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THE HIGH COST OF MOTHERHOOD: END-LACTATION SYNDROME IN SOUTHERN SEA OTTERS (*ENHYDRA LUTRIS NEREIS*) ON THE CENTRAL CALIFORNIA COAST, USA

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ABSTRACT: Sea otters (*Enhydra lutris*) have exceptionally high energetic requirements, which nearly double during lactation and pup care. Thus, females are extremely vulnerable to caloric insufficiency. Despite a number of compensatory strategies, the metabolic challenge of reproduction culminates in numerous maternal deaths annually. Massive depletion of energy reserves results in a case presentation that we define as end-lactation syndrome (ELS), characterized by moderate to severe emaciation not attributable to a concurrent, independent disease process in females dying during late pup care or postweaning. We compiled detailed data for 108 adult female southern sea otters (*Enhydra lutris nereis*) examined postmortem that stranded in California, US, 2005–12, and assessed pathology, reproductive status, and the location and timing of stranding. We introduce simple, grossly apparent, standardized physical criteria to assess reproductive stage for female sea otters. We also describe ELS, examine associated risk factors, and highlight female life history strategies that likely optimize reproduction and survival. Our data suggest that females can reset both the timing and energetic demands of reproduction through fetal loss, pup abandonment, or early weaning as part of specific physiologic checkpoints during each reproductive cycle. Females appear to preload nutritionally during delayed implantation and gestation to increase fitness and reproductive success. We found that ELS was a major cause of death, affecting 56% of enrolled adult females. Peak ELS prevalence occurred in late spring, possibly reflecting the population trend toward fall/winter pupping. Increasing age and number of pregnancies were associated with a higher risk of ELS. Although the proportion of ELS females was highest in areas with dense sea otter populations, cases were recovered throughout the range, suggesting that death from ELS is associated with, but not solely caused by, population resource limitation.

Key words: ELS, emaciation, end-lactation syndrome, *Enhydra lutris nereis*, lactation, metabolism, maternal care, reproductive cycle, southern sea otter.

INTRODUCTION

As the smallest marine mammal, sea otters (*Enhydra lutris*) exhibit the highest mass-specific metabolic demands of any mustelid or marine mammal (Morrison et al. 1974), with a resting metabolic rate 2.8–3.2 times higher than similarly sized terrestrial animals and double that of all other marine mammals (Costa and Kooyman 1984). A more recent evolutionary transition to the ocean environment is reflected by unique physical attributes, such as decreased streamlining and absence of blubber and countercurrent heat

exchangers (Berta et al. 2005), making marine survival more challenging (Williams 1989). Evolutionary strategies to overcome these metabolic challenges include development of the densest fur of any mammal and daily prey consumption equivalent to 20–25% of body mass (Costa and Kooyman 1982).

Female sea otter reproduction is composed of three phases that collectively span 1 yr: estrus, copulation, and delayed implantation (DI) (2–3 mo); implantation, gestation, and parturition (4–5 mo); and pup care through weaning (5–6 mo) (Riedman and Estes 1990).

Only females provide pup care, and the minimum maternal investment for successful weaning is 19–26 wk, with longer periods of care equating to higher pup survival (Jameson and Johnson 1993). The high energetic cost of lactation and pup rearing requires significant increases in maternal foraging activity in proportion to pup maturity and growth (Gelatt et al. 2002; Esslinger et al. 2014).

Unlike most mammals, sea otter pups continue nursing throughout 5–6 mo of dependency, while consuming large amounts of prey captured by their mothers (Gelatt et al. 2002). Females optimize neonatal (≤ 3 wk postpartum) pup care by decreasing foraging activity and dive depth, which negatively affects energy intake (Gelatt et al. 2002; Staedler 2011). Around 10 wk postpartum, females increase dive frequency and foraging intensity to offset substantial caloric deficits (Esslinger et al. 2014). During late pup care, maternal energetic demands increase by $>95\%$ (Thometz et al. 2014). Despite increased foraging, females are often emaciated during late pup dependency and postweaning (Monson et al. 2000) and may be more susceptible to death from exogenous stressors (Tinker et al. 2006). Survival strategies such as early weaning can reduce maternal caloric deficits, leaving females in better condition for survival and future reproduction, but significantly decreasing pup survival (Monson et al. 2000).

Because of the high caloric cost of homeostasis, reproduction and pup care pose substantial risk for female sea otters, especially when combined with disease, resource competition, or other factors that reduce foraging efficiency (Tinker et al. 2006). During each reproductive cycle, females must strike a balance between successfully rearing a pup and maintaining sufficient energy reserves to survive (Thometz et al. 2014). Given such a delicate balance, any additional stressors could tip the scales toward emaciation and death.

Approximately 40–50% of sea otters that die in California are recovered as beach-cast carcasses (Gerber et al. 2004), providing a valuable dataset for examining patterns and

causes of mortality (Kreuder et al. 2003). We used these data to develop criteria for classifying reproductive stage for female sea otters and to examine relationships between reproductive stage and selected risk factors.

