Biomechanical Energetics of Terrestrial Locomotion in California Sea Lions (*Zalophus californianus*)

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SUMMARY STATEMENT

Quadrupedal galloping in California sea lions shows intermediate energetic efficiency compared to more aquatic and fully terrestrial species during terrestrial locomotion.

ABSTRACT

Pinnipedia, an order of semi-aquatic marine mammals, adapted a body design that allows for efficient aquatic locomotion but limited terrestrial locomotion. Otariids, like the California sea lion (*Zalophus californianus*), have enlarged forelimbs and can bring their hindlimbs under the body to locomote quadrupedally on land. Phocids (true seals) have reduced forelimbs and are unable to bring their hindlimbs beneath them during terrestrial locomotion. Due to these differences, phocids are expected have greater energetic costs when moving on land compared to otariids. The mechanical costs of transport and power outputs of terrestrial locomotion were first obtained from one male and two female adult California sea lions through video recording locomotion sequences across a level runway. The center of mass, along with six other anatomical points, were digitized to obtain variables such as velocity (V), amplitude of heave (A), and the frequency (f) of oscillations during the locomotion cycle. These variables represent the principal parameters of a biomechanical model that computes the power output of individuals. The three

California sea lions in this study averaged a power output of 112.04 watts and a Cost of Transport of 0.63 J kg^{-1} m^{-1}. This footage was compared against video footage previously recorded of three phocid species (harbor seal, gray seal, and northern elephant seal). Power output and mechanical Cost of Transport were compared between all four pinniped species following the animals' center of mass. The quadrupedal gait of sea lions showed lower vertical displacements of the center of mass, and higher velocities compared to the terrestrial gait of phocids. Northern elephant seals, gray seal, and the harbor seal showed significantly higher Costs of Transport and power outputs from the sea lions. California sea lions locomote with lower energetic costs, and thus higher efficiency compared to phocids, proving that they are a mechanically intermediate species on land between terrestrial mammals and phocids. This study provides novel information on the mechanical energy exerted by pinnipeds, particularly California sea lions, to then be used in future research to better understand the limitations of these aquatic mammals.

INTRODUCTION

The suborder Pinnipedia is composed of three different families of semi-aquatic carnivorous mammals: Otariidae (sea lions and fur seals), Odobenidae (walruses), and Phocidae (true seals). All three families of pinnipeds use their flippers for both aquatic and terrestrial locomotion (English, 1976b; Gordon, 1981; Fish et al., 1988; Deméré and Yonas, 2009). Evolutionary changes to a more aquatic body type have been beneficial for aquatic locomotion, but limiting for terrestrial locomotion (Garrett and Fish, 2015).

The unique structure of otariids indicates adaptations for life both on land and in the water (English, 1976a, b). Being a marine mammal that is both semi-aquatic and semi-terrestrial comes with challenges and compromises. Otariids, like the California sea lion (*Zalophus californianus*), primarily swim using their foreflippers for propulsion by wing-like flapping with the hindflippers assuming a passive role (English, 1976b; Friedman and Leftwich, 2014).

California sea lions, including the other otariids, can "walk" on land alternating their limbs much like a terrestrial quadruped (King, 1964; Hildebrand, 1966; Peterson and Bartholomew, 1967; Tarasoff et al., 1972). The footfalls of a sea lion's walk are evenly spaced in time and are therefore symmetrical (English, 1976b). During a sea lion's walk, the contact of a

given hindlimb with the ground is followed by contact of the ipsilateral (lateral) rather than contralateral (diagonal) forefoot, therefore showing a lateral walk sequence (Fig. 1) (English, 1976b). As the sea lion walks, the heels of each of their hindlimbs contacts the ground first, the rest of the foot is dorsally flexed with their digits spread so that their hindlimbs do not contact the forefoot (Hildebrand, 1966). Hildebrand (1966) stated that lateral sequence gaits are "superior for avoiding interference between fore and hindfeet" (Hildebrand, 1966).

Otariids can also locomote in which they keep their hindlimbs moving together on one pivot with the fore flippers moving slightly out of phase for a faster gait (Fig. 1) (Peterson and Bartholomew, 1967; English 1976b; Beentjes, 1990; Heyward, 2010). Sea lions use their enlarged foreflippers as a propulsive lever when they are moving terrestrially, which may help them conserve energy as to not lift limbs in the vertical direction (Inman and Eberhart, 1953; English, 1976a, b). In California sea lions, their limbs both support their mass and propel them forward, and the foot pattern is necessary for their forward movement (English, 1976b).

Phocids are more aquatically adapted and therefore are unable to bring their hindlimbs underneath their body to walk. Phocids primarily move forwards by means of spinal flexion and crutching with the forelimbs, but they do not use their hindlimbs for terrestrial locomotion (Garrett and Fish, 2015). This forward progression using spinal undulations in phocids is very different from the quadrupedal gait of otariids (Backhouse, 1961; Kuhn and Frey, 2012; Garrett and Fish, 2015). Phocids demonstrate a lack of speed and have a high energetic cost for terrestrial locomotion (Fish, 2000; Garrett and Fish, 2015; Tennett et al., 2018). This limited performance is a clear example of evolutionary constraints. Morphological adaptations for more aquatic lifestyles although reducing the energetic cost of locomotion in water increases the energy required to move on land (Fish, 2000; Tennett et al., 2018).

Previous studies on the terrestrial locomotion of California sea lions and other otariids have described the kinematics of terrestrial locomotion, (Howell, 1929, 1930; Peterson and Bartholomew, 1967; Beentjes, 1990) but have not examined the energetic cost associated with walking or galloping. Although the energetics of swimming of otariids and phocids has been measured (Kruse, 1975; Williams and Kooyman, 1985; Feldkamp, 1987a, b; Fish et al., 1988), the northern elephant seal (*Mirounga angustirostris*) is the only pinniped for which the mechanical work of terrestrial locomotion has been calculated (Tennett et al., 2018). The present research addresses the kinematics and locomotor energetics of terrestrial locomotion in

California sea lions. The energetics of the California sea lion is compared to the mechanical effort of phocid seals, specifically the harbor seal (*Phoca vituline)*, gray seal (*Halichoerus grypus*), and the northern elephant seal. It is hypothesized that the quadrupedal gait of the California sea lion will be more efficient, showing a lower mechanical Cost of transport, when compared to the undulatory gait of the three phocid seals. Understanding the kinematics and mechanical energetics helps to understand the compromises of these amphibious marine mammals and how they locomote on land and in water (Biewener, 1990).

METHODS

Digital Video Analysis

Two adult female (Cali, Ariel) and one male (Nemo) adult California sea lions (*Zalophus californianus*, Lesson, 1828) were examined at SLEWTHS research center in Moss Landing, California. The sea lions were trained using classical and operant conditioning and positive reinforcement techniques using food as a reward. The sea lions were maintained on a diet of herring and capelin and were exercised daily and weighed weekly to ensure optimal body condition. All experiments on the sea lions were approved by the West University Institutional Animal Care and Use Committee (Protocol #201601).

The two adult female and adult male were trained to gallop across a level surface while being video recorded. Videos were recorded with a Canon EW-88C camera (24-70 mm lens) at 60 frames/s. Due to the size and speed of the animals, the video sampling frequency was adequate to determine the movements of selected points as with similar studies (Garrett and Fish, 2015; Tennett et al. 2018). The camera was mounted on a tripod and located approximately two meters away from the sea lion to record galloping strides. The field of view was sufficient to record at least three full strides. Individual sea lions galloped across the mat in the lateral view of a camera. The mat was constructed of 0.61 m x 0.61 m x 3.5 cm interlocking foam rubber tiles that were arranged as 3.66 m x 1.83 m covering an area of 6.7 m^2 so that the flipper tips were within the bounds of the mat for video recording and the safety of the animals. Videos where the sea lions did not complete a full stride cycle or walked instead of galloped were not used in the analysis. As opposed to galloping, the walking gait is associated with large lateral head and neck motions (Peterson and Bartholomew, 1967). These lateral motions would add substantial error to energetic calculations that depend on oscillatory motions in the vertical plane (see *Energetics*

Equation below) and could not be compared to the terrestrial locomotion of phocids. Prior to and after the recording sessions a 1/2-meter stick was placed in the field of view to scale the video recordings.

