeny. In general, oiling reduces the buoyant force of the pelt relative to intact pelage across all age classes (Fig. 3). This suggests that regardless of age, all sea otters are vulnerable to the disruption of their buoyancy when oiled, similar to what was found in a previous study on sea otter thermal function (Riordan et al., 2023b). Our study only focused on the physical effects of crude oil on the fur in a laboratory-based setting. In marine wildlife, exposure to crude oil can cause severe physiological

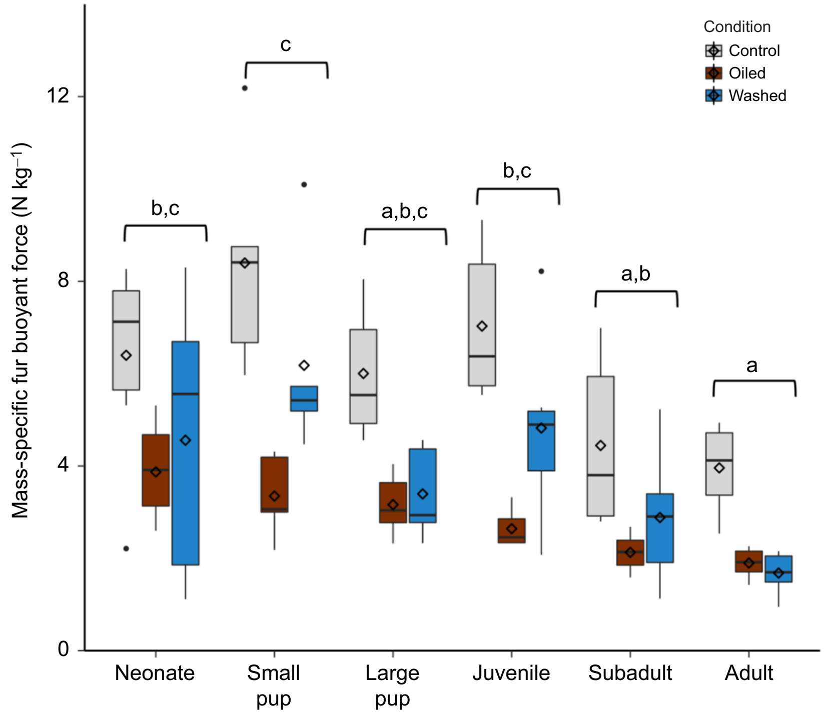

Fig. 4. Mass-specific fur buoyant force for southern sea otters. The mass-specific fur buoyant force (F_{ms}; N kg^{-1}) for southern sea otters (*E. lutris nereis*) across ontogeny, including neonates (<1 month, *N*=9), small pups (1–2 months, *N*=5), large pups (3–5 months, *N*=5), juveniles (6 months–1 year, *N*=6), subadults (1–3 years, *N*=6) and adults (4–9 years, *N*=6), and by pelage condition: control (gray), after oiling with crude oil (brown) and washed with Dawn® (blue). The horizontal line within each box indicates the median value and the box boundaries indicate the upper and lower interquartile range. Vertical lines indicate minimum and maximum values within 1.5 times the interquartile range. Individual points are outlier values >1.5 and <3 times the interquartile range. Diamonds within boxplots indicate the mean values for each age class. Different letters above the bars indicate statistically significant findings among age class means. F_{ms} decreased with age and as well with oiling; there were variable results when washed (*P*<0.0001–0.0018).