Postmortem examinations revealed a characteristic lesion pattern, as described in the upcoming text, suggestive of mortality related to the high energetic costs of lactation and pup care in reproductively active female southern sea otters. We named this condition end-lactation syndrome (ELS), and developed criteria to facilitate case recognition. Using detailed postmortem data, we assessed whether ELS prevalence was related to age, stranding location (possibly related to differential resource competition), and time period. Our study also characterizes the female reproductive cycle and highlights maternal strategies to optimize survival and reproductive success.

MATERIALS AND METHODS

Enrolled southern sea otters were fresh (<72 h postmortem) adult (4–10 yr old) or aged adult (>10 yr old) females that stranded 2005–12 and had received detailed postmortem examination with histopathology. Carcasses were opportunistically recovered from Año Nuevo ($37^{\circ}7'59''N$, $122^{\circ}19'59''W$) to Jalama Beach ($34^{\circ}30'39''N$, $120^{\circ}30'1''W$) along the central California coast, US. Reproductive status and nutritional condition were assessed using a suite of anatomical features (Figs. 1A–F, 2A–F). Reproductive activity was assessed through physical confirmation of current or recent lactation or presence of ovarian follicles (Fig. 1D), corpora lutea (CLs) (Fig. 1E), corpora albicantia (CAs) (Fig. 1F), or an enlarged uterus or uterine blood vessels reflective of current or past pregnancy (Fig. 2E, F).

Each female was classified according to length, weight, nutritional and pelage condition, and presence or absence of concurrent disease processes that could affect survival and nutritional status. As in prior studies (Kreuder et al. 2003), nutritional condition was determined by subcutaneous, intraperitoneal, and epicardial adipose stores and presence or absence of diffuse skeletal muscle atrophy indicative of cachexia. All females were classified with respect to nutritional condition as emaciated (none or scant adipose and marked diffuse muscle atrophy), fair (fair adipose, mild muscle atrophy), moderate (moderate adipose, no muscle atrophy), and excellent (abundant

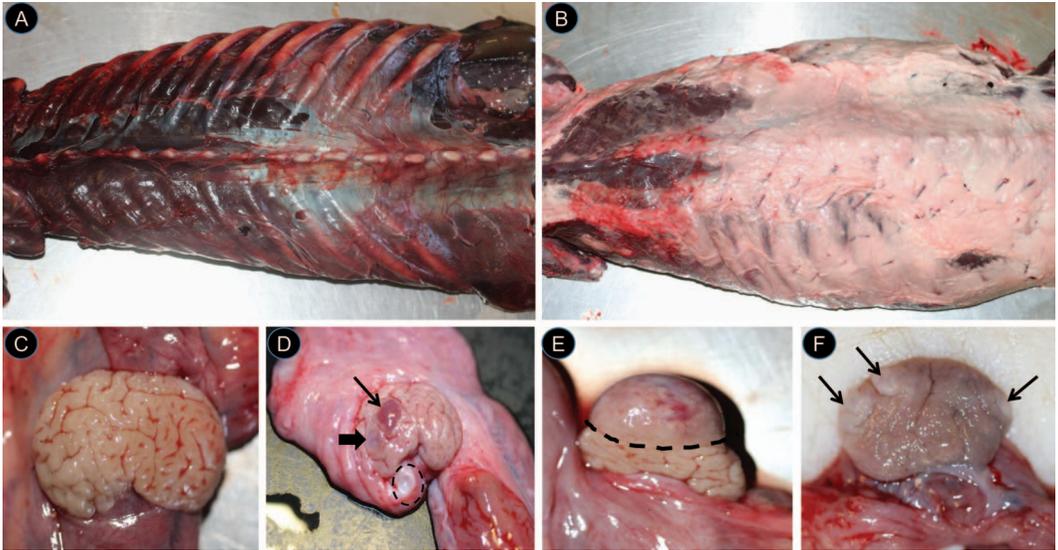


FIGURE 1. Gross findings used to assess nutritional status and reproductive stage based on ovarian structures. (A) Dorsal subcutis of an adult female southern sea otter (*Enhydra lutris nereis*) from the central California coast, USA, that died from end-lactation syndrome (ELS), showing severe, diffuse skeletal muscle atrophy and marked depletion of subcutaneous adipose tissue. (B) Dorsal subcutis of a pregnant adult female southern sea otter (non-ELS control), with no skeletal muscle atrophy and abundant subcutaneous adipose tissue. (C) The ovary of this subadult female sea otter is devoid of follicles, corpora lutea (CLs), or corpora albicantia (CAs). (D) Ovary of an estrus or postestrus otter with a central large, pink-red, raised follicle (thin arrow). Also visible are a CA, suggestive of past pregnancy (broad arrow), and a paraovarian cyst (inside dashed circle). (E) A large, rounded, yellow-pink, raised CL is present along the entire upper edge of this ovary (above dashed line) and is nearly the same size as the ovary, indicative of postimplantation pregnancy. (F) This ovary contains at least three firm, white, flat-topped CAs (arrows), suggestive of at least three prior pregnancies. The total number of previous pregnancies can be estimated in sea otters by counting the number of discrete CAs on both ovaries.

