Growth patterns of theoretical bite force and jaw musculature in southern sea otters (*Enhydra lutris nereis*)

Chris J. Law[1,2]

[1]Burke Museum and Department of Biology, University of Washington

[2]Department of Integrative Biology, University of California Berkeley

Abstract

The transition from milk to solid food requires equally drastic changes in the morphology of the feeding apparatus and biting performance. As durophagous mammals, southern sea otters exhibit significant ontogenetic changes in cranial and mandibular morphology to presumably enable them to feed on a variety of hard-shelled invertebrate prey. However, how quickly juvenile otters reach sufficient maturity in biting performances remained unknown. Here, I found that theoretical bite force of southern sea otters does not reach full maturity until during the adult stage at 3.6 and 5.0 years of age in females and males, respectively. The slow maturation of biting performance can be directly attributed to the slow growth and development of the cranium and the primary jaw adductor muscle (i.e., the temporalis) and may ultimately impact the survival of newly weaned juveniles by limiting their ability to process certain hard-shelled prey. Alterative foraging behaviors such as tool use, however, may mitigate the disadvantages of delayed maturation of biting performance. In analyses of sexual dimorphism, I found that growth in male bite force enables them to quickly reach sufficient biting performances needed to process prey early in life. This is followed by a slower growth phase towards bite force maturation that coincides with sexual maturity, thus enabling them to compete with other males for resources

and mates. Overall, this study demonstrates how the analysis of anatomical data can provide insight on the foraging ecologies and life histories of sea otters across ontogeny.

Key words: Carnivora, functional morphology, jaw biomechanics, ontogeny, performance, sexual dimorphism, skull morphology

Introduction

The growth and development of the vertebrate feeding apparatus often correspond to major ontogenetic shifts in diet and resource use (e.g., (Herrel and O'Reilly 2006; Baliga and Mehta 2014; Gignac and Erickson 2014; Santana and Miller 2016; Higgins et al. 2018; Chatar et al. 2024). In mammals, weaning is a major ontogenetic dietary shift, as juveniles must transition from a liquid food source (i.e., milk) during the nursing stage to a diet consisting of solid foods that must be obtained and processed for survival. Unsurprisingly, the mammalian feeding apparatus undergoes tremendous ontogenetic changes in skull morphology and musculature to accommodate these dietary shifts. Skull growth and development facilitate enlargement of jaw muscles and their attachment areas, increase in osteological robustness, and stronger biting performances (Tanner et al. 2010; Croix et al. 2011; Segura 2015; Forbes□Harper et al. 2017; Law et al. 2017; Law 2020; Stanchak et al. 2023). Furthermore, selection is expected to favor individuals that exhibit fast rates and/or short durations of growth and development, and thus more quickly become efficient foragers on adult diets (Herrel and Gibb 2006; Gignac and Santana 2016). The need for quick transitions to adult morphologies and performances may be particularly important for species with highly specialized diets such as durophagy, a diet that consists of hard or tough material including bamboo, bones, exoskeletons, or shells. Although

adults of durophagous species exhibit strong biting performances to specialize on hard material (Radinsky, 1981a, b; Christiansen & Wroe, 2007), these traits are often not fully developed in the skulls of juveniles and may constrain their ability to break into their hard, tough food items. Thus, how quickly durophagous juveniles reach sufficient maturity in biting performances requires further investigation.

Southern sea otters (*Enhydra lutris nereis*) are a great model species to examine the growth and development of biting performance and the underlying jaw musculature. This durophagous marine mustelid feeds on a variety of hard-shelled invertebrates such as clams, crabs, mussels, snails, and urchins (Riedman and Estes 1990). As one of the smallest marine mammals, sea otters exhibit the highest known mass-specific metabolic rates of marine mammals (Morrison et al. 1974; Costa and Kooyman 1984; Yeates et al. 2007) and consequently must spend 20–50% of the day foraging to consume 20–30% of their body mass in food per day (Morrison et al. 1974; Costa and Kooyman 1982; Estes et al. 1986; Ralls and Siniff 1990; Thometz et al. 2016). Thus, as adults, sea otters exhibit several cranial adaptations that facilitate durophagy and enable them to feed effectively including short, blunt skulls (Riley 1985); taller and wider mandibular rami (Timm-Davis et al. 2015); and bunodont dentition with fracture-resistant dental enamel (Constantino et al. 2011; Ziscovici et al. 2014). Southern sea otters exhibit dramatic changes in cranial and mandibular shape and size over ontogeny to reach these adult morphologies including the widening of the zygomatic arches and the mastoid processes, dorsoventral compression of the cranium, shortening of the jaw length, and anterodorsal expansion of the coronoid process (Law et al. 2017). These ontogenetic changes enable southern sea otters to exhibit positive allometric increases in bite force and underlying jaw adductor musculature with respect to body size and skull size (Law et al. 2016b). Southern sea otters

obtain most of their nourishment from nursing during the first few weeks of life (Payne & Jameson, 1984). However, by 6 weeks of age, pups begin soliciting small pieces of food from their mothers, and by 8.9 weeks of age, pups can catch and consume their own prey (Staedler, 2011). Pups can break open hard-shelled prey items by 14–20 weeks of age and are weaned and completely independent by 6–8 months of age (Payne & Jameson, 1984; Jameson & Johnson, 1993). Although significant ontogenetic changes in skull morphology occur during these first 6–8 months, the full growth and development of the skull does not occur well after weaning (Law et al. 2017). The mandible does not reach adult maturity until the subadult stage at 1–3 years old, and most aspects of cranial maturity does not occur until after mature body size is obtained during the adult stage at 4–5.5 years old (Law et al. 2017). Law et al. (Law et al. 2017) postulated that the slower maturation of the skull may hamper the ability of newly weaned juveniles to successfully process hard-shelled prey by constraining jaw adductor muscle size, and thus biting performance. Although positive allometry in bite force suggests fast growth to overcome the smaller, less developed morphology of the juvenile stage, the rate and duration of growth and development of biting performance remains to be quantified.

In this study, I quantified the age at which juvenile southern sea otters reach maturity in biting performance. To accomplish this goal, I conducted dissection-based estimations of theoretical bite forces (Davis et al. 2010; Santana et al. 2010) across an ontogenetic series of southern sea otters and generated a growth curve model of theoretical bite force. I also generated growth curves for the underlying jaw adductor musculature and lever mechanics known to contribute to bite force generation in mammals. Because southern sea otters exhibit sexual dimorphism in their skulls, I investigated whether these growth curves differed between the sexes.

Methods

Specimens and gross dissections

Osteological and muscular data were obtained from 74 southern sea otter specimens (35 females and 39 males). 55 of these specimens were previously analyzed by (Law et al. 2016b) and 19 specimens were added in this study. All 74 specimens originated from naturally deceased southern sea otters obtained from the California Department of Fish and Wildlife (CDFW) Marine Wildlife Veterinary Care and Research Center between October 2013 and June 2017. The age of each specimen was estimated by CDFW using a suite of morphological characteristics including total body length, tooth wear, and closure of cranial sutures (Nicholson et al. 2020). All specimens stranded along the central California coast, within and throughout the current southern sea otter range from Pigeon Point in the north to Gaviota in the south.