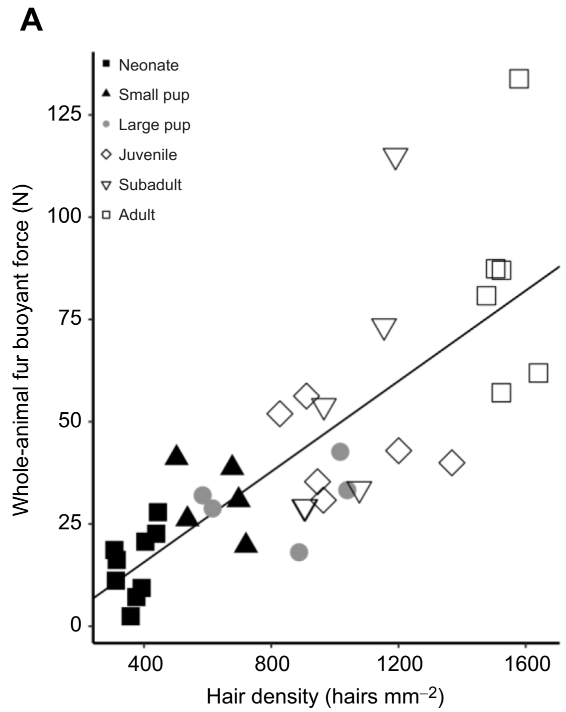

Fig. 5. Results of whole-animal and mass-specific buoyant force versus hair density for southern sea otters. The whole animal and mass-specific buoyant force versus hair density for southern sea otters (*E. lutris nereis*) across ontogeny, including neonates (<1 month, N=9), small pups (1–2 months, N=5), large pups (3–5 months, N=5), juveniles (6 months–1 year, N=6), subadults (1–3 years, N=6) and adults (4–9 years, N=6). (A) Relationship between the whole-animal fur buoyant force (F_{wa}; N) and hair density (hairs mm^{-2}) for southern sea otters. There was a significant positive correlation between F_{wa} and hair density (P<0.0001). (B) Relationship between mass-specific fur buoyant force (F_{ms}; N kg^{-1}) and hair density (hairs mm^{-2}) for southern sea otters. There was no significant correlation between F_{ms} and hair density (P=0.0641). For both analyses, each sample is represented by a single symbol, and different symbols and colors denote age classes. Lines represent the best-fit linear regression. Hair density values were used from a previous study (Riordan et al., 2023a).

impacts, and we did not investigate any internal toxicological impacts on sea otters.

The close proximity of southern sea otter populations to oil platforms off the coast of California makes sea otters vulnerable to the internal and external effects of oil spills. Special consideration should be made to ensure all the oil is removed from the fur, and Dawn® has been shown to be efficient at ridding the fur of oil when using proper wash techniques (Williams et al., 1988; Jessup et al., 2012). Washing the pelts with Dawn® sometimes restored the buoyant force, but the results were not consistent. Although the primary purpose of Dawn® is to clean the fur, this suggests that washing with Dawn® may not fully restore the air layer of the fur (Jessup et al., 2012). However, the sea otter pelt buoyant force values used to estimate F_{wa} and F_{ms} were from pelts in a laboratory setting, not for live animals, which have natural oils and groom consistently for proper fur hygiene and air layer maintenance (Williams et al., 1988; Davis et al., 1988). It is likely that some detergent was not fully removed from the sample, and it might take longer to completely rid the fur of soap because of the higher hair density present in the adult pelage (Riordan et al., 2023a). It is important that wildlife networks and rehabilitators carefully remove all detergent residue from the fur when washing oiled otters. Additionally, the amount of oil added to the pelts in our study mimics a heavily oiled sea otter, and it could require two wash cycles to fully clean the pelt in an actual rehabilitation scenario. Another possible limitation to our laboratory-based experiment could be that we used freshwater to clean the pelts. Our findings can still improve oiled sea otter care, as they support efforts to clean the oil from the fur using a cleaning detergent such as Dawn®. Surprisingly, there were no differences in the amount of Dawn® used to clean pelts and the clean time across age classes for our sea otter pelt samples (Table 2). Adult sea otter pelts have a higher hair density (Riordan et al., 2023a), and it may be expected to take longer and require a larger amount of Dawn® to thoroughly clean pelts with denser pelage. In the event of an oil spill, washing sea otter fur with Dawn® is likely to work to restore the air layer, partnered with extended time in rehabilitation to allow for the natural oils to be produced and for the sea otters to groom themselves.

Diving for sea otters is energetically costly because of their inefficient swimming mode, large lungs, buoyant fur and the high cost of thermoregulating at depth (Denison and Kooyman, 1973; Kooyman, 1973; Yeates et al., 2007; Ponganis, 2011). Sea otters typically forage at depths less than 25 m, and spend most of their time grooming, resting and eating at the surface (Riedman and Estes, 1990; Cashman, 2002). The behavior of sea otters may explain why these large quantities of air in the lungs and fur may be beneficial. An increased understanding of the relationship of sea otter body and lung size is key to assessing the overall effects of buoyancy across ontogeny. Future work should examine how these size differences affect sea otter buoyancy.

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Competing interests
The authors declare no competing or financial interests.

Author contributions
Conceptualization: K.R., N.M.T., F.I.B., H.E.M.L.; Methodology: K.R., H.E.M.L.; Formal analysis: K.R.; Investigation: K.R., A.E.D., S.J.K., H.E.M.L.; Resources: F.I.B., H.E.M.L.; Data curation: K.R., A.E.D., S.J.K., H.E.M.L.; Writing - original draft: K.R.; Writing - review & editing: A.E.D., S.J.K., N.M.T., F.I.B., H.E.M.L.; Visualization: K.R., H.E.M.L.; Supervision: H.E.M.L.; Project administration: K.R., H.E.M.L.; Funding acquisition: K.R., H.E.L.M.

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Data availability
All relevant data can be found within the article and its supplementary information.

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