Each sea lion was marked with zinc oxide dots on different anatomical points of reference on their bodies. The dots were placed on the center of mass (CM) (Fish et al., 2003), axillary region, iliac crest, ankle, wrist joint, and hind flipper tips on both sides of the body. These markings allowed for digital tracking (Fig. 2). CM was approximated from findings in previous studies, as well as through a mass distribution study in the current research. CM was previously determined according to the method of Domining and De Buffrenil (1991), where California sea lions laid on a wooden board resting on a cylindrical pipe. The board was rolled over the pipe until the animal was balanced. The balance point was then measured from the animal's nose to obtain the location of the CM (Fish et al. 2003).

The sea lions were recorded as they galloped across the rubber mat in both directions. Using ImageJ (NIH, ver. 1.51s) and Tracker software (Ver. 5.1.5), the oscillations of each anatomical point from the sea lions' gallops were tracked and digitized to visualize and measure the path of locomotion (Movie 1). For kinematic analyses, 10 videos for each sea lion were analyzed, digitizing oscillations for all seven anatomical points. Ten videos with the most clearly defined wave-like oscillations were chosen for each animal. For biomechanical energetic analyses, all 157 videos were used, tracking only CM.

Three species of phocids were used to compare the biomechanical energetics with the California sea lion. These phocids were the northern elephant seal (*Mirounga angustirostris*, Gill, 1866), the gray seal (*Halichoerus grypus*, Fabricius, 1791), and the harbor seal (*Phoca vitulina*, Linnaeus, 1758). Undulation patterns in phocids are the same at various speeds, there is not a distinction between walking and galloping as there is in terrestrial mammals as well as otariids. Undulation of phocid seals was recorded as they moved across a runway towards a fish reward, showing a typical movement pattern that has an incentive. The California sea lions were recorded galloping across a runway with the same fish incentive. Northern elephant seal data were obtained through prior footage of seals locomoting across a sandy beach at Año Nuevo State Park in California (Movie 2). Footage was recorded in 2015 to document the kinematics in northern elephant seal locomotion (Tennett et al., 2018). Ten videos of 10 different male elephant seals were used in the present study. Videos that represent a range of terrestrial

locomotion speeds with clearly defined oscillations were chosen. All 10 videos were analyzed with Tracker software to obtain the vertical oscillations of CM. As the elephant seals were wild animals, CM could not be marked. Therefore, the axilla (i.e., posterior insertion of the foreflipper) was tracked as a proxy for CM that could be accurately followed throughout the gallop sequences. When the axilla was not visible due to poor lighting, the eye was followed. The videos were scaled by placing a 1/2-meter stick in the field of view of the camera in the location where the seal had just traversed. Body lengths were determined from the scaled videos and measured with ImageJ.

Videos of one captive gray seal and one harbor seal locomoting under trainer control were obtained in 2011 at the Adventure Aquarium in Camden, New Jersey (Garrett and Fish, 2014). One adult gray seals, Kjya, was recorded for 34 locomotor sequences. One adult harbor seal, Spanky, was recorded for 6 locomotor sequences. Videos were tracked and digitized in Tracker software. Videos were tracked following the animals' axilla as a proxy for CM. Videos were scaled using a 0.61 m training pole in the frame.

Kinematics

Seven anatomical points of reference were tracked frame by frame in 10 different locomotor sequences for each adult sea lion (S3). Minimum, maximum, and average velocities (m/s), along with minimum, maximum, and average peak-to-peak (P-P) amplitudes (m) of each marked anatomical point during the gallop cycles. The P-P amplitude was determined by measuring the vertical displacement for each oscillation of the reference points in the sequence and finding the average P-P amplitude for that sequence. The P-P amplitude represents the vertical excursion of each the various tracked points within the sagittal plane of the body. The vertical oscillations of CM with respect to the horizontal movement of the animal is associated with the energy expended (Tennett et al., 2018). All velocity and P-P amplitude data were converted into body lengths (BL) to remove bias due to different body sizes.

Footfalls were studied during the galloping sequence of each individual sea lion to determine the specific gait used. Footfall diagrams were created as the percent of time each limb is on the ground during one complete gallop stride. One complete cycle started from the time that the left hind flipper contacted the ground to when it contacted the ground a second time (Hildebrand, 1989).

Biomechanical Energetics

Power output (W) and Cost of Transport (COT; J kg^{-1}m^{-1}) are important variables when calculating the biomechanical energetics of a system. The power output is the rate at which work is done during transport of the body at a certain velocity (Tucker, 1970). COT is typically the ratio of metabolic power input to the product of body mass and velocity (Tucker, 1970, 1975; Schmidt-Nielsen, 1972). As metabolic rate for power input was not examined in this study, the power output was used in its place to compute a mechanical COT (Tennett et al., 2018). Power outputs are dependent on the height of the oscillations that a system is making to determine the work expended for that movement. Therefore, P-P amplitude of the oscillations of CM during forward locomotion was used for every individual locomotion sequence by every individual of all four species California sea lion, northern elephant seal, gray seal, and harbor seal. Mass-specific Power output was also calculated for each species by dividing the animal's mass by their power output (W kg^{-1}).

Energetics Equations

To determine the mechanical power output (P) used by the California sea lions as they galloped, a custom computational biomechanical model was used (Tennett et al., 2018). There is an oscillatory wave-like motion that is created when a sea lion or a phocid is moving quickly, and therefore the analysis follows the energetics behind that undulatory motion. Variables input into the model included x (horizontal displacement) and y (vertical displacement) of marked body points, BL, M, absolute and transverse V (velocity), f (stride frequency), and A (P-P amplitude of their oscillations). As the vertical oscillations for all the pinnipeds examined were confined to the vertical plane, a two-dimensional analysis was appropriate for energetic calculations. Frequency was calculated as the inverse of the average period of step cycle (number of cycles/time to complete cycles). M and BL were provided for all the sea lions at SLEWTHS. M and BL lengths were also provided for the two gray seals and the harbor seal from the Adventure Aquarium. Elephant seal body lengths were measured from scaled images using ImageJ. Elephant seal masses (M) were estimated using the regression equation from Haley et al. (1991) as:

$$M = 301.34 SA^{1.32} BL^{0.54}$$

where SA (m^2) is the projected lateral area determined by tracing the outline of the fully extended body in ImageJ from the scaled video. Each of these variables were calculated for all locomotion sequences for each individual animal. Cali, adult female California sea lion, had 55 runs, Nemo had 55 runs, Ariel had 47 runs. There were 10 different runs for 10 different elephant seals, 29 runs for a gray seal, and 5 runs for a harbor seal.

As described in Tennett et al. (2018), the energetics equation shows that the vertical motion (y) of a traveling wave created when a sea lion or a phocid is moving quickly, can be approximated as a function of the horizontal component (x) and time (t) by:

$$y(x,t) = A\cos(kx - \omega t) = A\cos(\frac{2\pi x}{\lambda} - 2\pi f t)$$

where k is the wavenumber, λ is the wavelength, ω is the angular frequency, A is the P-P amplitude of the heave, and f is the frequency. Kinetic energy (dK) will be found through the equation:

$$dK = \frac{1}{2}(\mu dx)(\omega A)^2(\sin^2(kx - \omega t)$$

where $\mu = M/BL$ and $dM = \mu dBL = \mu dx$. As a function of dt, the rate at which kinetic energy passes through an oscillatory element of the seal will be obtained, which is the energy being carried and used by the animal. The oscillations carry potential kinetic energy as well. In any oscillatory system, the average kinetic energy equals the average potential energy (Full, 1989). Thus, the average power output, (P), which is the average rate at which both kinetic and potential energies are used by the animal, is then:

$$P = 2\left(\frac{dK}{dt}\right) = \frac{1}{2}\mu V \omega^2 A^2 = 2\pi^2 \mu V f^2 A^2$$

This model assumes that the animal is moving over flat ground. These variables are also found in other biomechanical publications such as Full and Tu (1990) on insects and Zani, Gottschall, and