I dissected the major jaw adductor muscles (superficial temporalis, deep temporalis, superficial masseter, deep masseter, and zygomaticomandibularis) following (Law et al. 2016b). While there was distinct separation between the superficial and deep temporalis, there was inadequate separation between the superficial masseter, deep masseter, and zygomaticomandibularis muscles (Scapino 1968; Law et al. 2016b). Therefore, I treated the three subdivisions as one muscle, the masseter (fig. 1A). I did not dissect the medial and lateral pterygoids because these muscles are positioned deep along the medial side of the mandible and cannot be excised intact fully. Muscles were removed from the left side of the skull, blotted dry, and weighed to the nearest 0.1 g using a digital scale. I measured the length and pennation angle of muscle fibers by digesting and separating the muscles in a solution of 15% aqueous nitric acid for 3–7 d depending on muscle size (Biewener and Full 1992). Muscle fiber lengths were

measured to the nearest 0.01 mm using a digital caliper. Skulls were subsequently cleaned by a dermestid beetle colony at the California Academy of Sciences or with a maceration tank at CDFW. I then photographed and digitally measured the condylobasal length (i.e., distance from the anteriormost point on the premaxillae to the plane of the posterior surface of the occipital condyles), zygomatic breadth (i.e., greatest distance across the zygomatic arches), and cranial height (i.e., distance perpendicular to the palate plane from the lateralmost point of the mastoid process to the point of the sagittal crest directly superior to the mastoid process) of each cranium using ImageJ (Schneider et al. 2012).

Estimating theoretical bite force

I calculated a theoretical bite force for each specimen by modeling the mandible as a static third-class lever (Davis et al. 2010). In this model, an axis passing through the temporomandibular joints (TMJs) serves as a fulcrum and muscle forces generated by contractions of the temporalis and masseter adductor muscles create rotation of the lower jaw about this fulcrum (Davis et al. 2010). Under static lever equilibrium, the force of biting balances the rotation of the lower jaw created by these muscle forces (fig. 1A, 1B). I first calculated the physiological cross sectional area (PCSA) for each muscle based on its mass (m), mean fiber length (f), muscle density (p = 1.06 g/cm (Mendez and Keys 1960)), and fiber pennation angle (θ) (Sacks et al. 1982):

$$PCSA = \frac{m}{p}\frac{\cos(\theta)}{f}$$

PCSA of the temporalis muscle was totaled as a sum of the PCSA calculated for the superficial and deep temporalis subdivisions and modeled as a single muscle. Following recommendations

of (Hartstone-Rose et al. 2018), I excluded pennation angle in estimations of PCSA because of the challenges of measuring pennation angle in multiple planes.

I then estimated muscle forces of the temporalis and masseter by multiplying the PCSA with a muscle stress value of 30 N/cm^2 (Davis et al. 2010). I modeled each muscle force as a single force vector (F_T and F_M) and applied them to the insertion points of the temporalis, the top of the coronoid process of the mandible, and the masseter, the mid-point between the anteriormost edge of the masseteric fossa and the angular process of the mandible. Estimations of muscle forces assumed that all of the jaw muscles were maximally activated.

I calculated the maximum theoretical bite force (BF) by adding the moment (product of the force vector and in-lever length) of each jaw adductor muscle, dividing by the out-lever ,and multiplying by 2 to account for bilateral biting:

$$BF = 2\frac{F_T * MAT + F_M * MAM}{OL}$$

where F_T and F_M are the force vectors of the temporalis and masseter, respectively; MAT is the perpendicular in-lever length measured from the temporalis muscle force vector to the TMJ; MAM is the perpendicular in-lever length measured from the masseter muscle force vector to the TMJ; and OL is the out-lever measured from the bite point and the TMJ (Davis et al. 2010). Muscle force vectors were estimated based on gape angles measured from the maxillary tip to the condyle to the mandibular tip. I used constant gape angles of 45˚, 55˚, 60˚, and 62˚ for pups, immatures, subadults, and adults, respectively following (Law et al. 2016b). I calculated theoretical bite forces in between the first and second molars of the lower jaw because the molars are used to crush items before consumption (Riedman and Estes 1990). All in-lever and out-lever measurements were taken from photographs of the lateral view of the mandible in ImageJ v. 1.48 (Schneider et al. 2012).

Statistical Analyses

I determined the rate and the age at which skull size, theoretical bite force, and underlying muscle parameters (i.e., PCSA, mass, and fiber length) reached maturity using Brody growth models:

$$x(t) = A(1 - Be^{-kt})$$

where *x(t)* is the trait of interest at time *t*, *A* is the asymptotic maturity, *k* is the growth rate and *B* is the scaling constant. I fit Brody models to each trait separately by sex because southern sea otters exhibit sexual dimorphism in the skull (Law et al. 2016a, 2017). I then determined whether the parameter estimates significantly differed between the sexes by comparing the mean values of one sex with the 95% confidence intervals of the mean with the other sex. I also reported the age of maturity of each trait as the estimated age at which the trait reached the lower limit of the 95% confidence interval for its asymptotic value (Zelditch et al. 2003).

Results

Asymptotic values of theoretical bite force significantly differed between male and female southern sea otters; adult males exhibited 142% greater theoretical bite forces ($BF_{♀}$ = 411.5 N; $BF_{♂}$ = 586.9 N) than adult females (Table 1; Fig. 1). Males displayed slower growth rates to reach their theoretical bite force, leading to later maturation (i.e., 95% of the asymptotic values) in theoretical bite force (5.0 years) compared to females (3.6 years). However, males reached the asymptotic value of theoretical bite force of females in 1.8 years.

Asymptotic values of the temporalis PCSA, mass, and fiber lengths also significantly differed between males and females (Table 1; Fig. 2). Adult male otters exhibited greater

temporalis PCSA, larger temporalis mass, and longer temporalis fiber lengths but displayed slower growth rates and thus later maturation in these traits compared to adult female otters (Table 1). Adult male otters also exhibited greater masseter PCSA and larger masseter mass than adult female otters; however, growth rates in these masseter traits did not significantly differ between the sexes, suggesting that increased growth duration rather than slower growth rate contributed to the larger PCSA and mass found in males. In contrast, asymptotic values of masseter fiber lengths did not significantly differ between the sexes.

Asymptotic values and growth rates of the mechanical advantage of jaw closing from either the temporalis or masseter did not differ between males and females (Table 1; Fig. 3). Both female and male otters reached mature mechanical advantage during weaning (6–12 months of age). Asymptotic values of temporalis in-lever (MAT) and out-lever to the molars (O) differed between the sexes; adult male otters exhibited significantly longer MAT and OL than females (Table 1; Fig. 3). In contrast, growth rates of masseter in-lever (MAM) differed between the sexes but not their asymptotic values (Table 1; Fig. 3).