adipose, no muscle atrophy). Grossly apparent characteristics of the integument, nipples, mammary glands, vagina, vulva, cervix, ovaries, and uterine horns were used to classify each sea otter as immature or sexually mature (Supplementary Material Table S1 and Figs. 1, 2). Only mature, reproductively active females were included, and all were subclassified as reproductive stage 1 through 5, based on grossly apparent characteristics unique to each stage of the reproductive cycle (see Supplementary Material Table S1). Each female was assigned the reproductive stage that best fit all reproductive characteristics, and consistent scoring was enforced through evaluation by multiple reviewers.

Because no diagnostic test exists to confirm ELS, diagnosis was based on exclusion of disease processes that could independently cause severe adipose tissue (adipose) depletion, emaciation, and marked muscle atrophy. Based on reproductive stage and postmortem examination findings, all enrolled females were classified as either ELS-positive (cases) or ELS-negative (controls). Minimum criteria for ELS cases included physical

attributes consistent with females in late pup care (stage 4) or early postweaning (stage 5) (see Supplementary Material Table S1), with moderate to severe emaciation not solely attributable to an independent disease process, such as acanthocephalan peritonitis. For some cases, ELS was the primary cause of death, whereas for others it was a major contributing factor. All ELS cases were pooled and were compared with time-matched, non-ELS controls.

Characteristics indicative of reproductive stage 4 or 5 females included evidence of recent lactation, substantial ($\geq 75\%$) mammary gland involution, and reduced or absent lactation (Fig. 2B). Additional criteria for stage 4 females included significant uterine involution since the most recent pregnancy (small, nearly symmetrical uterine horns) (Fig. 2D), a closed cervix, one or more relatively inconspicuous placental scars, absence of an implanted blastocyst, and one or more ovarian CAs.

Characteristics typical of stage 5 females included signs of estrus and copulation: acute or subacute mating trauma (e.g., nose wounds),