Kram (2005) on tortoises. COT was determined by dividing *P* by *M* and *V* in the following equation:

$$COT = P/M/V$$

Statistical analysis

All statistical analyses were performed in R (ver. 4.0.2), and all packages used were a part of R (R Core Team, 2020). Values for each individual's trials were expressed as means ± one SDs. Graphs were created in SPSS (ver. 24.0). The small sample size is a reflection of the availability of having access to trained sea lions that could be positioned appropriately for detailed data collection. Due to the low number of animals available, multiple experimental trails were made to provide and adequate statistical sample. For both kinematic and biomechanical analyses, analysis of variance tests (ANOVA) followed by TukeyHSD tests were done to compare variables. In kinematics, the amplitude, maximum velocity, and average velocity were compared against each anatomical body point (Table S1-2). In biomechanics, the COT was compared against power output, velocity, and amplitude for each of the three sea lions as well as between each of the four pinniped species (Table S4-5). Means ± one SDs were recorded as well as 95% confidence intervals (DiStefano, 2004). Additionally, least-square regressions and correlation coefficients were used to investigate frequency, as well as relationships between P-P amplitude and both the power output and COT. For biomechanical analyses, the sample size differed for each of the four species. Therefore, regressions were made following each of the species separately to normalize the sample size. In all statistical tests, a value of P<0.05 was considered significant (Whitlock and Schulter, 2015).

RESULTS

Kinematics

A total of 157 videos were recorded for the three adult sea lions. Each of the sea lions that were examined displayed a minimum of two full gallop cycles for each experimental sequence. Overall, mean velocities between the seven anatomical points of reference for all three sea lions together were statistically similar aside from hindflipper tips (df=6, F=7.348, P<0.05). However, the hindflipper tips traveled the fastest during galloping bouts, only showing similar velocities to the foreflipper and the rostrum. The hindflipper tips had a mean velocity of 2.37 ±

0.35 m s^{-1} for forward movement. The hindflipper tips had the fastest maximum velocity of 11.63 m s^{-1} during forward galloping (df=6, F=196.2, P<0.05). This was almost 6 m s^{-1} faster than the next highest maximum velocity displayed by the foreflipper. The foreflipper and the ankle show statistically similar maximum velocities (P<0.05). The anatomical points on both the fore- and hindflippers have the fastest maximum velocities and the slowest minimum velocities for moving the limbs forwards (Table S1-3). Minimum velocities for the fore- and hindflipper points were 0 m/s considering they rest on the ground at points during the gallop cycle and thus were not in constant motion. The rostrum, CM, axillary region, and iliac crest were in constant motion throughout the gallop cycle. CM and the rostrum displayed similar velocity trends over the gallop sequence.

The footfalls of each sea lion showed a transverse gallop with the right hindlimb touching the ground before the left hindlimb does, and the forelimbs moving slightly out of phase of one another as well (Fig. 3). The left and right hindlimbs were on the ground about 50% of the cycle, while the two forelimbs are on the ground each about 30% of the cycle. There are at least two limbs on the ground at the same time for about 90% of the cycle (Fig. 3).

All tracked anatomical points oscillated vertically, and all points showed a similar oscillation trend throughout the gallop cycle (Movie 1). There were statistical differences in amplitude between the body points (df=6, F=24.64, P<0.05). The greatest maximum P-P amplitude was displayed by the rostrum at 0.36 m (P < 0.05). The ankle displayed the smallest amplitude (P < 0.05) with a mean P-P amplitude of 0.07 m, which is 68% lower than the mean value of the rostrum. The foreflipper, CM, axillary region, iliac crest, and hind flipper tip showed statistically similar mean P-P amplitude values (P>0.05). The hindflipper tip showed the second highest maximum amplitude value after the rostrum (Table S2,3).

Biomechanical energetics of the California sea lion

The power output, mechanical COT, P-P amplitude, and velocity were calculated for the three adult sea lions based on the vertical displacements of CM. The pooled average power output for all sea lions was 112.04±18.94 W (Table 1, S7).

Nemo's COT was 51% lower than the two females, yet statistic difference between sexes was not recorded as there was only one male (Table 1, S6). The two females had similar COT values. The average velocity was statistically different for each sea lion (df=2, F=13.17, P<0.05)

(Table 1, S8). Amplitude differed for the sea lions individually (df=2, F=9.021, P<0.05). Ariel showed the greatest P-P amplitude for her CM (P<0.05), which was an 18% increase compared to Cali and Nemo. Cali and Nemo had statistically similar P-P amplitudes (P=0.37) (Table 1, S9).

The power output and the COT increased for each individual sea lion with vertical displacement about CM. P-P amplitude was highly correlated with COT and power output for each individual sea lion (Table S4).

Biomechanical energetics comparison to phocids

When corrected for body size, California sea lions showed significantly faster velocities, lower vertical displacements, and lower COT (P<0.01) compared to all three phocid species. Power outputs for the three phocid seals were significantly higher than that of the California sea lion (df=3, F=81.29, P<0.05). The northern elephant seal shows the highest power output (P<0.05) (Fig. 4, Table S5). Average power output for the California sea lions was 96% lower than that of the northern elephant seals, and 48% lower when corrected for body size (Table 2, S10). The mass-specific power outputs of the gray and harbor seal were significantly higher than the California sea lion as well (P<0.05). Power output for the gray seal and the harbor seal were 46% and 30% higher than the California sea lions, respectively (P<0.05) (Table 2). COT for the three phocid species was significantly higher than COT for California sea lions (df=3, F=40.32, P<0.05) (Table 2,S11; Fig. 5). COT for the three phocids species collectively was 69% higher than the California sea lions. The phocid species had statistically similar COTs (P>0.05) (Table 2).

All three phocid seals showed significantly higher P-P amplitudes compared to sea lions when corrected for body size (df=3, F=38.28, P<0.0001) (Fig. 5). The P-P amplitudes of the northern elephant seals, gray seal, and harbor seal were significantly greater (P<0.05) than the P-P amplitude of CM of the California sea lions (Table 2, S12). Similarly, the length-specific P-P amplitude of the California sea lion was statistically lower (P<0.05) than the values for the phocids. The harbor seal showed P-P amplitudes greater than the gray seal when corrected for body length (P<0.01), yet similar to the northern elephant seal (P=0.87). The harbor seal and northern elephant seal had an average length-specific P-P amplitude that was 46% higher than the sea lions. The gray seal had a P-P amplitude 25% higher than the sea lions, and 27% lower

than the other two seals (Table 2). As P-P amplitude increases, the power output as well as the COT increase with a positive correlation for the California sea lion, harbor seal, and gray seal. The northern elephant seal showed no correlation between its P-P amplitude and power output (R^2=0.002), as well as P-P amplitude and COT (R^2=0.261) (Fig. 6). Velocities were corrected for body size and showed a significant difference between the phocids and the California sea lions (df=3, F=75.63, P<0.05). The California sea lions had significantly faster velocities than each of the phocid species (P<0.05). There was no correlation between velocity and COT for California sea lions. However, there was a correlation for the harbor seal and the northern elephant seals (Fig. 7).

DISCUSSION

Galloping kinematics

A gait is a cyclic motion when moving on land. Gaits are described as either symmetrical or asymmetrical. Symmetrical gaits include various walks and trots, whereas asymmetrical gaits are gallops, and bounds (Howell, 1944; Hildebrand, 1966). California sea lions were described previously to gallop with a half-bound gait according to English (1976b). The half-bound is a primitive gait where the hindlimbs move in unison and the forelimbs have a staggered contact with the ground (Hildebrand, 1977, 1989). Observations by Beentjes (1990) noted that Hooker's sea lions (*Phocarctos hookeri*) gallop with all four flippers placed on the ground and then lifted independently, whereas the California sea lions did not display this pattern. California sea lions can gallop with their hindlimbs moving together in unison, the heels are used as a pivot while the foreflippers advance slightly out of phase (Peterson and Bartholomew, 1967). The head moves within the sagittal plane when galloping, bobbing vertically as opposed to side to side. The sea lions in the present study primarily displayed a transverse gallop where the hindlimbs land on the ground slightly out of phase of one another.