Discussion

The transition from milk to a diet consisting of hard-shelled invertebrate prey presumably requires equally drastic changes in the morphology of the feeding apparatus and biting performance. Although southern sea otters exhibit drastic ontogenetic changes in cranial and mandibular morphology, these morphologies do not reach full maturity until during the adult stage ~5.5 years of age for both sexes (Fig. 4; Table 1) (Law et al. 2017). In this current study, I further found that biting performances also do not reach full maturity until the adult stage (3.6 years old in females and 5.0 years old in males). The slow maturation of biting performance may

limit newly weaned juveniles from processing certain hard-shelled prey and may therefore impact their survival. The first year post-weaning age class often shows depressed survivorship (Monson et al. 2000; Tinker et al. 2006), as newly weaned otters exhibit the highest daily energy demands of all juvenile age classes (Thometz et al. 2014) but do not have the benefit of obtaining food from their mothers and must compete with conspecific adults for the same food resources (Riedman and Estes 1990) in already resource-poor environments (Tinker et al. 2008; Layman et al. 2015; Tinker and Hatfield 2015). Together, these results suggest that newly weaned southern sea otters are at a disadvantage in foraging until the early stages of adulthood when they reach adult skull morphologies and biting performances. Below, I discuss how alternative feeding behaviors, craniomandibular asynchronization, and sexual dimorphism may explain and help mitigate delayed maturation of biting performance.

Tool use may mitigate delayed maturation of biting performance

Alternative feeding behaviors can potentially provide pathways to foraging success even with suboptimal morphologies or performances such as a less developed feeding apparatus. One such feeding behavior found in southern sea otters is the use of rocks, shells, or other hard objects as hammers or anvils to crack open their hard-shelled prey (Riedman and Estes 1990). The use of tools varies greatly among individual otters and is associated with individual variation in diet specialization; for instance, frequent tool users specialize on snails or clams whereas non-tool users specialize tend to specialize on urchins, crabs, and small bivalves (Fujii et al. 2015, 2017). Overall, individual otters that used tools frequently are able to process to harder, larger prey items that are typically inaccessible with biting alone (Law et al. 2024b). Therefore, the use of tools could allow juvenile snail or clam specialists to overcome the mechanical constraints of

processing harder prey despite having relatively weak bite forces. In contrast, juveniles specializing on urchins, crabs, and small bivalves do not require tools as their bites generates sufficient force to break open their prey (Law et al. 2016b, 2024b). The benefits of tool use are particularly strong in female otters; despite their smaller crania and weaker bite forces (Law et al. 2016a,b), females that used tools consumed prey items that were 21–35% harder compared with males, both tool users and non–tool users (Law et al. 2024b). Therefore, tool use may serve as an essential behavior in facilitating prey access for individuals with weak bite forces that are still growing/developing or are smaller.

Effects of craniomandibular asynchronization on biting performance growth

Asynchronized growth and development between the cranium and mandible found in southern sea otters may explain the underlying factors that are affecting the maturation rate of biting performance. Compared to the mandible, the sea otter cranium exhibits slower growth and development of its morphology (Law et al. 2017). Because the cranium serves as the underlying structure that supports the primary jaw muscle (i.e., the temporalis muscle) used to generate bite force, the slow maturation of cranial size and shape directly contributes to the slow maturation of biting performance (3.6 years of age for females and 5.0 years of age for males). Specifically, broadening of the zygomatic arches, lengthening along the anteroposterior axis, and development of a more pronounced sagittal crest all provide additional attachment sites for the temporalis muscle (Scapino 1968; Turnbull 1970; Law and Mehta 2019; Law 2020; Stanchak et al. 2023). Cranial size maturity is not reached until 4.3 years of age for females and 3.3 years of age for males, cranial shape maturity is not reached 5.5 years of age for both sexes (Fig. 4; Table 1; Law et al. 2017), and correspondingly, physiological cross-sectional area of the temporalis does not

reach full maturity until 3.8 years of age for females and 4.8 years of age for males (Fig. 2; Fig. 4; Table 1). In contrast, the mandible reaches full maturity during the subadult class, much earlier than the cranium; full mandibular size and shape maturity is reached between 1.5 to 2.8 years of age (Fig. 4; Table 1; Law et al. 2017). Ontogenetic changes in mandibular shape of southern sea otters are associated with increasing jaw adductor muscle in-levers and the out-lever (Law et al. 2017); thus, these lever measurements along with mechanical advantage of jaw closure also reach full maturity during the subadult class (Fig. 3; Fig. 4; Table 1). The mandible also serves as the underlying structure that supports the masseter muscle. Unsurprisingly, physiological cross-sectional area of the masseter also reaches full maturity at 2.1 years of age for females and 3.3 years of age for males, on par with the mandibular morphologies (Fig. 2; Table 1). The earlier maturation of mandibular morphology and musculature in juvenile otters may contribute to positive allometric increases in bite force early in ontogeny (Law et al. 2016b) and provide a boost in biting performance during a period in which the cranium remains smaller and less developed and the temporalis has not yet reached full development.

The different functional roles of the cranium and mandible is often hypothesized to influence the asynchrony between their growth and/or development. The cranium is the more complex structure of the two, serving as a multifunctional structure that takes part in sensory functions, respiration, and brain protection in addition to feeding, whereas the mandible is involved primarily in feeding. Thus, the cranium may require slow, prolonged growth and/or development of its morphologies to accommodate its multiple functions. Although asynchrony has been quantified in only a handful of mammal species (Tanner et al. 2010; Croix et al. 2011; Segura et al. 2013; Segura 2015; Law et al. 2017), this phenomenon has also been uncovered at the macroevolutionary level. Decoupled evolutionary modes between the cranium and mandible

are found in various mammal clades (McLean et al. 2018; Arbour et al. 2019; Michaud et al. 2020; Cassini and Toledo 2021; Law et al. 2022, 2024a) despite strong integration between the cranium and mandible (Hautier et al. 2012; Figueirido et al. 2013; McLean et al. 2018; Michaud et al. 2020; Law et al. 2024a). A possible explanation is that the cranium exhibits more structural, functional, or phylogenetic constraints on its evolution, whereas the mandible may evolve more directly in response to dietary changes. For example, in bats, sensory functions (i.e., echolocation and vision) and phylogenetic structure are the most influential factors shaping cranial evolution, whereas diet has a stronger influence on mandibular evolution (Arbour et al. 2019). The comparison between asynchronous growth/development at the species level and decoupled evolution at the macroevolutionary level presents itself as an exciting avenue of future investigation in the factors influencing cranial and mandibular variation.