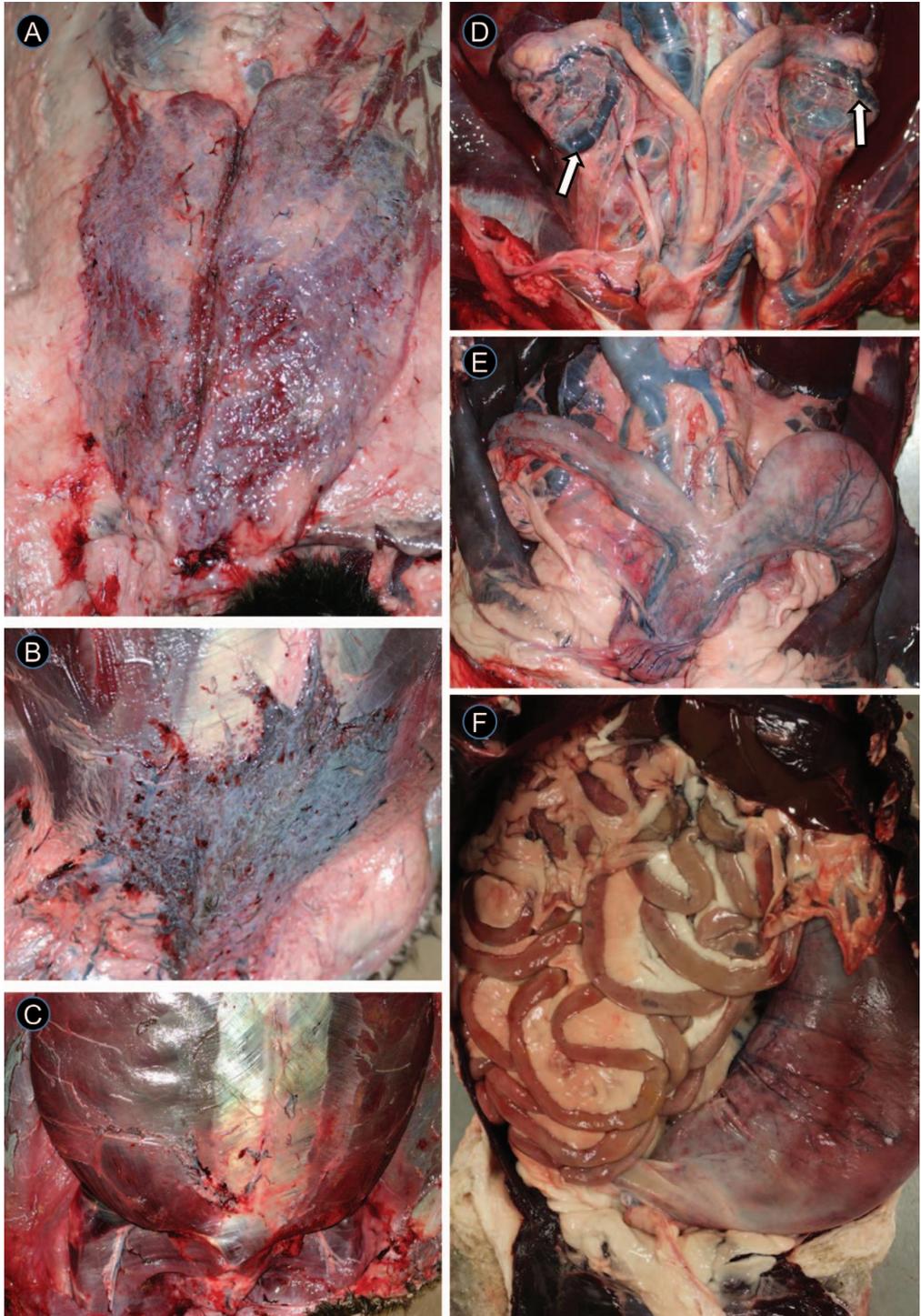


FIGURE 2. Gross findings used to assess reproductive stage of adult female southern sea otters (*Enhydra lutris nereis*) from the central California coast, USA, based on extent of mammary gland development and uterine size and symmetry. (A) Ventral abdominal subcutis showing the thick, pink, fused and bilobed mammary glands typical of adult females during late pregnancy or early postpartum. This female is not yet lactating. Lactation begins just before parturition. (B) Postweaning female showing marked, diffuse atrophy and gray-black

diffuse vulvar or cervical swelling (suggestive of estrus), plus/minus ovarian follicle(s) (Fig. 1D), or small cystic CLs. Recent copulation was indicated by vaginal dilation, bruising of the vagina or caudal cervical os, and matted perivulvar hair. We diagnosed ELS only after considering reproductive stage, nutritional condition, and potential nutritional effects of any concurrent disease processes.

Cases meeting ELS criteria were compared with non-ELS controls by age class, estimated age (average of age estimate in years, based on all physical characteristics) (Kreuder et al. 2003), prior number of pregnancies (based on counts of grossly apparent ovarian CAs), stranding month, nutritional condition, subcutaneous adipose (none, scant, fair, moderate, abundant) (Fig. 1A, B), and reproductive stage (1–5) at the time of death (see Supplementary Material Table S1). Given the unique reproductive biology of sea otters and the number and distribution of males, it is extremely unlikely that any females would enter estrus and not be bred. Observational studies also suggest that females virtually always become pregnant upon entering estrus, with a birth rate approximating one pup per year (Jameson and Johnson 1993; Riedman et al. 1994). Blinded CA counts during postmortem examination of tagged otters with known life histories also support this assessment (M.A.M. unpubl. data). Thus, ovarian CA counts are considered to provide a reasonable approximation of prior pregnancies in sea otters.

Logistic regression was used to test for effects of age and number of previous pregnancies on the likelihood of ELS (ELS as a binomial response variable, where 1=ELS case, and 0=control). We also compiled known and estimated (within 3-wk accuracy) birth dates of all pups born to females in previous telemetry studies from just north of Monterey Bay to the Santa Barbara Channel (Staedler 2011; Tinker et al. 2013) to compare temporal trends for pup births with trends for recovery of stranded ELS females.

Finally, stranding locations (by 0.5-km coastal segment) were compared with local population density estimates (otters/km²), based on time-matched, smoothed, 3-yr average spring survey

data (Tinker and Hatfield 2015). Logistic regression was used to test for linear and quadratic effects of local population density on ELS status as defined above, and the model with the highest R^2 value was retained.

RESULTS

Pooled cases and controls consisted of 108 females (94 adults and 14 aged adults) from 4 to ≥ 15 yr old (mean 8 ± 2). The number of prior pregnancies ranged from 0 to ≥ 10 (mean 3 ± 2). The CA counts were unknown for two animals. Case and control distribution ranged from 11 to 16 per year from 2005 to 2012. Nutritional condition varied from emaciated (67%) to fair (4%), good (10%), or excellent (19%) and subcutaneous adipose from none (52%) to scant (15%), moderate (9%), or abundant (19%). The distribution by reproductive stage 1–5 was 9% (early pregnancy), 11% (late pregnancy), 10% (early pup care), 21% (late pup care), and 48% (weaning, estrus, and DI), respectively.

Of 108 adult females, more than half ($n=61$) had ELS, including 44% ($n=27$) with ELS as the primary cause of death and 56% ($n=34$) with ELS as a major contributing factor. Sixty-nine percent ($n=75$) of females died during late pup care or after pup weaning (stages 4 and 5), with 80% ($n=60$) diagnosed with ELS.

