

RESEARCH ARTICLE

Biomechanical energetics of terrestrial locomotion in California sea lions (*Zalophus californianus*)

Sarah J. Kerr^{1,*}, Frank E. Fish¹, Anthony J. Nicastro¹, Jenifer A. Zeligs², Stephanie Skrovan² and Megan C. Leftwich³

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, but phocids (true seals) have reduced forelimbs and are unable to bring their hindlimbs beneath them during terrestrial locomotion. Because of these differences, phocids are expected to have greater energetic costs when moving on land compared with otariids. The mechanical costs of transport (COT) 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 W and a COT 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 COT were compared for all four pinniped species by tracking the animals' center of mass. The quadrupedal gait of sea lions showed lower vertical displacements of the center of mass, and higher velocities compared with the terrestrial gait of phocids. Northern elephant seals, gray seals and harbor seals showed significantly higher COT and power outputs than the sea lions. California sea lions locomote with lower energetic costs, and thus higher efficiency compared with 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.

KEY WORDS: Biomechanics, Energetics, Galloping, *Zalophus*, Pinniped, Locomotion

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 by 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 by keeping 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). Sea lions use their enlarged foreflippers as a propulsive lever when they are moving terrestrially, which may help them conserve energy by avoiding lifting limbs in the vertical direction (Saunders et al., 1953; English, 1976b). 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;

¹Department of Biology, West Chester University, West Chester, PA 19383, USA.

²Moss Landing Marine Laboratories, Moss Landing, CA 95039, USA. ³George Washington University, Washington, DC 20052, USA.

*Author for correspondence (sjkerr96@gmail.com)

 S.J.K., 0000-0003-0512-905X

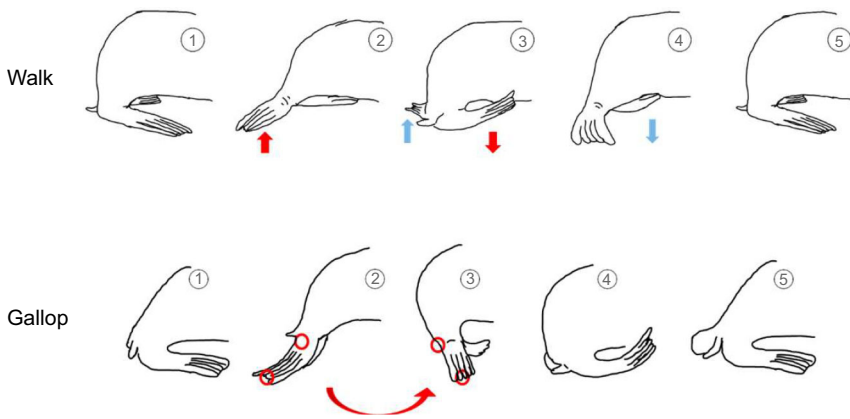


Fig. 1. The hindflippers of a California sea lion move independently during walking, but they move in unison during galloping. In the walking phase, the red arrows depict how the front flipper is moving; the blue arrows indicate how the back flipper is moving. In the gallop phase, the red arrow indicates 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 1–5 follow the locomotion sequence in order across a cycle.

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 (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 vitulina*), 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 (COT), when compared with the undulatory gait of the three phocid seals. Understanding the kinematics and mechanical energetics helps researchers to appreciate the compromises of these amphibious marine mammals and how they locomote on land and in water (Biewener, 1990).

MATERIALS AND METHODS

Digital video analysis

Two 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 Chester University Institutional Animal Care and Use Committee (Protocol #201601).

The two adult females 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^{-1} . Owing to the size and speed of the animals, the video sampling frequency was adequate to determine the movements of selected points as reported by 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 the camera. The mat was constructed of 61 cm×61 cm×3.5 cm interlocking foam rubber tiles that were arranged as 3.66 m×1.83 m covering an area of 6.7 m² 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 (Eqn 2) below] and could not be compared to the terrestrial locomotion of phocids. Prior to and after the recording sessions a 0.5 m rule 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