Effects of sexual dimorphism on biting performance growth

Like many species within the order Carnivora (Lindenfors et al. 2007; Law 2019), a combination of sexual selection and niche divergence is hypothesized to drive sexual dimorphism in sea otters in which males are bigger. Despite their larger size, male southern sea otters displayed faster growth and developmental rates in craniomandibular morphology compared to females (Law et al. 2017). Presumably, reaching maturation of craniomandibular morphology earlier enables males to reach maximum biting performance faster, which may lead to competitive advantages in processing hard-shelled prey and in male–male agonistic interactions. However, the growth curves of theoretical bite force provide a more nuanced pattern that displayed both faster and slower growth (Fig. 1; Table 1). Within their first two years, male otters exhibited fast growth in biting performance and reached the asymptotic value

of theoretical bite force of females (411.5 N) in just 1.8 years (compared to 3.6 years for females). Subsequent growth of biting performance slows down and takes an additional >3 years for males to reach their asymptotic value of theoretical bite force (586.9 N). Biphasic growth of biting performance may be advantageous for males, which must compete to establish reproductive territories, aggressively exclude other mature males, and maintain exclusive access to estrous females (Ames et al. 1983; Jameson 1989; Ralls et al. 1996; Pearson and Davis 2005). In the first phase, quickly reaching biting performances on par with female bite forces enables males to compete with conspecifics in obtaining and processing the energy required to further grow and develop. In the second phase, continual growth of biting performance is slowed, likely because muscle tissue is energetically costly to grow (Millward et al. 1976). Consistently, the mass of the temporalis muscles is the last element associated with the feeding apparatus to reach full maturation (Fig. 2; Table 1). During this period, males do not have territories and instead congregate in ‘bachelor areas’ where they take part in extensive male–male interactions ranging from playful to aggressive that may be important for the development of fighting skills and possibly even the establishment of social hierarchies (Jameson 1989; Lafferty and Tinker 2014). Because biting is the primary weapon used in territorial conflicts between males, males that attain stronger biting performances faster may rise through the hierarchical ranks and begin to venture out of bachelor groups to establish their own reproductive territories. The ability to maintain these territories has lifetime reproductive consequences as males that maintained their territories for the longest sired the most pups (Tarjan and Tinker 2016). That full maturation of theoretical bite force and the onset of sexual maturity and body size maturity occur at the same time at five years of age in males suggest biting performance has an important influence on reproductive success. Females, in contrast, exhibit weaker bite forces than males due to their

smaller sizes. However, these bite forces may be sufficient to process hard-shelled prey because female otters tend to use tools more frequently than male otters, providing them an alternative method to forage effectively (Law et al. 2024b).

Conclusion

The ability to feed is paramount to survival; therefore, it is critical to understand the growth and development of the feeding apparatus and its impact on the maturation of biting performance. In this study, I found that southern sea otters exhibit slow maturation of biting performance that may limit newly weaned juveniles from processing certain hard-shelled prey and may thus impact their survival. However, tool using behavior, asynchronous growth and development of the cranium and mandible, and sexual dimorphism may explain and help mitigate the delayed maturation of feeding performance. This study demonstrates how the analysis of anatomical data can provide insight on the foraging ecologies of sea otters across ontogeny. Future work integrating the functional morphology of the feeding apparatus, biomechanics of tool using behavior, and changes in prey characteristics will elucidate the processes that improve feeding performances through ontogeny.

Acknowledgements

I am grateful to the staff of the California Department of Fish & Wildlife (Colleen Young, Erin Dodd, and Francesca Batac) and California Academy of Sciences (Moe Flannery and Sue Pemberton) for access to specimens; Lilian Carswell (US Fish and Wildlife Service) for permitting logistics; and Tim Tinker (US Geological Survey) and Rita Mehta (University of California Santa Cruz) for helpful discussions on sea otter life history. Funding was provided

partly by a Grant-in-Aid of Research from the American Society of Mammalogists, a Lerner-Gray Fund through the American Museum of Natural History, a Rebecca and Steve Sooy Graduate Research Fellowship for Marine Mammals, and the National Science Foundation (NSF DBI-2128146).

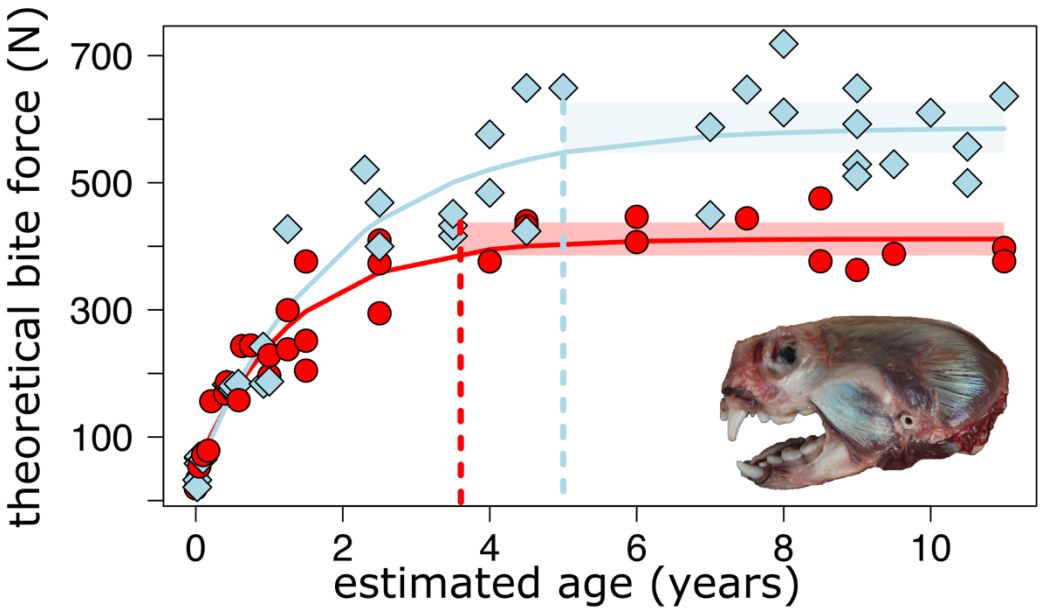

Fig. 1. Growth curve for theoretical bite force. Red circles and growth curves represent female otters and blue diamonds and growth curves represent male otters. Red and blue dashed lines indicate the times at which traits reach 95% of their asymptotic values for females and males, respectively.