Plots of reproductive stage by nutritional condition suggest progressive improvement from postimplantation pregnancy (stage 1) through early pup care (stage 3) (Figs. 2D–F, 3A). This trend reversed abruptly between early (stage 3) and late (stage 4) pup rearing. Nearing the end of pup care 83% ($n=19$) of females in stage 4 and 90% ($n=52$) of otters in stage 5 were emaciated. Similarly, $>90\%$

←
discoloration of the mammary gland as it involutes between successive pregnancies. Note absence of milk production. (C) Ventral abdominal subcutis, demonstrating absence or near absence of discernible mammary tissue. This is typical during delayed implantation and early postimplantation pregnancy. (D) Ventral view of the abdomen of an adult female, demonstrating the small, slender, bilaterally symmetrical uterine horns typical of females from late pup care through postweaning and delayed implantation periods. The prominent, dilated veins near each ovary (arrows) confirm at least one prior pregnancy. (E) Uterus during early pregnancy, characterized by progressive uterine horn asymmetry and dilation of the central portion of the pregnant uterine horn (center right). (F) Ventral abdominal view of a pregnant, late-gestation uterus (center right). The nonpregnant uterine horn is often small and hard to see at this stage. Note the progressive and marked increase in internal adipose stores during gestation.

($n=51$) of females with no adipose were classified as ELS as a primary or major contributing cause of death, whereas 77% ($n=36$) of non-ELS females had fair to excellent subcutaneous adipose (Fig. 1B).

Adult females stranded during all months, with a large peak in March–June and a smaller peak in August–October (Fig. 3B). Similarly, 61% ($n=37$) of ELS cases stranded March–June. Pregnant females (stages 1 and 2) stranded during all months except April. The proportion of females stranding during late pup care (stage 4) and postweaning (stage 5) was highest in late spring/early summer, with $\geq 70\%$ of adult females examined postmortem in stage 4 or 5 each month from March to June, corresponding temporally with the peak in ELS cases. Seventy-five percent of females examined May–June had recently weaned pups, and 80% of those were ELS cases, whereas 75% of females examined during August were pregnant or in early pup care. Pup births (based on concurrent monitoring of live, radio-tagged otters) peaked October–January (Fig. 3C).

Logistic regression models indicated a significant increase in ELS occurrence in relation to female age ($\chi^2=14.3$, $P=0.0002$; Fig. 4A) and number of previous pregnancies ($\chi^2=18.8$, $P=0.0001$; Fig. 4B). Females were also more likely to meet criteria for ELS when recovered from coastal locations with higher sea otter population densities (Fig. 4C): a logistic model with a positive quadratic term ($\beta=0.007$) was significant ($\chi^2=5.12$, $P=0.024$) and provided a better fit than a linear model ($R^2=0.040$ vs. 0.027), indicating an accelerating rate of ELS occurrence at higher sea otter population density. The probability of females examined postmortem having ELS was 0.91 (95% confidence interval [CI₉₅]=0.57–0.99) in the highest density areas (~ 18 otters/km²), compared with 0.49 (CI₉₅=0.38–0.61) in low-density areas (~ 1 otter/km²). However, carcass recovery was biased toward urbanized coastlines and areas with greater shoreline access, and some areas with lower otter population density were not represented.

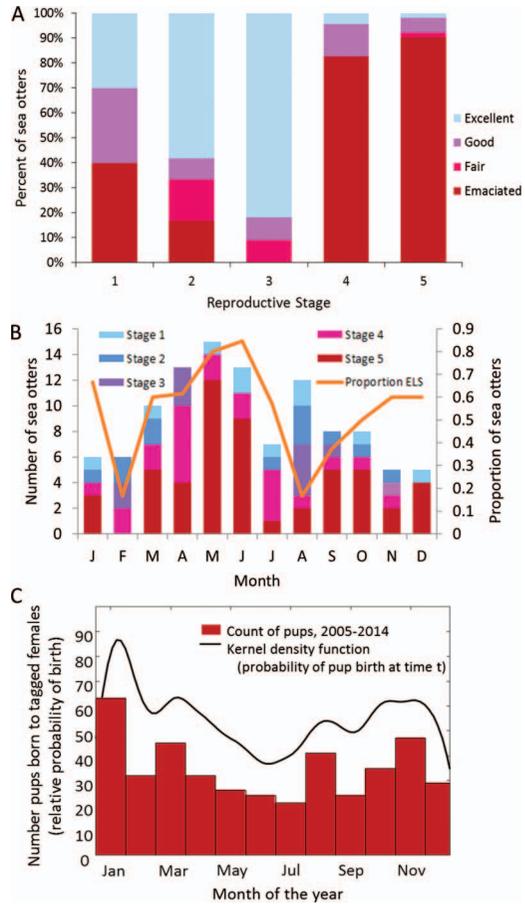


FIGURE 3. (A) Distribution of pooled end-lactation syndrome (ELS) cases and controls based on reproductive stage^a and nutritional condition. (B) Distribution of cases and controls by reproductive stage^a and stranding month, with superimposed line indicating proportion of ELS cases (2005–12) ($n=108$). (C) Known or estimated (± 3 wk) birth dates (to the nearest month) for all sea otter (*Enhydra lutris nereis*) pups born during long-term radiotelemetry studies in California (2005–14) (bars), with superimposed, smoothed (to the nearest week) probabilities of pup birth at time t (continuous line).