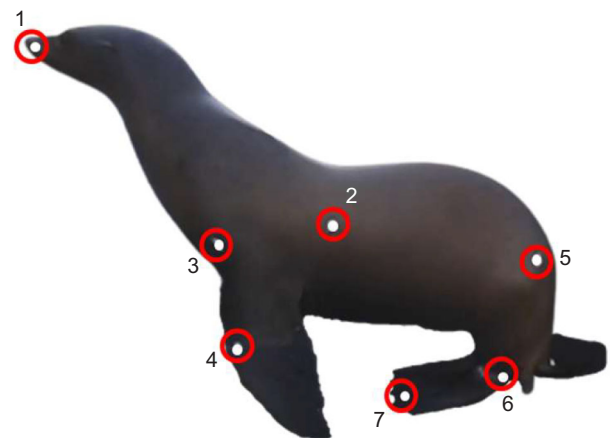


Fig. 2. Diagram of the seven anatomical points of reference that were marked on the sea lions with zinc oxide. The marks were digitized and tracked in Tracker software. Anatomical points included: rostrum, center of mass, axillary region, wrist joint, iliac crest, ankle and hind flipper tips.

mass distribution study in the current research. CM was previously determined according to the method of Doming and de Bruffénil (1991), where California sea lions lay 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, v. 1.51 s) and Tracker software (v. 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 7 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 because of poor lighting, the eye was followed. The videos were scaled by placing a 0.50 m rule in the field of view of the camera in the location that 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, 2015). One adult gray seal, Kija, 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. Minimum, maximum, and average velocities (m s^{-1}), 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 percentage 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; $\text{J kg}^{-1} \text{m}^{-1}$) 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 (M) 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 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 mass was estimated using the regression equation from Haley et al. (1991) as:

$$M = 301.34SA^{1.32}BL^{0.54}, \quad (1)$$

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 was calculated for all locomotion sequences for each individual animal. Cali, an 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, 34 runs for a gray seal and 6 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:

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

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:

$$dK = \frac{1}{2} (\mu dx) (\omega A)^2 (\sin^2(kx - \omega t)), \quad (3)$$

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:

$$P = 2 \left(\frac{dK}{dt} \right) = \frac{1}{2} \mu V \omega^2 A^2 = 2\pi^2 \mu V f^2 A^2. \quad (4)$$

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

$$\text{COT} = \frac{P}{MV}. \quad (5)$$

Statistical analysis

All statistical analyses were performed in R (v. 4.0.2; <https://www.r-project.org/>), and all packages used were a part of R. Values for each individual's trials were expressed as mean±s.d. The small sample size reflects the availability of trained sea lions that could be positioned appropriately for detailed data collection. Owing to the low number of animals available, multiple experimental trials were made to provide an adequate statistical sample. For both kinematic and biomechanical analyses, analysis of variance tests (ANOVAs) followed by Tukey HSD tests were done to compare variables. In kinematics, the amplitude, maximum velocity and average velocity were compared against each anatomical body point (Tables S1,S2). 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 (Tables S4,S5). Means±s.d 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 Schluter, 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 (d.f.=6, $F=7.348$, $P < 0.05$). However, the

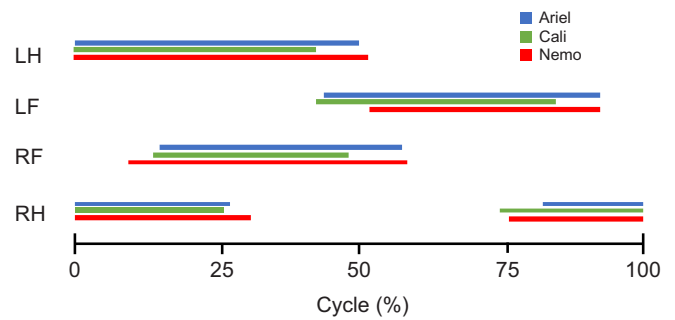


Fig. 3. Footfall diagram following the left hindlimb for one complete cycle in three individual California sea lions. LH, left hindlimb; LF, left forelimb; RF, right forelimb; RH, right hindlimb. Blue, green and red lines follow one complete cycle from Ariel, Cali and Nemo, respectively.

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 $2.37 \pm 0.35 \text{ m s}^{-1}$ for forward movement. The hindflipper tips had the fastest maximum velocity of 11.63 m s^{-1} during forward galloping (d.f.=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 (Tables S1–S3). Minimum velocities for the fore- and hindflipper points were 0 m s^{-1} 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 also moving slightly out of phase of one another (Fig. 3). The left and right hindlimbs were on the ground for ~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 ~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 (d.f.=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 (Tables S2,S3).

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 $112.04 \pm 18.94 \text{ W}$ (Table 1, Table S7).

Nemo's COT was 51% lower than COT in the two females, yet statistic difference between sexes was not recorded as there was only one male (Table 1, Table S6). The two females had similar COT values. The average velocity was statistically different for each sea lion (d.f.=2, $F=13.17$, $P < 0.05$) (Table 1, Table S8). Amplitude differed for the sea lions individually (d.f.=2, $F=9.021$, $P < 0.05$).