Differences in gait are likely due to differing habitats and substrates. California sea lions will use more bounding gaits when moving over rocky terrain (English, 1976b; Beentjes, 1990). As a California sea lion walks, their hindlimbs make short strides as they cannot move independently of each other for a long distance. With each step, the sea lion's hips and shoulders rotate while their head moves sinuously from side to side (Peterson and Bartholomew, 1967). On wet ground, California sea lions will often move forwards using only their forelimbs with their

abdomens on the ground, and their hindlimbs dragging behind. This movement allows faster strides across wet sand or shallow water (Peterson and Bartholomew, 1967). On smooth ground, a bull California sea lion can outrun a man, maintaining a speed of 6.7 m/s for a short distance (Peterson and Bartholomew, 1967). At slow speeds, otariids can maintain a terrestrial gallop for long distances. Fur seals have been documented galloping for up to three quarters of a mile (Bartholomew and Wilke, 1956).

Locomotion by terrestrial carnivores (fissipeds; e.g., dogs, cats) mirrors the same sequences as sea lions for forelimb movements (English, 1976). The foreflippers of sea lions are enlarged when compared to a terrestrial carnivore's forelimb in relation to respective body sizes. Except when dragging the posterior body across wet sand, sea lions extensively move their axial skeleton during terrestrial locomotion due to their aquatically adapted body shape. Fissiped carnivores get all the thrust they need from their hindlimbs when walking (Hildebrand, 1959; Goslow et al., 1973). Carnivores such as the cheetah and dogs gallop utilized substantial flexion and extension of the axial skeleton when moving at high speed (English, 1976). The flexion and extension of the axial skeleton of galloping sea lions is similar to terrestrial carnivores. The body design and use of the axial skeleton in sea lions were found to increase energy consumption compared to terrestrial mammals. However, despite their amphibious body design, sea lions can reach high speeds on land while still maintaining their aquatic efficiency (Hildebrand, 1959; Goslow et al., 1973; English, 1976b). The ability to travel over land with some proficiency may allow otariids to escape predators and move on land.

There is a wide range of footfall patterns that animals use with some quadrupeds bearing more mass on their forelimbs or on their hindlimbs (Hildebrand, 1976). Footfall pattern and body mass distribution may allow larger oscillations of CM than predicted with larger energy exchanges (Griffon et al., 2004). California sea lions have their CM positioned anteriorly on the body, close to the pectoral flippers, thus producing relatively large oscillations of their CM (Fish et al., 2002; Fish et al., 2003; English, 1976a). Large oscillations are necessary, because a sea lion's limbs are unable to swing freely due to the elongation of the digits of the flipper. In this study, the hindflipper tips showed the second highest maximum amplitude value after the rostrum, most likely due to the length of the elongated digits reaching above the hindlimb as it rotates around the ankle joint during galloping bouts.

Biomechanical Energetics

During quadrupedal gaits in mammals, speed and vertical oscillations about CM change even if the average speed is constant and the path of locomotion linear. These changes are responsible for kinetic and potential energy changes, which compose the mechanical work that an animal's muscles perform to maintain locomotion (Cavagna et al., 1976). Walking gaits rely on the out-of-phase fluctuations in vertical position and forward speed of CM (Cavagna et al., 1977; Griffon et al., 2004). During walking when CM is at its highest vertical position, potential energy is at its greatest and kinetic energy is at its lowest, and *vice versa*. Many animals reduce the muscular work of walking by exchanging the gravitational potential energy and kinetic energy of CM, like an inverted pendulum (Cavagna et al., 1976; Griffin et al., 2004). During running gaits (e.g., galloping), a spring-mass model applies, where kinetic and potential energies are in phase with one another, similar to a bouncing ball (Cavagna et al., 1976).

These energy fluctuations mainly come from muscular force generated to support an animal's weight and work associated with movement of CM (Biewener, 2003). Quadrupedal animals use bounding gaits to conserve energy during faster locomotion, whereas the exchange between potential and kinetic energies is used to conserve energy during walking gaits. Gait changes conserve energetic costs as faster gaits reduce vertical oscillations of CM and thus allow large quadrupeds to avoid costly aerial periods (Lee and Harris, 2018).

Past studies examined different modes of terrestrial locomotion in various pinniped species, focusing on physiological and behavioral characteristics, but with only few studies on biomechanics (Backhouse, 1961; O'Gorman, 1963; Ray, 1963, Tarasoff and Fisher, 1970, Tarasoff et al., 1972, Gordon, 1981, Kuhn and Frey, 2012; Garrett and Fish, 2015; Tennett et al., 2018). The mechanical energetics of an animal moving on land are associated with the forces that are applied to the ground to support the animal and push forward CM (Giovanni et al., 1977). The energetics of locomotion by an animal can be performed by measurement of metabolic rate from oxygen consumption, respiratory frequency, and heart rate (e.g., Williams et al., 1992). However, the mechanical energetics for terrestrial locomotion can be determined through examination of the physics of an animal's gait (Fish, 1982; Williams et al., 1992; Tennett et al., 2018). To measure the mechanical power output of pinnipeds moving on land, the P-P amplitude of the oscillating CM and its velocity can be determined (Tennett et al., 2018). The power outputs calculated by Tennett et al. (2018) for 70 northern elephant seals averaged

3,290 W at a velocity of 0.6 BL s^{-1} (2.16 m s^{-1}), and 5,530 W at maximum velocity of 0.71 BL s^{-1} (2.56 m s^{-1}) with a P-P amplitude of 0.31 m.

In the present study, mechanical COT was calculated using the power output from the energetics equation. While this computational model is accurate, there are limitations. The model assumes the animals are running on level ground, which was the case for all captive sea lions studied. This model tracks CM of an animal to get the average power output. Some other parts of the animals may be oscillating with higher power outputs, but only CM was recorded for the power outputs here. The reason for using CM was that the analysis used a parameter M BL^{-1}. That parameter was treated as a constant. However, M BL^{-1} of an animal is not constant. When the CM was used, the non-uniformities average out. The model assumed that the oscillatory motion of the CM of the animal moved in a perfect sinusoidal fashion. However, the motion was not perfectly sinusoidal although extremely close.

Biomechanics was assessed in three individual captive sea lions. While this gives novel insight into the mechanical energy costs in terrestrial locomotion of California sea lions, further research is necessary for a mechanical energy cost to represent all otariids. Considering the limitations on the availability of trained otariids, any novel research will impact the range of knowledge on terrestrial locomotion in these mammals. There were also limitations for the performance of the individual animals studied as well. Nemo was the largest of the three sea lions examined and displayed the lowest COT. However, Nemo would not move at high speed when asked to perform gallops. Cali and Ariel galloped as directed. Although these captive sea lions were able to perform gallops in front of the camera, they were only given a short runway in which to reach a high speed. Wild sea lions have more space to gallop and will often gallop due to a disturbance, or to charge at a possible threat. Due to these differences in the motivation for galloping, wild sea lions would most likely gallop at faster speeds than the captive sea lions.

The northern elephant seals in this study were the only wild phocids examined. The captive gray and harbor seals were following commands to receive a food reward and might have behaved differently than their wild counterparts. The harbor seal in this study was overweight for his age and body length, and did not use his foreflippers to aid in forward locomotion. Harbor seals in the wild were observed to move over land with greater ease, utilizing their foreflippers (Garrett and Fish, 2014). The harbor seal had a P-P amplitude similar to that of the northern

elephant seals but different from the gray seal. Therefore as only this harbor seal was examined, its results might not accurately reflect those of wild harbor seals.

Phocid species showed a higher vertical oscillation and thus larger mechanical energetic costs when compared with the California sea lions. Phocids use a slow 'inchworm' type of locomotion to move on land without the use of the hindlimbs (Backhouse, 1961; Ray, 1963; Deméré and Yonas, 2009; Garrett and Fish, 2015; Tennett et al., 2018). The high vertical oscillations of phocids occurred due to locomoting strictly through crutching of the foreflippers and undulations of their axial skeleton without the use of their hindlimbs (Backhouse, 1961; Kuhn and Frey, 2012; Garrett and Fish, 2015; Tennett et al., 2018).