^a Reproductive stage: 1=first half of implanted pregnancy; 2=second half of implanted pregnancy through parturition; 3=first half of postpartum pup care; 4=latter half of pup care through weaning; 5=interval spanning pup separation, estrus, copulation, and delayed implantation.

DISCUSSION

The reproductive physiology of sea otters is unique among marine and terrestrial mammals (Williams 1989). The resting metabolic rate is outside of their thermal-neutral zone,

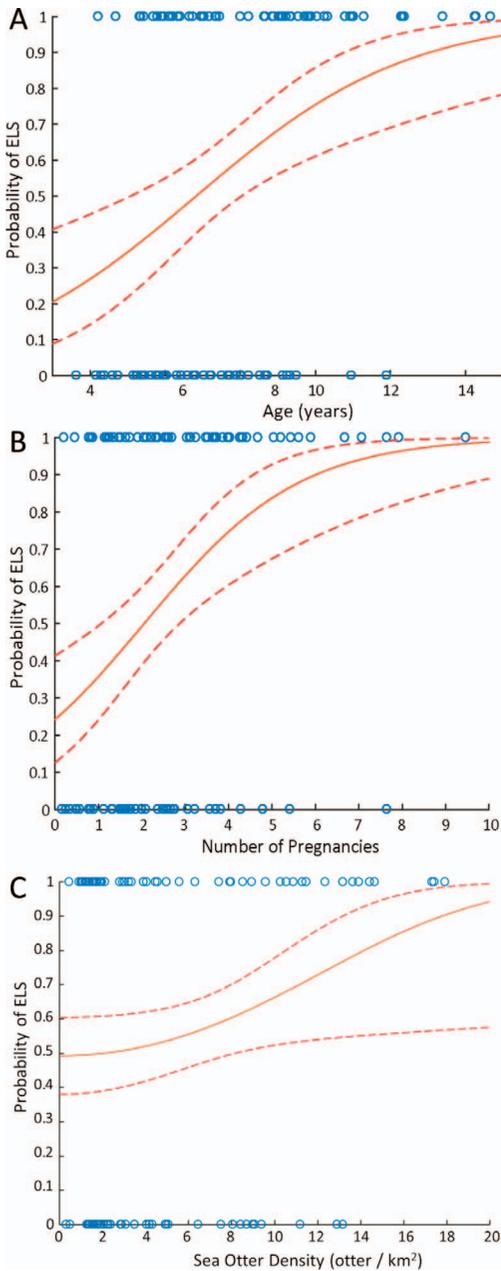


FIGURE 4. Probability of adult female southern sea otters (*Enhydra lutris nereis*) dying from end-lactation syndrome (ELS) as a function of three covariates: (A) female age, (B) the minimum number of prior pregnancies (as determined by counts of ovarian corpora albicantia), and (C) location and time-matched population density (otters/km²). Logistic regression models (solid lines) were fit to data from postmortem examinations of sea otter cases from 2005 to 2012 (circles, 1=ELS and 0=other cause of death). Dashed lines around each function indicate 95% confidence interval.

necessitating high and continuous energy expenditures to maintain thermoregulation and homeostasis. Additionally, sea otters have altricial young that require 5–6 mo of lactation and postpartum care to optimize survival (Hanson et al. 1993). Energy expenditures for pup care nearly double maternal caloric requirements (Thometz et al. 2014). Collectively these attributes make female sea otters especially vulnerable to caloric depletion.

Our findings suggest that ELS represents a common and significant outcome of the high energetic costs of reproduction for female southern sea otters. From 2005 to 2012, 69% of reproductively active females were in stage 4 or 5 (just before or after pup weaning, respectively) at postmortem examination, indicating that the majority of adult females die during this critical end-lactation period. Additionally, ELS was diagnosed as a primary or major contributing cause of death for 56% of adult females. Given this high prevalence, the effects of ELS-associated female mortality on southern sea otter population trends could be substantial.

Some attributes of the sea otter reproductive cycle likely exacerbate energetic costs that contribute to ELS. Once sexually mature, female sea otters are almost always pregnant or caring for young, with little allowance for physiologic and metabolic recovery except during DI and pregnancy. At weaning, or after pup loss, females enter estrus and initiate their next reproductive cycle (Riedman et al. 1994). During estrus, aggressive mating activities can exacerbate nutritional and physiologic stress (Staedler and Riedman 1993) during a period when females are least capable of withstanding these exogenous nutritional demands. Mating activity can also cause significant trauma, impairing foraging efficiency and increasing risk of opportunistic infection (Foott 1970).