Table 1. Power, cost of transport (COT), amplitude and velocity for three individual sea lions

	Cali	Nemo	Ariel	Mean (all sea lions)
Power (W)	111.42±73.48	93.41±51.73	131.28±79.26	112.04±18.94
COT (J kg ⁻¹ m ⁻¹)	0.76±0.48	0.37±0.19	0.76±0.44	0.63±0.23
Amplitude (m)	0.11±0.04	0.12±0.029	0.14±0.05	0.12±0.02
Velocity (m s ⁻¹)	1.95±0.18	1.78±0.32	2.01±0.15	1.92±0.12

Means±s.d. are reported.

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, Table 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 with all three phocid species. Power outputs for the three phocid seals were significantly higher than that of the California sea lion (d.f.=3, $F=81.29$, $P<0.05$). The northern elephant seal shows the highest power output ($P<0.05$) (Fig. 4A,

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, Table 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 (d.f.=3, $F=40.32$, $P<0.05$) (Table 2, Table S11; Fig. 4B). COT for the three phocids species collectively was 69% higher than COT in the California sea lions. The phocid species had statistically similar COT ($P>0.05$) (Table 2).

All three phocid seals showed significantly higher P–P amplitudes compared with sea lions when corrected for body size (d.f.=3, $F=38.28$, $P<0.0001$) (Fig. 5A, Table 2). 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, Table 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 ($P<0.01$), but 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 increased 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. 5A). Velocities were corrected for body size and showed a significant difference between the phocids and the California sea lions (d.f.=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. 5B).

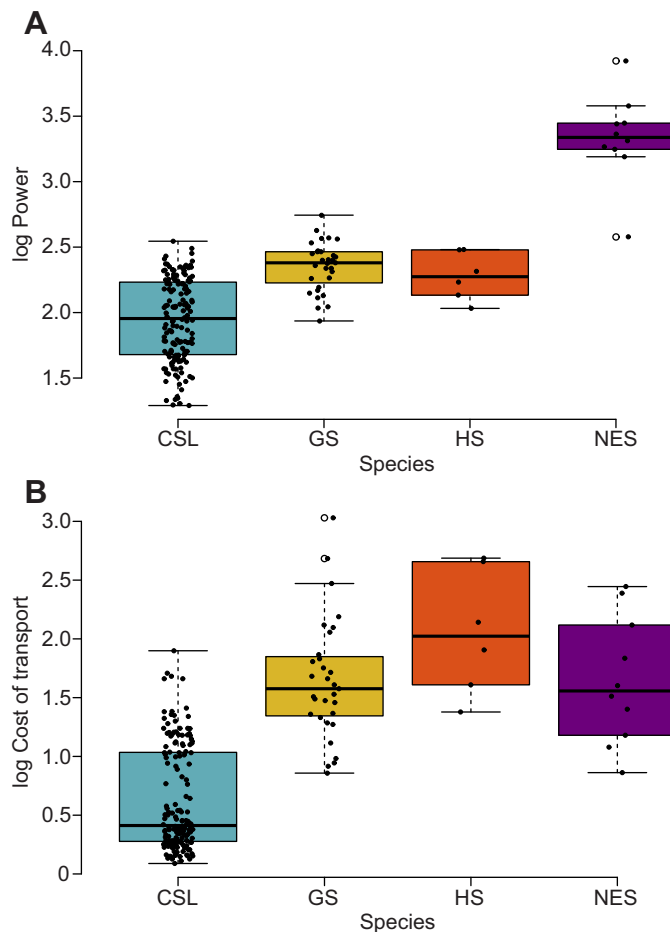


Fig. 4. Power output and cost of transport in four pinniped species. (A) Power outputs (W) and (B) COT (J kg⁻¹ m⁻¹) in California sea lion (CSL), gray seal (GS), harbor seal (HS) and northern elephant seal (NES). Dots indicate individual data points.

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 (*Phocarcctos 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

Table 2. Costs of transport (COT), power output, mass-specific power output (W kg^{-1}), vertical amplitude and velocities averaged for each of the four pinniped species

	California sea lion ($n=3$)	Northern elephant seal ($n=10$)	Gray seal ($n=1$)	Harbor seal ($n=1$)
COT ($\text{J kg}^{-1} \text{m}^{-1}$)	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})	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^{-1})	0.96±0.14	0.44±0.23	0.49±0.15	0.69±0.11

Values are means±s.d. Amplitudes and velocities measured in body lengths to correct for size.

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 each other.