A direct relationship was seen between the P-P amplitude and power output and COT ($R^2 = 0.96$). The relationship between P-P amplitude of CM and COT infers that having a low COT is dependent on minimizing the vertical oscillations of CM in a locomotor sequence. Having a high P-P amplitude about CM during terrestrial galloping increases the biomechanical work and energetic expenditure than animals with low vertical displacements (Maynard-Smith and Savage, 1956). COT was also compared against velocity for all four species. There was no correlation between velocity and COT for the California sea lions, as there was for the northern elephant seals. Faster speeds could require an increase of energy usage for phocids which cannot locomote on land with the use of their hindlimbs. Maintaining COT through velocity increases could be further proof that California sea lions are more efficient on land having the ability to locomote like a terrestrial mammal. Both otariids and phocids evolved to be highly aquatically adapted and have energetic limitations when trying to sustain rapid terrestrial locomotion (Garrett and Fish, 2014; Tennett et al., 2018). Sea lions, while having the ability that to pull their hindlimbs underneath their bodies to gallop quadrupedally, still have limitations for terrestrial galloping. Having aquatically adapted and enlarged limbs causes otariids to have these large oscillations about their CM in order to lift and protract their limbs (Beentjes, 1990). This limitation causes an increased COT but is not a limitation of terrestrial mammals. In terrestrial mammals, the vertical displacement of CM is minimal, lowering their COT. Although a sea lion's unique gait is necessary for its amphibious lifestyle, their gait is costly when compared to its terrestrial mammal ancestors (Beentjes, 1990).

Terrestrial mammals move with less energetic expense than the pinnipeds in this study by locomoting with a lower vertical displacement of CM. The mechanical COT for Asian elephants (*Elephas maximus*) was determined to be about 0.2 J kg^{-1} m^{-1} over a range of speeds (Genin et al. 2010). With increasing speed, the elephants decrease the vertical oscillation of the CM from about 3 cm to 1 cm (Genin et al. 2010). Although a larger animal, the vertical oscillations of CM for the elephant was over 9 cm smaller than for California sea lions, and nearly 31 cm smaller than for the northern elephant seal. Humans have a comparatively small mechanical COT of approximately 0.05 J kg^{-1} m^{-1} (Lee and Harris, 2018). The mechanical COT for a chipmunk and a large dog (100 kg) were 0.46 J kg^{-1} m^{-1} and 0.35 J kg^{-1} m^{-1} (Heglund et al. 1982). These values, while only slightly lower than that of a California sea lion, are considerably lower than for phocid seals.

Terrestrial mammals can also reduce energetic cost when galloping through the storage and recovery of elastic energy in tendons and ligaments (Biewener, 2003). However, the aquatic body design of pinnipeds does not show evidence for elastic energy storage (Fish and Garrett, 2014). The tendon makeup in the limbs of terrestrial mammals allows for recovery of mechanical work and lower COT compared to pinnipeds (Biewener, 2003).

Conclusions

California sea lions locomote on land with gaits similar to terrestrial mammals (transverse gallop). The ability to pull the hindlimbs underneath the body and stand upright with the both sets of limbs entirely supporting the weight of the body reduces the vertical displacement of CM during galloping. This research shows that a lower vertical oscillation of CM allows for lower power outputs and mechanical COT. When compared to phocid species that lack the ability to tuck their hindlimbs underneath their body, sea lions moved over land with higher velocities, smaller vertical amplitudes, and lower COT. Quadrupedal galloping of the California sea lion is more efficient than the undulations of phocid seals. However, the aquatically adapted morphology of the California sea lion does incur a higher energetic cost for movement on land compared to fully terrestrial mammals. Thus with respect to terrestrial locomotion, the sea lions are intermediate between fully terrestrial mammals and phocids. This intermediate position for sea lions means that compromises are made to function in both aquatic and terrestrial environments (Williams, 1999; Fish, 2000).

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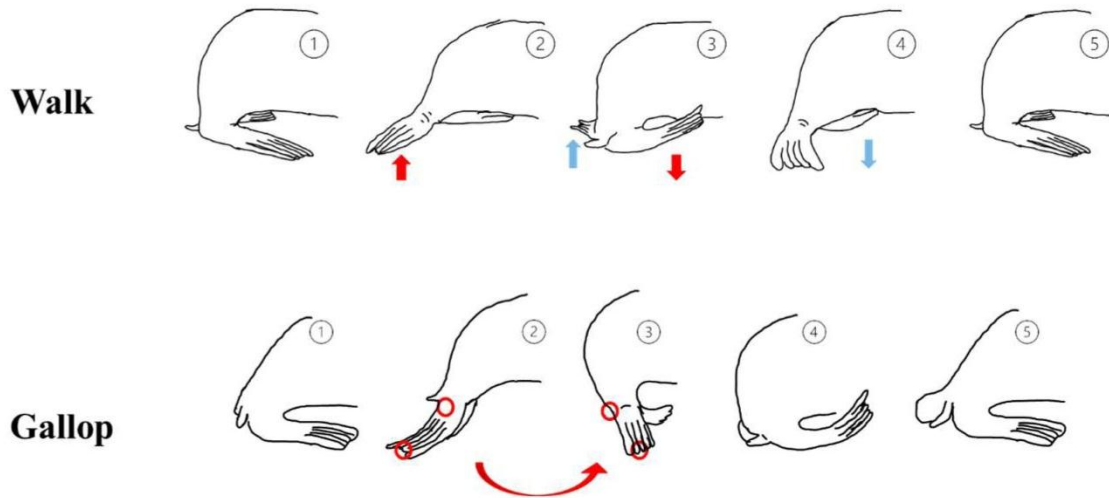
Figures and Tables

Fig. 1. When walking, the hindflippers of a California sea lion move independently of one another. When galloping, the hindflippers move in unison. In the walking phase the red arrows depict how the front flipper is moving; the blue arrows indicate how the back flipper is moving. In the gallop phase, the red arrow indicates the hindflippers moving in unison. The red circles in the gallop phase indicate which body parts move the fastest (the hindflipper tips and the ankle joint). The numbers follow the locomotion sequence in order across a cycle.
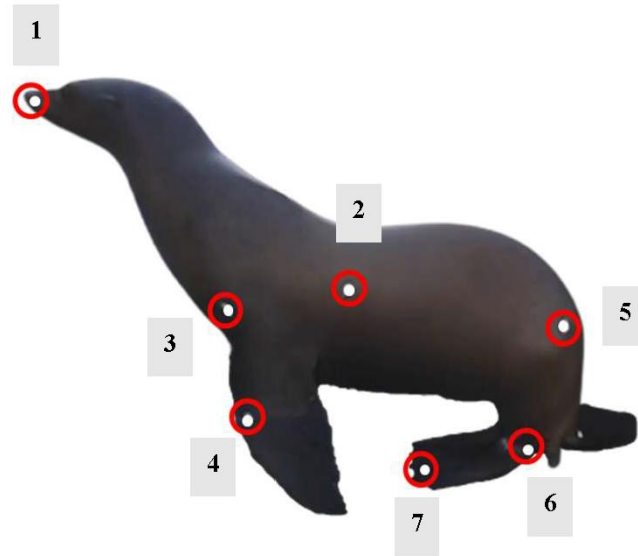
Fig. 2. Diagram of the seven anatomical points of reference that were marked on the sea lions with zinc oxide. The marks were digitized and tracked in Tracker software. Anatomical points included, rostrum, center of mass, axillary region, wrist joint, iliac crest, ankle, and hind flipper tips.
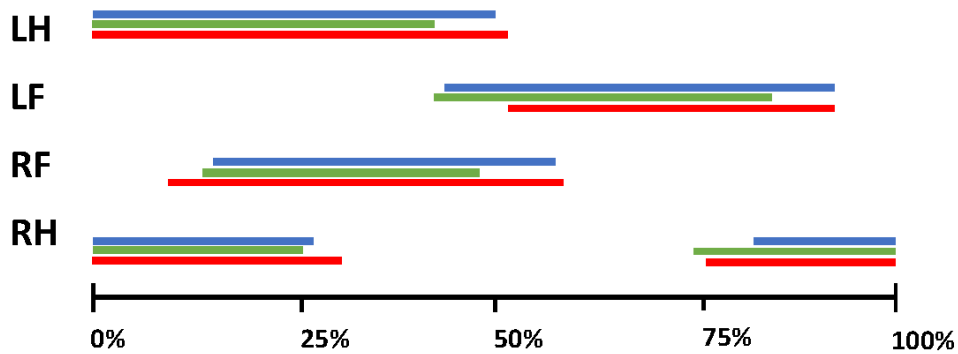