Once present, emaciation can inhibit metabolic recovery through the negative effects of muscle catabolism, protein deficiency, anemia, and an increasingly inefficient surface area to body mass ratio, triggering collateral effects on thermoregulation, hydrodynamics, foraging efficiency, and immune competency.

Any concurrent conditions that reduce fitness and foraging efficiency, including infection, biotoxin ingestion, or trauma, could further enhance risk of ELS expression through synergistic effects. Finally, pollution and anthropogenic disturbance could also contribute to ELS risk.

Stranding month and connections with peak pupping period

Although southern sea otter reproduction occurs year round, observational data (Fig. 3C) suggest that pupping peaks October–January. At postmortem examination, ELS cases were identified during all months, but peak prevalence occurred March–June. A fall–winter pupping peak corresponds temporally with a peak in ELS cases 5–6 mo later (when pups would be weaned), possibly reflecting population-level reproductive trends. Adverse winter weather or seasonal fluctuations in preferred prey could also increase energetic demands for females caring for pups October–January, contributing to peak ELS prevalence 5–6 mo later (Tinker et al. 2006; Oftedal et al. 2007). These same factors could also negatively influence the nutritional preloading (period of maximal adipose deposition) that occurs for pregnant females before pupping in late fall. Such has been described for capital breeding pinnipeds including grey seals (*Halichoerus grypus*) (Boyd 2000) and northern elephant seals (*Mirounga angustirostris*) (Crocker et al. 2001), where body reserves (i.e., adiposity) were a major determinant of reproductive effort.

Associations between ELS and age

Our documentation of increased ELS prevalence in older females at postmortem examination mirrors prior reports of increased weaning success for older, live-tagged sea otters (Monson et al. 2000; Tinker et al. 2006). One likely explanation is that older females are more likely to complete the pup dependency period, whereas younger females have a higher rate of premature pup loss, with most losses occurring within the first few weeks

after birth (Tinker et al. 2006). Younger females in poor condition may also abandon a pup to increase their own likelihood of survival and future reproductive success (Monson et al. 2000). Based on the life history concept of declining residual reproductive value, older females may be more likely to follow through with pup rearing, even when in poor condition, because they are under strong selective pressure to invest in current reproductive effort, even at the expense of future survival (Williams 1966).

Alternatively, or perhaps in combination with the notion of residual reproductive value, some metabolic costs may disproportionately affect older animals, enhancing the risk of ELS. Adult female sea otters have extremely high metabolic rates and reproduce continuously upon reaching sexual maturity, resulting in a uniquely high and, possibly, cumulative metabolic cost of reproduction. A cumulative cost of reproduction in mammals has been suggested but rarely studied (Clutton-Brock et al. 1983). Some health conditions can accumulate over a lifespan or emerge with age, such as tooth wear, infection, and trauma (Kreuder et al. 2003), and could hamper a female's ability to accommodate the increased energetic costs of reproduction. Finally, younger females could be more likely to die from non-ELS causes (Kreuder et al. 2003), contributing to an apparent increase in ELS prevalence with increasing age.

Associations between ELS and population density

Analysis of ELS case distribution in relation to local population size (Fig. 4C) indicates that the probability of death from ELS is highest in areas of greater sea otter population density. This density-dependent increase in ELS corresponds with reports of decreased foraging success and prey abundance in coastal areas with high numbers of sea otters (Tinker et al. 2008, 2012) and suggests that ELS could contribute to population regulation. Our models also confirm ELS occurrence across the entire mainland California sea otter population gradient (although some peripheral areas with very low densities were

not represented). This suggests that although resource limitation accentuates ELS risk in adult females, it is not the sole cause of ELS expression. Any condition that impairs individual fitness and foraging efficiency, including infection, intoxication, or trauma, could enhance risk of death from ELS. Finally, factors (in addition to competition) that affect prey abundance, such as periodic, seasonal, or interannual trends in marine invertebrate recruitment or survival, could also influence ELS expression.

Little is known about the importance of ELS in sea otter populations outside of California. It is likely that ELS occurs in other sea otter subpopulations, but because of its nonspecific presentation, this condition could be easily missed if not viewed in the context of each animal's reproductive stage. An ELS-like syndrome has been described for northern sea otters (*Enhydra lutris kenyoni*) from a region of Alaska where the population is also approaching carrying capacity (Garshelis and Garshelis 1987).