Differences in gait are likely to be 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 for a long distance. With each step, the sea lion's hips and shoulders rotate while their head moves sinusoidally 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^{-1} 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 (1.2 km) (Bartholomew and Wilke, 1956).

Locomotion by terrestrial carnivores (fissipeds; e.g. dogs, cats) mirrors the same sequences as sea lions for forelimb movements (English, 1976a,b). The foreflippers of sea lions are enlarged when compared with 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 because of their aquatically adapted body shape. Fissiped carnivores get all the thrust they need from their hindlimbs when walking (Hildebrand, 1959). Carnivores such as the cheetah and dogs gallop utilizing substantial flexion and extension of the axial skeleton when moving at high speed (English, 1976a,b). 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 with terrestrial mammals. However, despite their amphibious body design, sea lions can reach high speeds on land while still maintaining their aquatic efficiency (Hildebrand, 1959; English, 1976b). The ability to travel over land with some proficiency may allow otariids to escape predators.

There is a wide range of footfall patterns, with some quadrupeds bearing more mass on their forelimbs or on their hindlimbs (Hildebrand, 1977). Footfall pattern and body mass distribution may allow larger oscillations of CM than predicted with larger energy exchanges (Griffin 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., 2003; English, 1976b). Large oscillations are necessary, because a sea lion's limbs are unable to swing freely owing to the elongation of the digits of the flipper. In this study, the hindflipper tips showed the second highest maximum amplitude value after the

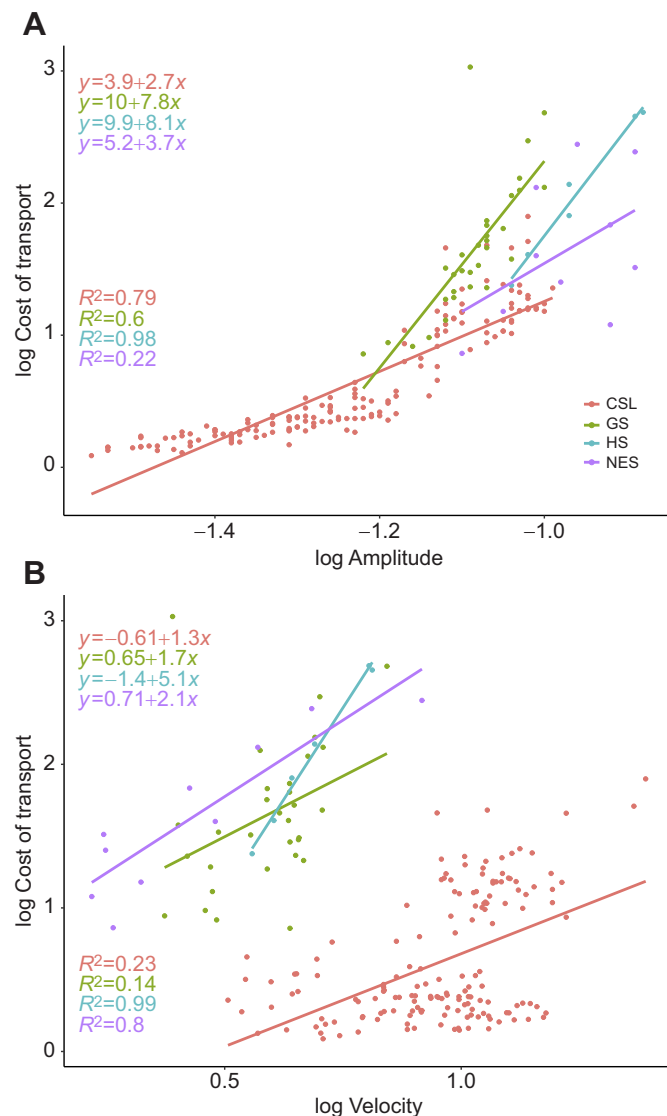


Fig. 5. Cost of transport as a function of amplitude and velocity in four pinniped species. (A) COT ($\text{J kg}^{-1} \text{m}^{-1}$) for all species, except the elephant seal (NES) shows a positive correlation with amplitude (BL). (B) COT shows a positive correlation with velocity (BL s^{-1}) for NES and harbor seal (HS) but not for California sea lion (CSL) or gray seal (GS).