Fig. 3. Footfall diagram following the left hindlimb for one complete cycle of three individual California sea lions. LH= left hind; LF= left fore; RF= right fore; RH= right hind. Blue follows one cycle from Ariel, green follows one cycle from Cali, and red follows one cycle from Nemo.
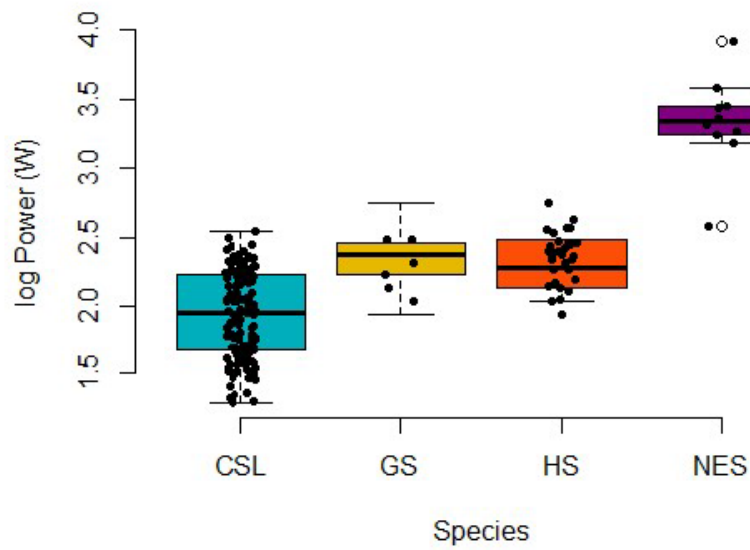
Fig. 4. Log power outputs (W) for each of the four species. Letters indicate statistical significance. Dots indicate induvial data points.
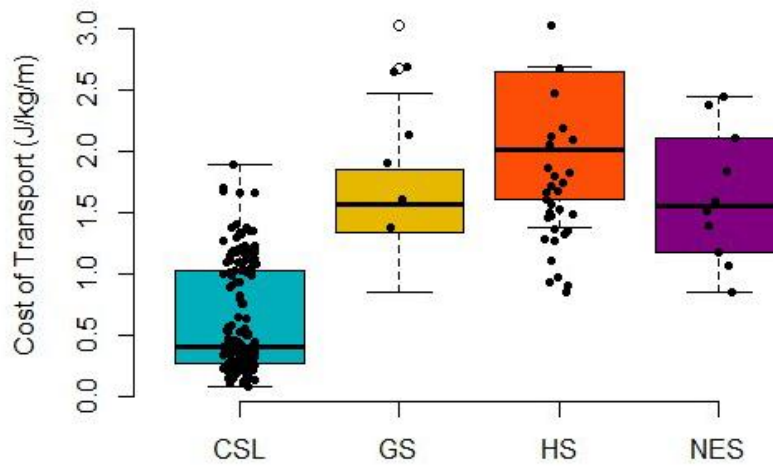

Fig. 5. Cost of Transport (J/kg/m) for each of the four species. Letters indicate statistical significance. Dots indicate individual data points.
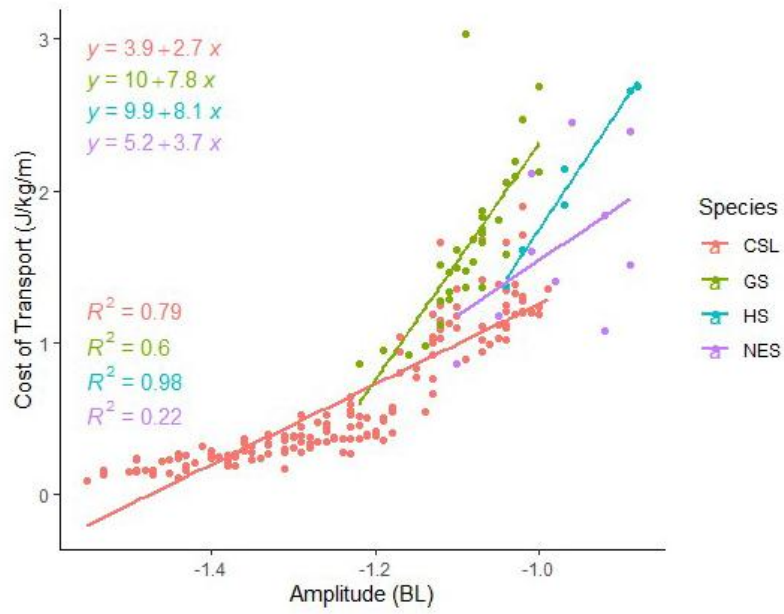
Fig. 6. Log Cost of Transport (J/kg/m) for each of the four species, except elephant seal (NES) shows a positive correlation with amplitude.
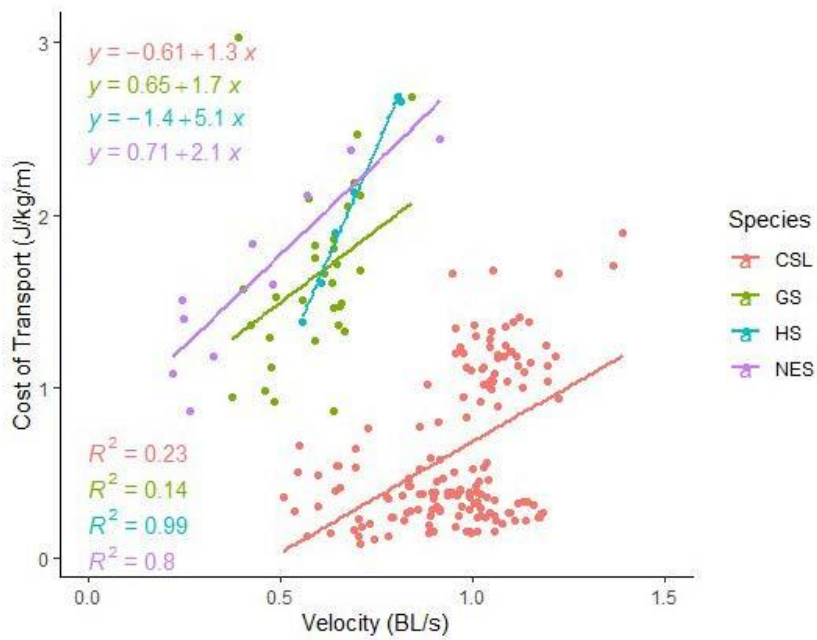
Fig. 7. Log Cost of Transport (J/kg/m) for each of the four species shows a positive correlation with velocity (BL) for elephant seal (NES) and harbor seal (HS); not for California sea lion (CSL).

Table 1. Power, Cost of transport, amplitude, and velocity for individual sea lion. Means ± one standard deviation are reported as well as mean values.

Column1	Power	Cost of transport	Amplitude	Velocity
	W	$J\ kg^{-1}\ m^{-1}$	m	$m\ s^{-1}$
Cali	111.42±73.48	0.76±0.48	0.11±0.04	1.95±0.18
Nemo	93.41±51.73	0.37±0.19	0.12±0.029	1.78±0.32
Ariel	131.28±79.26	0.76±0.44	0.14±0.05	2.01±0.15
Mean	112.04±18.94	0.63±0.23	0.12±0.02	1.92±0.12

Table 2. Costs of transport (COT), power output, mass-specific power output (W/kg), vertical amplitude, and velocities averaged for each of the four pinniped species with means ± one standard deviation. Amplitudes and velocities measured in body lengths to correct for size. CSL= California sea lion (n=3); NES = northern elephant seal (n=10); GS = gray seal (n=1); HS = harbor seal (n=1).