Strategies for survival

Given their substantial metabolic obstacles for successful reproduction, sea otters appear to have evolved numerous methods to optimize survival and reproductive success, including only having one pup at a time (Sinha et al. 1966; Kenyon 1969) and nutritional preloading before parturition. We found that 60% of females were in fair to excellent nutritional condition in early pregnancy, transitioning to 100% during early pup care. This trend reversed abruptly as pup care continued, when 83% of females in late pup care, and 90% of postweaning females were emaciated. In combination with results from prior studies (Monson et al. 2000, 2015; Thometz et al. 2014), our findings suggest that southern sea otters utilize both capital (Stearns 1989) and income (Costa 1993) reproductive provisioning strategies, exhibiting significant nutritional preloading during DI and gestation and markedly increased foraging activity during pup care. Nutritional preloading (which spans >50% of the female

reproductive cycle) should improve maternal survival and ensure that pup care can continue long enough to optimize reproductive success. Monson et al. (2015) reported a decrease in core body temperature of sea otters during the final 3 mo of gestation (reproductive stage 2), a possible adaptation to decrease metabolic rate and maximize energy stores during pregnancy to maximize maternal and pup survival.

Females appear to navigate through various nutritional or physiologic "checkpoints" as they progress through the reproductive cycle (Monson et al. 2000; Thometz et al. 2014). These checkpoints likely correspond to focal points of life history trade-offs: times at which females are under strong selective pressure to optimize energetic allocations between current and future reproductive success. After estrus and copulation, the first checkpoint may occur during the period of DI. Delayed implantation permits uncoupling of mating and parturition, thus allowing more freedom to select breeding and parturition periods that maximize reproductive success and survival (Mead 1989; Sandell 1990).

Although sea otters exhibit DI, their expression of this reproductive strategy differs from most other mustelids and marine mammals where estrus, fertilization, and initiation of DI occur immediately after parturition when the female is in optimal nutritional condition. In contrast, sea otters enter estrus, copulate, and undergo DI following 5–6 mo of intensive pup care. Females mate immediately postweaning (Riedman et al. 1994) during a period of severe nutritional deficit. Because southern sea otters have an ill-defined mating period and pupping season (Riedman and Estes 1990), any seasonal advantages for expressing DI are unclear. Delayed implantation may provide these adult females with a period of comparatively low nutritional demand that expedites physiologic recovery between sequential reproductive cycles. Although the trigger for blastocyst implantation varies between species, physiologic recovery beyond a basic nutritional threshold may be part of this requirement, as has been reported for Australian fur seals (*Arctocephalus pusillus*

doriferus) (Gibbens and Arnould 2009), South African fur seals (*Arctocephalus pusillus*) (Guinet et al. 1998), and terrestrial mustelids (Ferguson et al. 2006).

A second potential checkpoint is the ability to reset the reproductive cycle. Our long-term data from postmortem examinations suggest that pregnant sea otters may respond to stressful conditions through fetal loss (e.g., fetal resorption or abortion), thus resetting the timing and energetic demands of reproduction. Additional support for this hypothesis is provided through observation of tagged, wild female sea otters, where temporal discordancy between witnessed copulation and pupping dates is common (M.M.S. unpubl. data).

In contrast with reproductive strategies employed by female sea otters during DI and pregnancy, checkpoints associated with female-pup interactions have been well characterized (Gelatt et al. 2002; Staedler 2011). One postpartum reproductive strategy that female sea otters commonly use is “bet-hedging,” either through abandonment of pups shortly after birth or by shortening the period of maternal care (Monson et al. 2000). In response to unpredictable environmental factors, females may provide less care to any single pup than is physiologically necessary for pup survival to optimize their own survival and ensure future reproductive success. This bet-hedging strategy requires periodic assessment of maternal nutritional reserves relative to pup survival. The greatest probability of pup mortality, in part from abandonment, occurs immediately postpartum, with a secondary peak 3–6 wk later when the pup begins to supplement milk with solid food (Tinker et al. 2013).

Summary

Our results illustrate the importance of interpreting findings from wildlife mortality investigations in the context of each animal’s biology and subpopulation/population-level dynamics. We introduce simple, grossly apparent criteria to assess reproductive stage for female sea otters, provide a case definition for end-lactation syndrome, highlight potential risk

factors for sea otter death due to ELS, and explore strategies employed by females to optimize reproduction and survival. The first half of the sea otter reproductive cycle (DI through parturition) appears to be geared toward preloading energy reserves to optimize survival and reproductive success during the extremely metabolically demanding period of pup care that follows. When faced with suboptimal environmental or physiologic conditions, females may reset the timing and energetic demands of reproduction through a prolonged period of DI, fetal loss, pup abandonment, or early weaning. Older females tend to complete pup rearing despite poor nutritional condition because of declining reproductive longevity, possibly explaining why ELS frequency was highest in older females and those with the most prior pregnancies.

Our work highlights the plasticity and complexity of sea otter reproduction and broadens our understanding of survival strategies utilized by females during portions of the reproductive cycle that precede the well-characterized pup care period. Because necropsy facilitates examination of the integument, uterus, ovaries, and mammary glands, more precise assessment of reproductive status is possible. Division of the female reproductive cycle into stages based on simple, grossly apparent physical characteristics, as we described, will facilitate future studies of reproduction and ELS in sea otters.

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SUPPLEMENTARY MATERIAL

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