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; Griffin 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, similarly 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 (Cavagna 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, 1999). However, the mechanical energetics for terrestrial locomotion can be determined through examination of the physics of an animal's gait (Fish, 1982; Williams, 1999; 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 3290 W at a velocity of 0.6 BL s^{-1} (2.16 m s^{-1}) and 5530 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 the parameter $M \text{ BL}^{-1}$, which was treated as a constant. However, $M \text{ BL}^{-1}$ 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. 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 upon disturbance, or to charge at a possible threat. Owing 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, 2015). 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 is 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 using their hindlimbs. Maintaining COT through velocity increases could be further proof that California sea lions are more efficient on land and can 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, 2015; Tennett et al., 2018). Sea lions, while having the ability 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 with 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 $\sim 0.2 \text{ J kg}^{-1} \text{ m}^{-1}$ 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 elephants are larger animals, their vertical oscillations of CM were 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 $0.05 \text{ J kg}^{-1} \text{ m}^{-1}$ (Lee and Harris, 2018). The mechanical COT for a chipmunk and a large dog (100 kg) were $0.46 \text{ J kg}^{-1} \text{ m}^{-1}$ and $0.35 \text{ J kg}^{-1} \text{ m}^{-1}$, respectively (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 (Garrett and Fish, 2015). The tendon makeup in the limbs of terrestrial mammals allows for recovery of mechanical work and lower COT compared with 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 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 with 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 with 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).

Acknowledgements

We thank the staff and animals at SLEWTHS research center who worked with us to make this research possible. This manuscript references the West Chester University Master's thesis of S.J.K. We also thank the thesis committee, Jennifer Maresh and Michael Rosario, who aided with statistical analysis.

Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: S.J.K.; Methodology: S.J.K., J.Z., S.S.; Software: S.J.K.; Validation: M.J.L.; Formal analysis: S.J.K., A.J.N.; Resources: J.Z., S.S.; Data curation: S.J.K.; Writing - original draft: S.J.K.; Writing - review & editing: F.E.F.; Visualization: S.J.K.; Supervision: F.E.F.; Project administration: F.E.F.

Funding

This research was supported by grants from the Office of Naval Research (N000141712312; program manager Thomas McKenna to M.C.L.).