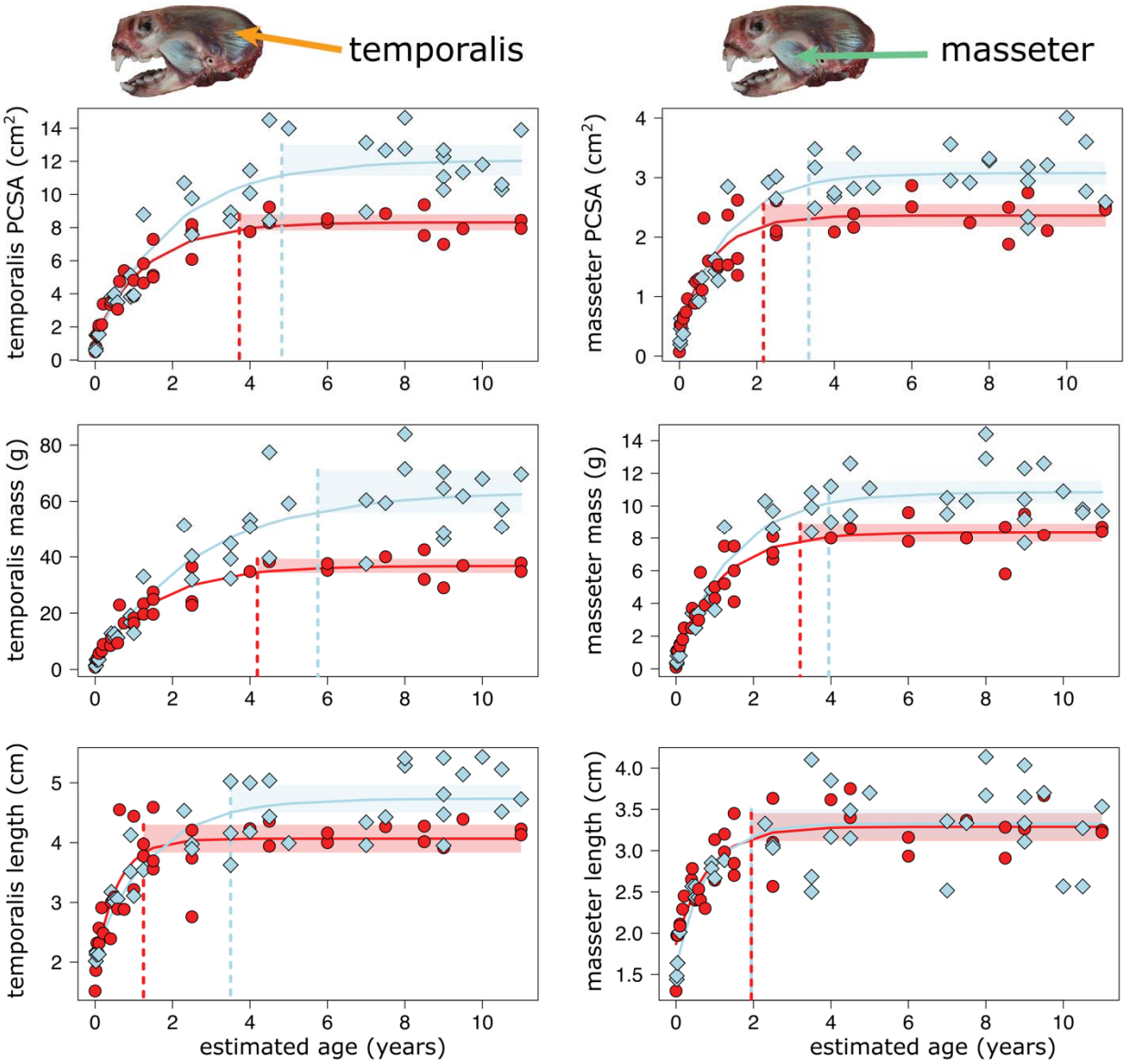

Fig. 2. Growth curves for PCSA, mass, and fiber length of the temporalis and masseter muscles. Red circles and growth curves represent female otters, and blue diamonds and growth curves represent male otters. Red and blue dashed lines indicate the times at which traits reach 95% of their asymptotic values for females and males, respectively.

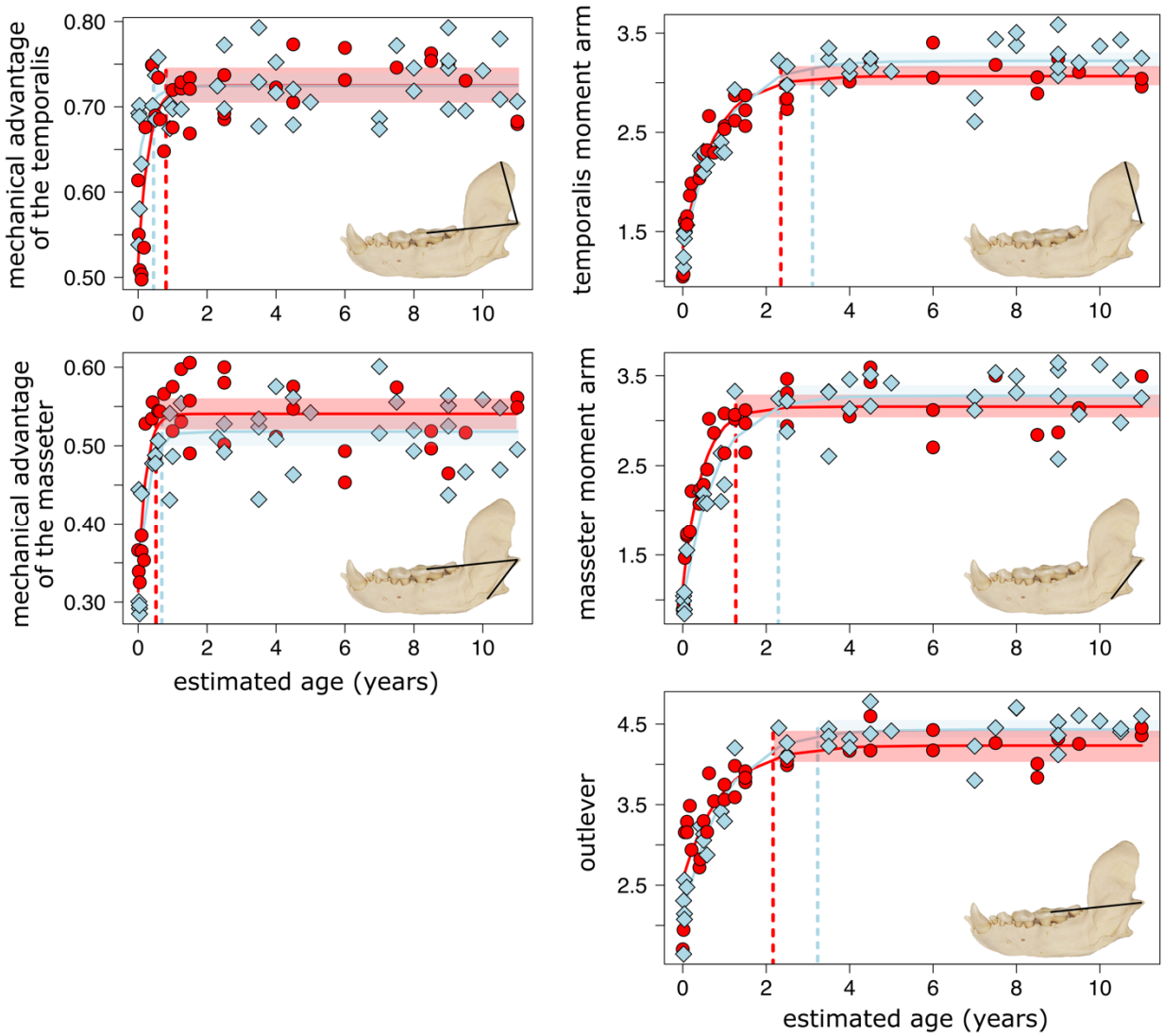

Fig. 3. Growth curves for mechanical advantage of jaw closure from the temporalis and masseter muscles. Red circles and growth curves represent female otters and blue diamonds and growth curves represent male otters. Red and blue dashed lines indicate the times at which traits reach 95% of their asymptotic values for females and males, respectively.