Species	CSL	NES	GS	HS
COT *($J\ kg^{-1}\ m^{-1}$)*	0.63±0.23	1.64±0.55	2.32±1.01	2.06±0.54
Power *(W)*	112.04±18.94	2762.41±2163.20	302.64±86.60	204.12±82.72
Power *(W/kg)*	1.24±0.50	2.38±1.82	2.31±0.26	1.78±0.72
Amplitude *(m)*	0.12±0.02	0.34±0.06	0.17±0.01	0.13±0.02
Amplitude *(BL)*	0.06±0.01	0.11±0.02	0.08±0.00	0.11±0.02
Velocity *($m\ s^{-1}$)*	1.92±0.12	1.35±0.67	1.06±0.33	0.84±0.13
Velocity *(BL/s)*	0.96±0.14	0.44±0.23	0.49±0.15	0.69±0.11

Table S1. Maximum and minimum velocities for all seven anatomical points of reference for all three sea lions. Means (± S.D.) of each measurement as well as 95% confidence intervals are also provided.

	Minimum velocity	**Maximum velocity**	**Mean velocity**	**95% Confidence Interval**	
	m/s	*m/s*	*m/s*	*Lower*	*Upper*
Rostrum	0.24	4.81	2.03 ± 0.42	1.01	3.04
Iliac crest	0.11	3.93	1.85 ± 0.34	1.24	2.46
Center of mass	0.20	3.60	1.95 ± 0.32	1.33	2.57
Axillary region	0.13	4.04	1.97 ± 0.35	1.21	2.73
Foreflipper	0.00	5.65	1.97 ± 0.37	1.16	2.92
Ankle	0.00	5.41	1.86 ± 0.33	1.32	2.40
Hindflipper tip	0.00	11.63	2.37 ± 0.35	2.15	2.59

Table S2. Maximum and minimum amplitudes for all seven anatomical points of reference for three California sea lions. Means (± S.D.) of each measurement as well as 95% confidence intervals are also provided.

	Minimum amplitude	**Maximum amplitude**	**Mean amplitude**	**95% Confidence Interval**	
	m	*m*	*m*	*Lower*	*Upper*
Rostrum	0.10	0.36	0.22 ± 0.06	-0.03	0.46
Iliac crest	0.07	0.18	0.11 ± 0.03	0.06	0.17
Center of mass	0.09	0.20	0.14 ± 0.03	0.08	0.20
Axillary region	0.10	0.19	0.14 ± 0.02	0.09	0.20
Foreflipper	0.07	0.19	0.13 ± 0.03	0.05	0.20
Ankle	0.04	0.13	0.07 ± 0.02	0.06	0.08
Hindflipper tip	0.04	0.28	0.13 ± 0.06	0.09	0.16

R-Script for Kinematic comparisons in the California sea lions

Compute the analysis of variance for Velocity
V.aov <- aov(avg.vel ~ as.factor(part), data = rawdata)
Summary of the analysis
summary(V.aov)
Df Sum Sq Mean Sq F value Pr(>F)
as.factor(part) 6 5.51 0.9183 7.348 4e-07 ***
Residuals 203 25.37 0.1250

 Tukeytest
TukeyHSD(V.aov)
Tukey multiple comparisons of means
95% family-wise confidence level
Fit: aov(formula = avg.vel ~ as.factor(part), data = rawdata)
$`as.factor(part)`

Table S3. Statistical results from ANOVA test between the average velocity and the anatomical body part in the three individual California sea lions. Maximum velocity and amplitude were also compared against body part in the same way.

	Diff	Lwr	Upr	P adj
2-1	-0.08740355	-0.35923592	0.18442881	0.9622961
3-1	-0.06923580	-0.34106816	0.20259656	0.9884683
4-1	-0.17574333	-0.44757570	0.09608903	0.4659663
5-1	-0.18807333	-0.45990570	0.08375903	0.3803263
6-1	-0.01144433	-0.28327670	0.26038803	0.9999997
7-1	0.33245433	0.06062197	0.60428670	0.0062319
3-2	0.01816775	-0.25366461	0.29000012	0.9999947
4-2	-0.08833978	-0.36017214	0.18349258	0.9602932
5-2	-0.10066978	-0.37250214	0.17116258	0.9266581
6-2	0.07595922	-0.19587314	0.34779158	0.9813227
7-2	0.41985789	0.14802552	0.69169025	0.0001495
4-3	-0.10650753	-0.37833990	0.16532483	0.9057042
5-3	-0.11883753	-0.39066990	0.15299483	0.8504274
6-3	0.05779147	-0.21404090	0.32962383	0.9956408
7-3	0.40169013	0.12985777	0.67352250	0.0003458
5-4	-0.01233000	-0.28416236	0.25950236	0.9999995
6-4	0.16429900	-0.10753336	0.43613136	0.5495926
7-4	0.50819767	0.23636530	0.78003003	0.0000017
6-5	0.17662900	-0.09520336	0.44846136	0.4596182
7-5	0.52052767	0.24869530	0.79236003	0.0000009
7-6	0.34389867	0.07206630	0.61573103	0.0040028

Compute the analysis of variance for COT
M.aov <- aov(max.vel ~ as.factor(part), data = rawdata)
Summary of the analysis
summary(M.aov)
Df Sum Sq Mean Sq F value Pr(>F)
as.factor(part) 6 603.2 100.53 196.2 <2e-16 ***
Residuals 203 104.0 0.51

Tukeytest
TukeyHSD(M.aov)
Tukey multiple comparisons of means
95% family-wise confidence level
Fit: aov(formula = max.vel ~ as.factor(part), data = rawdata)
$`as.factor(part)`

Compute the analysis of variance for Amplitude in BL
Amp.aov <- aov(amp ~ as.factor(part), data = rawdata)

Summary of the analysis
summary(Amp.aov)
Df Sum Sq Mean Sq F value Pr(>F)
  as.factor(part) 6 0.3447 0.05744 24.64 <2e-16 ***
  Residuals 203 0.4733 0.00233

Tukeytest
TukeyHSD(Amp.aov)
  Tukey multiple comparisons of means
  95% family-wise confidence level

  Fit: aov(formula = amp ~ as.factor(part), data = rawdata)

  $`as.factor(part)`
  diff lwr upr p adj

<u>R script for biomechanics of 3 adult California sea lions</u>

Compute the analysis of variance for Power
C.aov <- aov(COT ~ as.factor(CSL), data = rawdata)

Summary of the analysis
```
summary(C.aov)
  Df Sum Sq Mean Sq F value Pr(>F)
  as.factor(CSL) 2 5.537 2.7686 17.25 1.69e-07 ***
  Residuals 157 25.196 0.1605
```

Tukeytest
```
TukeyHSD(C.aov)
  Tukey multiple comparisons of means
  95% family-wise confidence level

  Fit: aov(formula = COT ~ as.factor(CSL), data = rawdata)

  $`as.factor(CSL)`
```

Table S4. Statistical results between the Cost of Transport and each individual California sea lion. Power outputs, velocity, and amplitude were compared against each sea lion in the same way.

	Diff	Lwr	Upr	P adj
2-1	-0.387803571	-0.5669387	-0.2086684	0.0000026
3-1	0.004764881	-0.1816849	0.1912147	0.9979861
3-2	0.392568452	0.2061187	0.5790182	0.0000049

Compute the analysis of variance for COT
P.aov <- aov(Power ~ as.factor(CSL), data = rawdata)

Summary of the analysis
```
summary(P.aov)
  Df Sum Sq Mean Sq F value Pr(>F)
  as.factor(CSL) 2 37072 18536 3.62 0.029 *
  Residuals 157 803803 5120
```

Tukeytest
```
TukeyHSD(P.aov)
  Tukey multiple comparisons of means
  95% family-wise confidence level

  Fit: aov(formula = Power ~ as.factor(CSL), data = rawdata)

  $`as.factor(CSL)
```

Compute the analysis of variance for Amplitude in BL
V.aov <- aov(Vel ~ as.factor(CSL), data = rawdata)

Summary of the analysis
summary(V.aov)
  Df Sum Sq Mean Sq F value Pr(>F)
  as.factor(CSL) 2 1.430 0.7151 13.17 5.17e-06 ***
  Residuals 157 8.528 0.0543

Tukeytest
TukeyHSD(V.aov)
  Tukey multiple comparisons of means
  95% family-wise confidence level

  Fit: aov(formula = Vel ~ as.factor(CSL), data = rawdata)