References

- Backhouse, K. M.** (1961). Locomotion of seals with particular reference to the forelimb. *Symp. Zool. Soc. Lond.* **5**, 59-75.
- Bartholomew, G. A. and Wilke, F.** (1956). Body temperature in the northern fur seal, *Callorhinus ursinus*. *J. Mammal.* **37**, 327-337. doi:10.2307/1376731
- Beentjes, M. P.** (1990). Comparative terrestrial locomotion of the Hooker's sea lion (*Phocartos hookeri*) and the New Zealand fur seal (*Arctocephalus forsteri*): evolutionary and ecological implications. *Zool. J. Linn. Soc.* **98**, 307-325. doi:10.1111/j.1096-3642.1990.tb01204.x
- Biewener, A. A.** (1990). Biomechanics of mammalian terrestrial locomotion. *Science* **250**, 1097-1103. doi:10.1126/science.2251499
- Biewener, A. A.** (2003). *Animal Locomotion*. Oxford: Oxford University Press.
- Cavagna, G. A., Thys, H. and Zamboni, A.** (1976). The sources of external work in level walking and running. *J. Physiol.* **262**, 639-657. doi:10.1113/jphysiol.1976.sp011613
- Cavagna, G. A., Heglund, N. C. and Taylor, C. R.** (1977). Walking, running, and galloping: mechanical similarities between different animals. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 111-125. London: Academic Press.
- Deméré, T. A. and Yonas, J. H.** (2009). Locomotion. Terrestrial. In *Encyclopedia of Marine Mammals*, 2nd edn. (ed. W. F. Perrin, B. Würsig and J. G. M. Thewissen), pp. 672-673. San Diego, CA: Academic Press.
- DiStefano, J.** (2004). A confidence interval approach to data analysis. *For. Ecol. Manag.* **187**, 173-183. doi:10.1016/S0378-1127(03)00331-1
- Domingo, D. P. and de Bruffénil, V.** (1991). Hydrostasis in the sirenia quantitative data and functional interpretations. *Mar. Mamm. Sci.* **7**, 331-368. doi:10.1111/j.1748-7692.1991.tb00111.x
- English, A. M.** (1976a). Functional anatomy of the hands of fur seals and sea lions. *Am. J. Anat.* **147**, 1-18. doi:10.1002/ajpa.1001470102
- English, A. W.** (1976b). Limb movements and locomotor function in the California sea lion (*Zalophus californianus*). *J. Zool.* **178**, 341-364. doi:10.1111/j.1469-7998.1976.tb02274.x
- Feldkamp, S. D.** (1987a). Swimming in the California sea lion: morphometrics, drag and energetics. *J. Exp. Biol.* **131**, 117-135. doi:10.1242/jeb.131.1.117
- Feldkamp, S. D.** (1987b). Foreflipper propulsion in the California sea lion, *Zalophus californianus*. *J. Zool.* **212**, 43-57. doi:10.1111/j.1469-7998.1987.tb05113.x
- Fish, F. E.** (1982). Aerobic energetics of surface swimming in the muskrat *Ondatra zibethicus*. *Physiol. Zool.* **55**, 180-189. doi:10.1086/physzool.55.2.30155854
- Fish, F. E.** (2000). Biomechanics and energetics in aquatic and semiaquatic mammals: platypus to whale. *Physiol. Biochem. Zool.* **73**, 683-698. doi:10.1086/318108
- Fish, F. E., Innes, S. and Ronald, K.** (1988). Kinematics and estimated thrust production of swimming harp and ringed seals. *J. Exp. Biol.* **137**, 157-173. doi:10.1242/jeb.137.1.157
- Fish, F. E., Hurley, J. and Costa, D. P.** (2003). Maneuverability by the sea lion *Zalophus californianus*: turning performance of an unstable body design. *J. Exp. Biol.* **206**, 667-674. doi:10.1242/jeb.00144
- Friedman, C. and Leftwich, M. C.** (2014). The kinematics of the California sea lion foreflipper during forward swimming. *Bioinspir. Biomim.* **9**, 046010. doi:10.1088/1748-3182/9/4/046010
- Full, R. J.** (1989). Mechanics and energetic of terrestrial locomotion: bipeds to polypeds. In *Energy Transformations in Cells and Organisms* (ed. W. Wieser and E. Gnaiger), pp. 175-182. Stuttgart, Germany: Thieme.
- Full, R. J. and Tu, M. S.** (1990). Mechanics of six-legged runners. *J. Exp. Biol.* **148**, 129-146. doi:10.1242/jeb.148.1.129
- Garrett, J. N. and Fish, F. E.** (2015). Kinematics of terrestrial locomotion in harbor seals and gray seals: importance of spinal flexion by amphibious phocids. *Mar. Mamm. Sci.* **31**, 459-478. doi:10.1111/mms.12170
- Genin, J. J., Willems, P. A., Cavagna, G. A., Lair, R. and Heglund, N. C.** (2010). Biomechanics of locomotion of Asian elephants. *J. Exp. Biol.* **213**, 694-706. doi:10.1242/jeb.035436
- Gordon, K. R.** (1981). Locomotor behaviour of the walrus (*Odobenus*). *J. Zool.* **195**, 349-367. doi:10.1111/j.1469-7998.1981.tb03470.x
- Griffin, T. M., Main, R. P. and Farley, C. T.** (2004). Biomechanics of quadrupedal walking: how do four-legged animals achieve inverted pendulum-like movements? *J. Exp. Biol.* **207**, 3545-3558. doi:10.1242/jeb.01177
- Haley, M. P., Deutsch, C. J. and Boeuf, B. J. L.** (1991). A method for estimating mass of large pinnipeds. *Mar. Mamm. Sci.* **7**, 157-164. doi:10.1111/j.1748-7692.1991.tb00562.x
- Heglund, N. C., Fedak, M. A., Taylor, C. R. and Cavagna, G. A.** (1982). Energetics and mechanics of terrestrial locomotion. *J. Exp. Biol.* **97**, 57-66. doi:10.1242/jeb.97.1.57
- Hildebrand, M.** (1959). Motions of the running cheetah and horse. *J. Mammal.* **40**, 481-495. doi:10.2307/1376265
- Hildebrand, M.** (1966). Analysis of the symmetrical gaits of tetrapods. *Folia Biotheor.* **6**, 9-22.