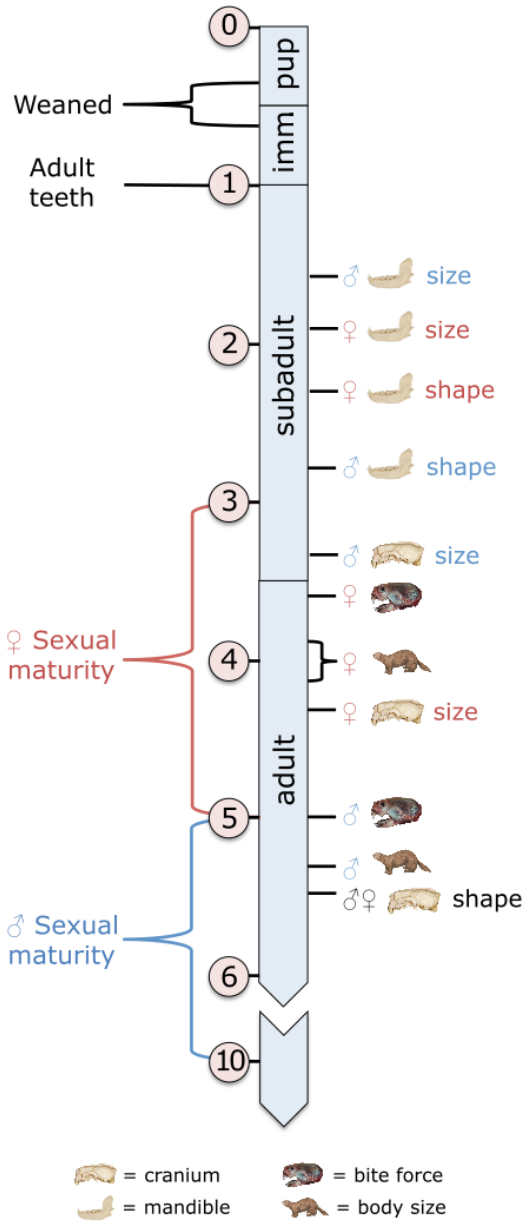

Figure 4. Timeline illustrating the maturation ages of southern sea otter skull morphology (Law et al. 2017) and theoretical bite force in relation to major life-history events. Maturation age was defined as the age at which the trait reached 95% of their asymptotic values. Imm = immature pup.

Table 1. Parameter estimates of growth curves generated with a Brody model. *A* is the asymptotic value, *K* is the growth rate constant, and *B* is the scaling constant. 95% confidence intervals are given in parentheses. Bold values indicate significant differences between male and female parameters. Age of maturity indicates the ages (in years) at which element reach 95% of their respective asymptotic values.

	sex	A	B	K	Age of maturity
bite force	F	**411.51 (385.39, 437.62)**	0.88 (0.80, 0.96)	**0.77 (0.55, 0.99)**	3.60
	M	**586.86 (546.99, 626.73)**	0.93 (0.84, 1.02)	**0.53 (0.36, 0.70)**	5.00
temporalis PCSA	F	**8.32 (7.83, 8.81)**	0.84 (0.77, 0.92)	**0.75 (0.54, 0.95)**	3.80
	M	**12.07 (11.13, 13.01)**	0.92 (0.82, 1.01)	**0.51 (0.32, 0.70)**	4.80
masseter PCSA	F	**2.36 (2.17, 2.55)**	0.83 (0.70, 0.96)	**1.15 (0.67, 1.62)**	2.10
	M	**3.08 (2.88, 3.27)**	0.92 (0.81, 1.03)	0.82 (0.52, 1.12)	3.30
temporalis mass	F	**36.77 (34.25, 39.29)**	0.93 (0.85, 1.01)	**0.64 (0.46, 0.82)**	4.20
	M	**63.47 (55.91, 71.04)**	0.98 (0.87, 1.09)	**0.38 (0.21, 0.54)**	5.80
masseter mass	F	**8.34 (7.77, 8.92)**	0.90 (0.81, 1.00)	0.85 (0.59, 1.11)	3.20
	M	**10.85 (10.14, 11.56)**	0.99 (0.88, 1.09)	0.70 (0.46, 0.94)	3.90
temporalis length	F	**4.07 (3.83, 4.30)**	0.53 (0.42, 0.64)	**1.76 (0.81, 2.70)**	1.30
	M	**4.74 (4.50, 4.97)**	0.55 (0.47, 0.62)	**0.69 (0.38, 1.00)**	3.50
masseter length	F	3.29 (3.12, 3.45)	0.43 (0.35, 0.52)	1.21 (0.60, 1.82)	1.90
	M	3.33 (3.15, 3.50)	0.53 (0.42, 0.64)	1.30 (0.53, 2.08)	1.90
temporalis MA	F	0.73 (0.70, 0.75)	**0.29 (0.21, 0.36)**	3.32 (1.15, 5.50)	0.90
	M	0.72 (0.71, 0.74)	**0.14 (0.07, 020)**	3.72 (-2.09, 9.54)	0.60
masseter MA	F	0.54 (0.52, 0.56)	0.42 (0.31, 0.53)	4.70 (1.69, 7.72)	0.50
	M	0.52 (0.50, 0.54)	0.40 (0.29, 0.50)	3.66 (0.55, 6.77)	0.70
temporalis in-lever	F	**3.07 (2.97, 3.16)**	0.56 (0.51, 0.62)	1.36 (1.03, 1.70)	2.30
	M	**3.22 (3.13, 3.31)**	0.59 (0.53, 0.64)	1.07 (0.77, 1.36)	3.10
masseter in-lever	F	3.16 (3.03, 3.29)	0.64 (0.55, 0.73)	**2.20 (1.43, 2.96)**	1.60
	M	3.28 (3.16, 3.40)	0.71 (0.60, 0.78)	**1.27 (0.88, 1.66)**	2.20
out-lever	F	**4.23 (4.04, 4.42)**	**0.39 (0.32, 0.47)**	1.09 (0.56, 1.61)	2.10
	M	**4.43 (4.33, 4.54)**	**0.52 (0.48, 0.57)**	1.03 (0.76, 1.30)	3.20

References

Ames, J. A., R. A. Hardy, and F. E. Wendell. 1983. Tagging materials and methods for sea otters, Enhydra lutris. California Fish and Game 69:243–252.