  $`as.factor(CSL)`

Compute the analysis of variance for Velocity in BL/s
A.aov <- aov(Amp ~ as.factor(CSL), data = rawdata)

Summary of the analysis
summary(A.aov)
  Df Sum Sq Mean Sq F value Pr(>F)
  as.factor(CSL) 2 0.02409 0.012044 9.021 0.000196 ***
  Residuals 157 0.20961 0.001335

Tukeytest
TukeyHSD(A.aov)
  Tukey multiple comparisons of means
  95% family-wise confidence level

  Fit: aov(formula = Amp ~ as.factor(CSL), data = rawdata)

  $`as.factor(CSL)`

R script for biomechanics of all species

Compute the analysis of variance for Power
P.aov <- aov(Log.Power ~ as.factor(Species), data = rawdata)

Summary of the analysis
summary(P.aov)
  Df Sum Sq Mean Sq F value Pr(>F)
  as.factor(Species) 3 21.30 7.102 81.29 <2e-16 ***
  Residuals 203 17.73 0.087

Tukeytest
TukeyHSD(P.aov)
  Tukey multiple comparisons of means
  95% family-wise confidence level

  Fit: aov(formula = Log.Power ~ as.factor(Species), data = rawdata)

  $`as.factor(Species)`

Table S5. Statistical results between the power output and each of the four pinniped species. 1=California sea lion; 2=gray seal; 3=harbor seal; 4=northern elephant seal. Results for Cost of Transport, velocity, and amplitude were compared against each species in the same way.

	Diff	Lwr	Upr	P adj
2-1	0.33429167	0.01590392	0.6526794	0.0354786
3-1	0.40956048	0.25931073	0.5598102	0.0000000
4-1	1.39262500	1.14304925	1.6422008	0.0000000
3-2	0.07526882	-0.26622458	0.4167622	0.9406253
4-2	1.05833333	0.66294642	1.4537202	0.0000000
4-3	0.98306452	0.70461337	1.2615157	0.0000000

Compute the analysis of variance for COT
COT.aov <- aov(Log.COT ~ as.factor(Species), data = rawdata)

Summary of the analysis
summary(COT.aov)
  Df Sum Sq Mean Sq F value Pr(>F)
  as.factor(Species) 3 10.06 3.353 40.32 <2e-16 ***
  Residuals 203 16.88 0.083

Tukeytest
TukeyHSD(COT.aov)
  Tukey multiple comparisons of means
  95% family-wise confidence level

Fit: aov(formula = Log.COT ~ as.factor(Species), data = rawdata)

$`as.factor(Species)`

Compute the Analysis of variance for amplitude
Amp.aov <- aov(Amplitude ~ as.factor(Species), data = rawdata)

Summary of the analysis
summary(Amp.aov)
  Df Sum Sq Mean Sq F value Pr(>F)
  as.factor(Species) 3 0.03980 0.013267 38.28 <2e-16 ***
  Residuals 203 0.07036 0.000347

Tukeytest
TukeyHSD(Amp.aov)
  Tukey multiple comparisons of means
  95% family-wise confidence level

  Fit: aov(formula = Amplitude ~ as.factor(Species), data = rawdata)

  $`as.factor(Species)`

Compute the Analysis of variance for velocity
Vel.aov <- aov(Velocity ~ as.factor(Species), data = rawdata)

Summary of the analysis
summary(Vel.aov)
  Df Sum Sq Mean Sq F value Pr(>F)
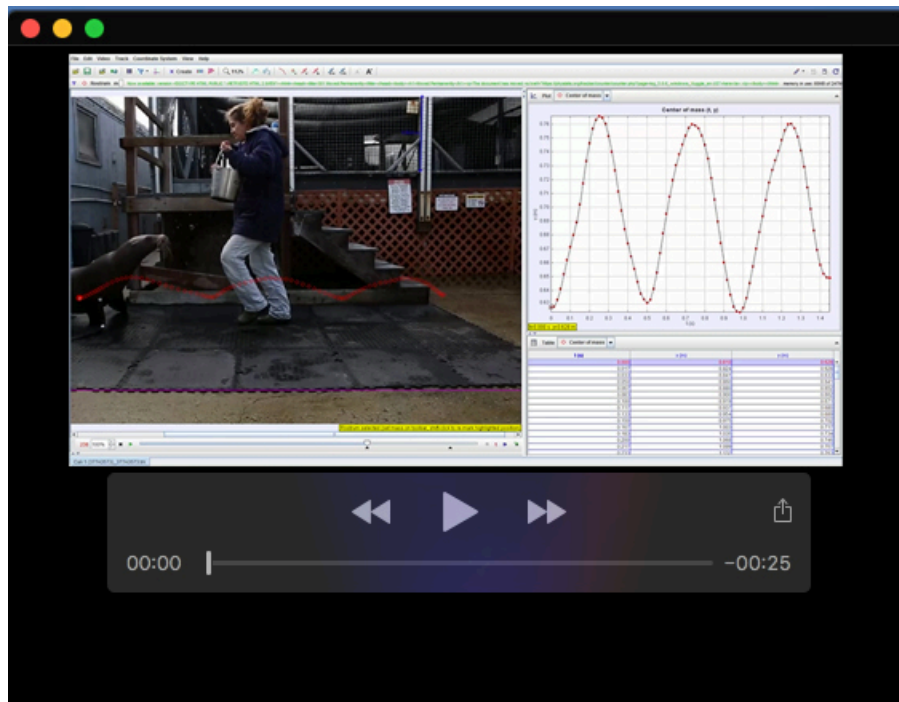 as.factor(Species) 3 5.627 1.8756 75.63 <2e-16 ***
  Residuals 203 5.034 0.0248

Tukeytest
TukeyHSD(Vel.aov)
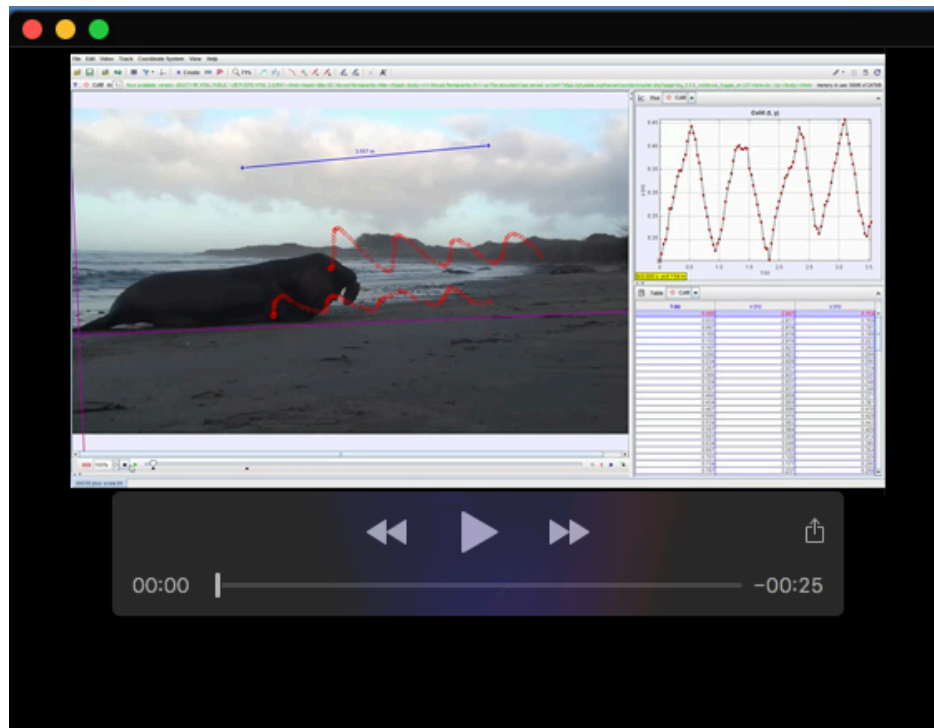 Tukey multiple comparisons of means
  95% family-wise confidence level

  Fit: aov(formula = Velocity ~ as.factor(Species), data = rawdata)

  $`as.factor(Species)`

Movie 1. Terrestrial locomotion of California sea lion.

Movie 2. Terrestrial locomotion video of adult California sea lion with anatomical points of reference showing oscillatory patterns during movement cycle.