- Hildebrand, M.** (1977). Analysis of asymmetrical gaits. *J. Mammal.* **58**, 131-156. doi:10.2307/1379571
- Hildebrand, M.** (1989). The quadrupedal gaits of vertebrates. *Bioscience* **39**, 766-775. doi:10.2307/1311182
- Howell, A. B.** (1929). Contribution to the comparative anatomy of the eared and earless seals (genera *Zalophus* and *Phoca*). *Proc. US Natl. Mus.* **73**, 1-142. doi:10.5479/si.00963801.73-2736.1
- Howell, A. B.** (1930). *Aquatic Mammals*. Springfield, IL: Charles C. Thomas.
- Howell, A. B.** (1944). *Speed in Animals*. Chicago: University of Chicago.
- King, J. E.** (1964). A note on the increasing specialization of the seal fore flipper. *Proc. Anat. Soc. G. Br. Irel.* **98**, 476-477.
- Kuhn, C. and Frey, E.** (2012). Walking like caterpillars, flying like bats—pinniped locomotion. *Palaeobiodivers. Palaeoenviron.* **92**, 197-210. doi:10.1007/s12549-012-0077-5
- Lee, D. V. and Harris, S. L.** (2018). Linking gait dynamics to mechanical cost of legged locomotion. *Front. Rob. AI* **5**, 111. doi:10.3389/frobt.2018.00111
- Maynard Smith, J. and Savage, R. J. G.** (1956). Some locomotory adaptations in mammals. *Zool. J. Linn. Soc.* **42**, 603-622. doi:10.1111/j.1096-3642.1956.tb02220.x
- O'Gorman, F.** (1963). Observations on terrestrial locomotion in Antarctic seals. *Proc. Zool. Soc. Lond.* **141**, 837-850. doi:10.1111/j.1469-7998.1963.tb01630.x
- Peterson, R. S. and Bartholomew, G. A.** (1967). *The Natural History and Behavior of the California Sea Lion*. Special Publication No. 1, American Society of Mammalogists.
- Ray, C.** (1963). Locomotion in pinnipeds: swimming methods relate to food habits. *Nat. Hist.* **72**, 10-21.
- Saunders, J. B., Inman, V. T. and Eberhart, H. D.** (1953). The major determinants in normal and pathological gait. *J. Bone Joint Surg. Am.* **35**, 543-558. doi:10.2106/0004623-195335030-00003
- Schmidt-Nielsen, K.** (1972). Locomotion: energy cost of swimming, flying, and running. *Science* **177**, 222-228. doi:10.1126/science.177.4045.222
- Tarasoff, F. J. and Fisher, H. D.** (1970). Anatomy of the hind flippers of two species of seals with reference to thermoregulation. *Can. J. Zool.* **48**, 821-829. doi:10.1139/z70-144
- Tarasoff, F. J., Bisailon, A., Piérard, J. and Whitt, A. P.** (1972). Locomotory patterns and external morphology of the river otter, sea otter, and harp seal (Mammalia). *Can. J. Zool.* **50**, 915-929. doi:10.1139/z72-124
- Tennett, K. A., Costa, D. P., Nicastro, A. J. and Fish, F. E.** (2018). Terrestrial locomotion of the northern elephant seal (*Mirounga angustirostris*): limitation of large aquatically adapted seals on land? *J. Exp. Biol.* **221**, jeb180117. doi:10.1242/jeb.180117
- Tucker, V. A.** (1970). Energetic cost of locomotion in animals. *Comp. Biochem. Physiol.* **34**, 841-846. doi:10.1016/0010-406X(70)91006-6
- Tucker, V. A.** (1975). The energetic cost of moving about. *Am. Sci.* **63**, 413-419.
- Whitlock, W. C. and Schluter, D.** (2015). *The Analysis of Biological Data*, 2nd edn. New York: W. H. Freeman and Company.
- Williams, T. M.** (1999). The evolution of cost efficient swimming in marine mammals: limits to energetic optimization. *Philos. Trans. R. Soc. Lond.* **354**, 193-201. doi:10.1098/rstb.1999.0371
- Williams, T. M. and Kooyman, G. L.** (1985). Swimming performance and hydrodynamic characteristics of harbor seals *Phoca vitulina*. *Physiol. Zool.* **58**, 576-589. doi:10.1086/physzool.58.5.30158584
- Zani, P. A., Gottschall, J. S. and Kram, R.** (2005). Giant Galápagos tortoises walk without inverted pendulum mechanical-energy exchange. *J. Exp. Biol.* **208**, 1489-1494. doi:10.1242/jeb.01554

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

	Minimum velocity	Maximum velocity	Mean velocity	95% Confidence Interval	
	<i>m/s</i>	<i>m/s</i>	<i>m/s</i>	<i>Lower</i>	<i>Upper</i>
Rostrum	0.24	4.81	2.03 \pm 0.42	1.01	3.04
Iliac crest	0.11	3.93	1.85 \pm 0.34	1.24	2.46
Center of mass	0.20	3.60	1.95 \pm 0.32	1.33	2.57
Axillary region	0.13	4.04	1.97 \pm 0.35	1.21	2.73
Foreflipper	0.00	5.65	1.97 \pm 0.37	1.16	2.92
Ankle	0.00	5.41	1.86 \pm 0.33	1.32	2.40
Hindflipper tip	0.00	11.63	2.37 \pm 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 (\pm S.D.) of each measurement as well as 95% confidence intervals are also provided.