Arbour, J. H., A. A. Curtis, and S. E. Santana. 2019. Signatures of echolocation and dietary ecology in the adaptive evolution of skull shape in bats. Nat Commun 10:2036.

Baliga, V. B., and R. S. Mehta. 2014. Scaling patterns inform ontogenetic transitions away from cleaning in Thalassoma wrasses. J. Exp. Biol. 217:3597–3606.

Biewener, A. A., and R. J. Full. 1992. Force platform and kinematic analysis. Pp. 45–73 *in* A. A. Biewener, ed. Biomechanics Structures and Systems. A Practical Approach. Biomechanics Structures and Systems. A Practical Approach.

Cassini, G. H., and N. Toledo. 2021. An Ecomorphological Approach to Craniomandibular Integration in Neotropical Deer. J Mamm Evol 28:111–123.

Chatar, N., R. Boman, V. Fischer, V. Segura, C. Julémont, and Z. J. Tseng. 2024. Growing sabers: Mandibular shape and biomechanical performance trajectories during the ontogeny of Smilodon fatalis. Anat. Rec., doi: 10.1002/ar.25504.

Constantino, P. J., J. J. W. Lee, D. Morris, P. W. Lucas, A. Hartstone-Rose, W.-K. Lee, N. J. Dominy, A. Cunningham, M. Wagner, and B. R. Lawn. 2011. Adaptation to hard-object feeding in sea otters and hominins. J. Hum. Evol. 61:89–96.

Costa, D. P., and G. L. Kooyman. 1984. Contribution of specific dynamic action to heat-balance and thermoregulation in the sea otter Enhydra lutris. Physiol. Zool. 57:199–203.

Costa, D. P., and G. L. Kooyman. 1982. Oxygen consumption, thermoregulation, and the effect of fur oiling and washing on the sea otter, Enhydra lutris. Can. J. Zool. 60:2761–2767.

Croix, S. L., M. L. Zelditch, J. A. Shivik, B. L. Lundrigan, and K. E. Holekamp. 2011. Ontogeny of feeding performance and biomechanics in coyotes. J Zool 285:301–315.

Davis, J. L., S. E. Santana, E. R. Dumont, and I. R. Grosse. 2010. Predicting bite force in mammals: two-dimensional versus three-dimensional lever models. J. Exp. Biol. 213:1844–1851.

Estes, J. A., K. E. Underwood, and M. J. Karmann. 1986. Activity-time budgets of sea otters in California. J. Wildl. Manage. 50:626–636.

Figueirido, B., Z. J. Tseng, and A. Martín-Serra. 2013. Skull shape evolution in durophagous carnivorans. Evolution 67:1975–1993.

Forbes□Harper, J. L., H. M. Crawford, S. J. Dundas, N. M. Warburton, P. J. Adams, P. W. Bateman, M. C. Calver, and P. A. Fleming. 2017. Diet and bite force in red foxes: ontogenetic and sex differences in an invasive carnivore. J. Zoo□l. 303:54–63.

Fujii, J. A., K. Ralls, and M. T. Tinker. 2017. Food abundance, prey morphology, and diet specialization influence individual sea otter tool use. Behav Ecol 28:1206–1216.

Fujii, J. A., K. Ralls, M. T. Tinker, and M. T. Tinker. 2015. Ecological drivers of variation in tool-use frequency across sea otter populations. Behav Ecol 26:519–526.

Gignac, P. M., and G. M. Erickson. 2014. Ontogenetic changes in dental form and tooth pressures facilitate developmental niche shifts in American alligators. J Zool 295:132–142.

Gignac, P. M., and S. E. Santana. 2016. A bigger picture: organismal function at the nexus of development, ecology, and evolution: an introduction to the symposium. Integr Comp Biol 56:369–372.

Hartstone-Rose, A., A. R. Deutsch, C. L. Leischner, and F. Pastor. 2018. Dietary correlates of primate masticatory muscle fiber architecture. Anat. Rec. 301:311–324.

Hautier, L., R. Lebrun, and P. G. Cox. 2012. Patterns of Covariation in the Masticatory Apparatus of Hystricognathous Rodents: Implications for Evolution and Diversification. J Morpho 273:1319–1337.

Herrel, A., and A. C. Gibb. 2006. Ontogeny of Performance in Vertebrates*. Physiol Biochem Zool 79:1–6.

Herrel, A., and J. C. O'Reilly. 2006. Ontogenetic scaling of bite force in lizards and turtles. Physiol Biochem Zool 79:31–42.

Higgins, B. A., C. J. Law, and R. S. Mehta. 2018. Eat whole and less often: ontogenetic shift reveals size specialization on kelp bass by the California moray eel, Gymnothorax mordax. Oecologia 101:1–13.

Jameson, R. J. 1989. Movements, home range and territories of male sea otters off central California. Mar Mammal Sci 5:159–172.

Lafferty, K. D., and M. T. Tinker. 2014. Sea otters are recolonizing southern California in fits and starts. Ecosphere 5:1–11.

Law, C. J. 2020. Sex□specific ontogenetic patterns of cranial morphology, theoretical bite force, and underlying jaw musculature in fishers and American martens. J Anat 237:727–740.

Law, C. J. 2019. Solitary meat-eaters: solitary, carnivorous carnivorans exhibit the highest degree of sexual size dimorphism. Sci Rep-uk 9:15344.

Law, C. J., V. B. Baliga, M. T. Tinker, and R. S. Mehta. 2017. Asynchrony in craniomandibular development and growth in Enhydra lutris nereis (Carnivora: Mustelidae): are southern sea otters born to bite? Biol J Linn Soc 121:420–438.

Law, C. J., E. A. Blackwell, A. A. Curtis, E. Dickinson, A. Hartstone□Rose, and S. E. Santana. 2022. Decoupled evolution of the cranium and mandible in carnivoran mammals. Evolution 76:2959–2974.

Law, C. J., L. J. Hlusko, and Z. J. Tseng. 2024a. Uncovering the mosaic evolution of the carnivoran skeletal system. Biol. Lett. 20:20230526.

Law, C. J., and R. S. Mehta. 2019. Dry versus wet and gross: Comparisons between the dry skull method and gross dissection in estimations of jaw muscle cross□sectional area and bite forces in sea otters. J Morphol 280:1706–1713.

Law, C. J., M. T. Tinker, J. A. Fujii, T. Nicholson, M. Staedler, J. A. Tomoleoni, C. Young, and R. S. Mehta. 2024b. Tool use increases mechanical foraging success and tooth health in southern sea otters (Enhydra lutris nereis). Science 384:798–802.

Law, C. J., V. Venkatram, and R. S. Mehta. 2016a. Sexual dimorphism in craniomandibular morphology of southern sea otters (Enhydra lutris nereis). J Mammal 97:1764–1773.

Law, C. J., C. Young, and R. S. Mehta. 2016b. Ontogenetic scaling of theoretical bite force in southern sea otters (Enhydra lutris nereis). Physiol Biochem Zool 89:347–363.

Layman, C. A., S. D. Newsome, and T. G. Crawford. 2015. Individual-level niche specialization within populations: emerging areas of study. Oecologia 178:1–4.

Lindenfors, P., J. L. Gittleman, and K. E. Jones. 2007. Sexual size dimorphism in mammals. Pp. 16–26 *in* Sex, size and gender roles: evolutionary studies of sexual size dimorphism.

McLean, B. S., K. M. Helgen, H. T. Goodwin, and J. A. Cook. 2018. Trait-specific processes of convergence and conservatism shape ecomorphological evolution in ground-dwelling squirrels. Evolution 72:473–489.

Mendez, J., and A. Keys. 1960. Density and composition of mammalian muscle. Metab. Clin. Exp. 9:184–188.

Michaud, M., G. Veron, and A. Fabre. 2020. Phenotypic integration in feliform carnivores: Covariation patterns and disparity in hypercarnivores versus generalists. Evolution 74:2681–2702.

Millward, D. J., P. J. Garlick, and P. J. Reeds. 1976. The energy cost of growth. Proc. Nutr. Soc. 35:339–349.

Monson, D. H., J. A. Estes, J. L. Bodkin, and D. B. Siniff. 2000. Life history plasticity and population regulation in sea otters. Oikos 90:457–468.

Morrison, P., M. Rosenmann, and J. A. Estes. 1974. Metabolism and thermoregulation in the sea otter. Physiol. Zool. 47:218-229.

Nicholson, T. E., K. A. Mayer, M. M. Staedler, T. O. Gagné, M. J. Murray, M. A. Young, J. A. Tomoleoni, M. T. Tinker, and K. S. V. Houtan. 2020. Robust age estimation of southern sea otters from multiple morphometrics. Ecol Evol 10:8592–8609.

Pearson, H. C., and R. W. Davis. 2005. Behavior of territorial male sea otters Enhydra lutris in Prince William Sound, Alaska. aquatic mammals 31:226–233.

Ralls, K., T. C. Eagle, and D. B. Siniff. 1996. Movement and spatial use patterns of California sea otters. Can J Zool 74:1841–1849.

Ralls, K., and D. B. Siniff. 1990. Time budgets and activity patterns in California sea otters. J. Wildl. Manage. 54:251–259.

Riedman, M., and J. A. Estes. 1990. The sea otter (Enhydra lutris): behavior, ecology, and natural history. Biological Report 90:1–117.

Riley, M. A. 1985. An analysis of masticatory form and function in three mustelids (Martes americana, Lutra canadensis, Enhydra lutris). J Mammal 66:519–528.

Sacks, R. D., R. D. Sacks, R. R. Roy, and R. R. Roy. 1982. Architecture of the hind limb muscles of cats: Functional significance. J Morpho 173:185–195.

Santana, S. E., E. R. Dumont, E. Dumont, and J. L. Davis. 2010. Mechanics of bite force production and its relationship to diet in bats. Funct. Ecol. 24:776–784.

Santana, S. E., and K. E. Miller. 2016. Extreme postnatal scaling in bat feeding performance: a view of ecomorphology from ontogenetic and macroevolutionary perspectives. Integr Comp Biol icw075-10.

Scapino, R. P. 1968. Biomechanics of Feeding in Carnivora.

Schneider, C. A., W. S. Rasband, and K. W. Eliceiri. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat Meth 9:671–675.

Segura, V. 2015. A three-dimensional skull ontogeny in the bobcat (Lynx rufus) (Carnivora: Felidae): a comparison with other carnivores. Canadian Journal of Zoology 93:225–237.

Segura, V., F. Prevosti, and G. Cassini. 2013. Cranial ontogeny in the Puma lineage, Puma concolor, Herpailurus yagouaroundi, and Acinonyx jubatus(Carnivora: Felidae): a three-dimensional geometric morphometric approach. Zool J Linn Soc 169:235–250.

Stanchak, K. E., P. A. Faure, and S. E. Santana. 2023. Ontogeny of cranial musculoskeletal anatomy and its relationship to allometric increase in bite force in an insectivorous bat (Eptesicus fuscus). Anat. Rec. 306:2842–2852.

Tanner, J. B., M. L. Zelditch, and B. L. Lundrigan. 2010. Ontogenetic change in skull morphology and mechanical advantage in the spotted hyena (Crocuta crocuta). J Morpho 271:353–365.

Tarjan, L. M., and M. T. Tinker. 2016. Permissible home range estimation (PHRE) in restricted habitats: a new algorithm and an evaluation for sea otters. PLoS ONE 11:e0150547-20.

Thometz, N. M., T. L. Kendall, B. P. Richter, and T. M. Williams. 2016. The high cost of reproduction in sea otters necessitates unique physiological adaptations. J. Exp. Biol. 219:2260–2264.

Thometz, N. M., M. T. Tinker, M. T. Tinker, M. M. Staedler, M. Staedler, K. A. Mayer, T. M. Williams, and T. M. Williams. 2014. Energetic demands of immature sea otters from birth to weaning: implications for maternal costs, reproductive behavior and population-level trends. J Exp Biol 217:2053–2061.

Timm-Davis, L. L., T. J. DeWitt, and C. D. Marshall. 2015. Divergent skull morphology supports two trophic specializations in otters (Lutrinae). PLoS ONE 10:e0143236-18.

Tinker, M. T., G. Bentall, and J. A. Estes. 2008. Food limitation leads to behavioral diversification and dietary specialization in sea otters. Proc Natl Acad Sci USA 105:560–565.

Tinker, M. T., D. F. Doak, J. A. Estes, B. B. Hatfield, M. M. Staedler, and J. L. Bodkin. 2006. Incorporating diverse data and realistic complexity into demographic estimation procedures for sea otters. Ecological Applications 16:2293–2312.

Tinker, M. T., and B. B. Hatfield. 2015. Southwest U.S. Southern sea otter annual range-wide census results: U.S. Geological Survey data release.

Turnbull, W. D. 1970. Mammalian masticatory apparatus.

Yeates, L. C., T. M. Williams, and T. L. Fink. 2007. Diving and foraging energetics of the smallest marine mammal, the sea otter (Enhydra lutris). J Exp Biol 210:1960–1970.

Zelditch, M. L., B. L. Lundrigan, H. D. Sheets, and T. Garland. 2003. Do precocial mammals develop at a faster rate? A comparison of rates of skull development in Sigmodon fulviventer and Mus musculus domesticus. Journal of Evolutionary Biology 16:708–720.

Ziscovici, C., P. W. Lucas, P. J. Constantino, T. G. Bromage, and A. van Casteren. 2014. Sea otter dental enamel is highly resistant to chipping due to its microstructure. Biol. Lett. 10:20140484–20140484.