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

R script for biomechanics of 3 adult California sea lions

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

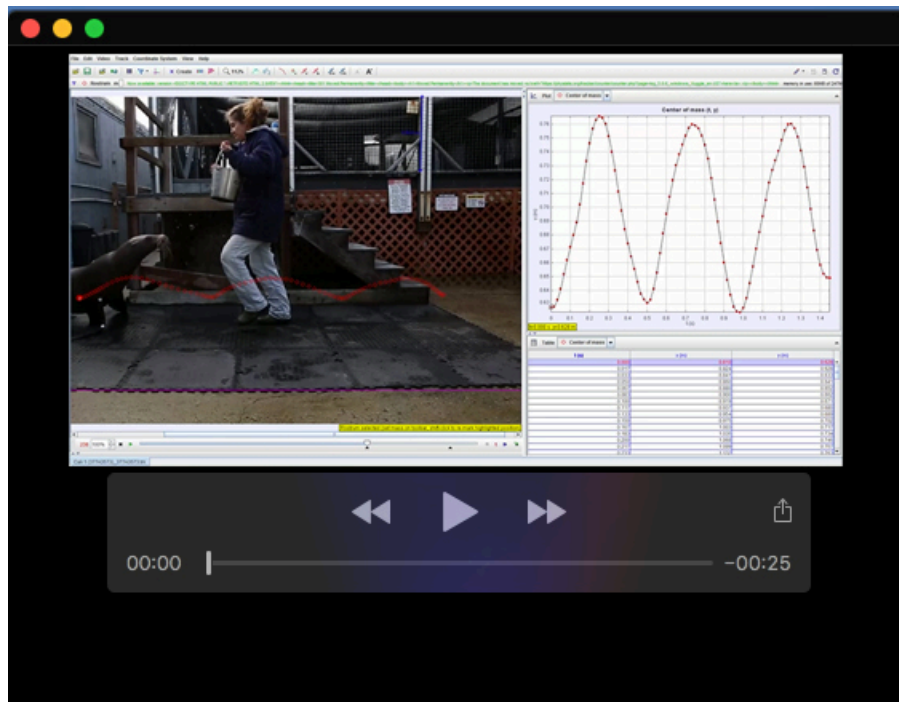
```
TukeyHSD(Vel.aov)
```

Tukey multiple comparisons of means

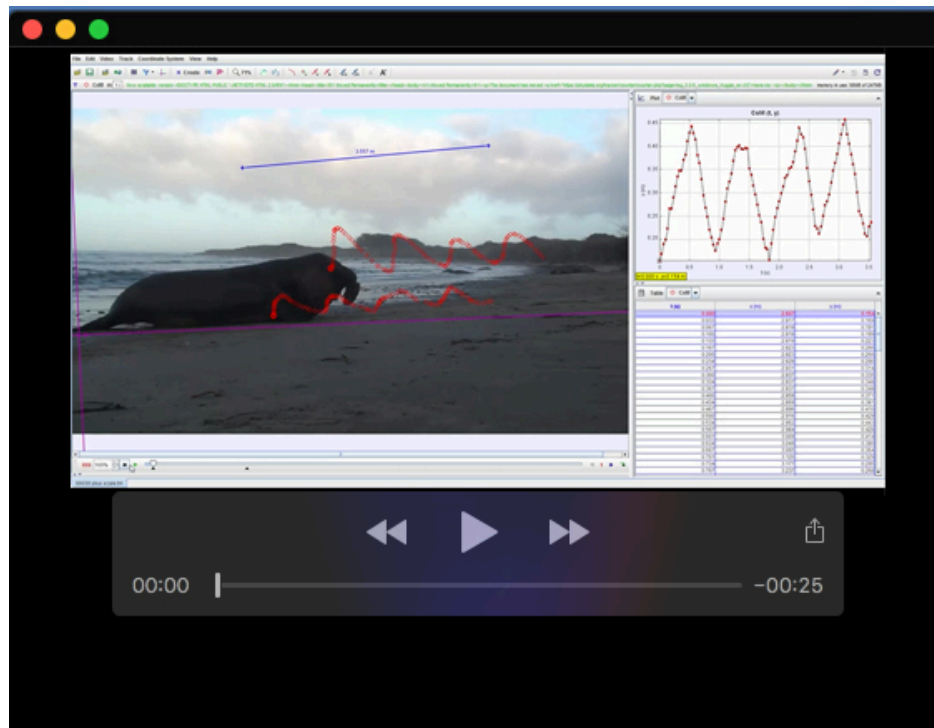
95% family-wise confidence level

```
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.