

**Running Mechanics of the
New Zealand sea lion (*Phocarctos hookeri*):
changes with speed and size**

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A thesis submitted for the degree of
Master of Science
at the University of Otago, Dunedin
New Zealand

3rd December 2010

Abstract

The Otariidae New Zealand sea lion (*Phocarctos hookeri*) is an understudied terrestrial locomotor whose body morphology has been modified by the aquatic environment with distinct environmental pressures. Despite morphological differences the NZ sea lion's locomotion on land is comparable with other terrestrial locomotors. Even though the NZ sea lion has distinctive-looking gaits they can be defined within the anteroposterior sequence (APS) method, a lateral walk and a transverse gallop. While the NZ sea lion does achieve many of the standards defining a run gait, it inconsistently achieves an aerial phase. Further consideration of the NZ sea lion gait suggests its forelimbs and hindlimbs may be using different gaits. The NZ sea lion uses a large sagittal flexion phase to allow its hindlimbs to match pace to its forelimbs. The NZ sea lion gait parameters more closely resemble that of the non-cursorial mammals. If the NZ sea lion is non-cursorial it would be the largest on record. Descriptions of gait and locomotion allow for informed conservation and management decisions regarding this large "nationally critical" marine mammal.

Acknowledgments

I would firstly like to thank my supervisor Dr. Chris L alas who was integral in just about every aspect of this project from the first assessments of its feasibility to the many editorial changes needed to make the final paper comprehensible and concise. Though Chris allowed me the freedom to develop and construct my own solutions to the many difficulties and setback involved in this project he was also always available when I needed a fresh look or feedback. For this I am forever grateful. I would also like to thank my departmental supervisor Dr. Abby Smith who smoothly stepped in at the end of this project for editorial assistance and time management oversight.

I need to thank the Department of Conservation in general and specifically Jim Fyfe at the Dunedin office for their support in what was an unusual project. I would also like to thank Jim Fyfe for his advice and help which was always available when I needed it. This project would never have been possible with out the gracious use of the McKay family property. Both David and Sarah's hospitality and their keen interest in both my project and the general conservation of the many marine species that habitat their piece of the Otago peninsula was inspiring. It is amazing to me what a single family can do for the betterment of their local environment.

This project would have been much more difficult with out the help of many of my fellow classmates who assisted in the filming aspects of this project in particular as well as general advice and assistance. In no particular order, thank you to; Rob, Sarah, Jess, Abe, Ashely, the Toms, my housemates Thom and Alex and lastly Sam. A special thanks to both Ani who, although she wanted nothing to do with 100 pound plus sea lions, was always available for advice and Rachel who also assisted in filming.

Lastly I would like to thank everyone at the Marine Science department at Otago University who assisted in many ways both small and large. Thank you all.

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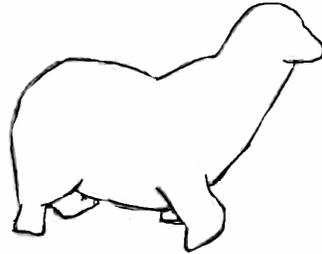
Chapter 1: Introduction

1.1 Locomotion in pinnipeds

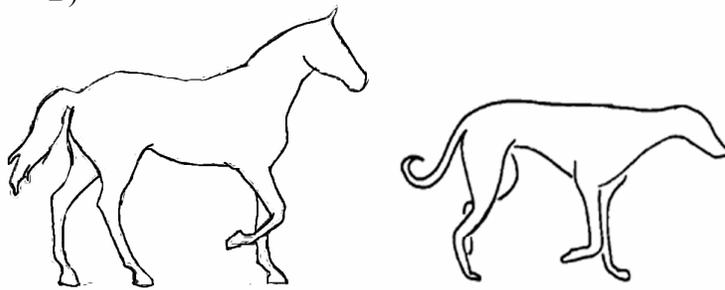
The pinnipeds are a superfamily made up of three families: the Phocidae (phocids; true seals), the Otariidae (otariids; fur seals and sea lions) and the Odobenidae (walrus). The Phocidae are comprised of 19 species in both hemispheres and all major oceans. The Otariidae are comprised of 16 species, with most restricted to the southern hemisphere. The Odobenidae contain only one species, (*Odobenus rosmarus*), with a range restricted to the Arctic region. Origins of the families is contested with recent evidence suggesting the Phocidae arise from a bear-like ancestor and the Otariidae from a otter-like ancestor (Sato et al., 2006; Rybczynski et al., 2009)

Pinnipeds are predatory mammals that rely almost exclusively on the aquatic environment for food, while being dependent on land or ice for rest and breeding (Reidman, 1990). When traversing these two environments pinnipeds must work against different forces: the terrestrial environment is governed by gravity and friction, but the aquatic environment is governed by drag and buoyancy, with hydrostatic forces playing an increasing role at depth (Fish, 2000; Williams, 2001; Alexander 2003). Pinnipeds have evolved to reduce the affects of the major forces of the aquatic environment. This is accomplished by a streamlined body shape and shortened limbs; an increased surface area of limbs transforming them into flippers to facilitate propulsion through water, a feature most prominent in otariids and increased fat stores for thermoregulation with neutral buoyancy, a feature most prominent in phocids (Fish, 1993; 2000).

A)



B)



C)



Fig. 1.1. Contrasts in shape between sea lions, cursorial and non-cursorial quadrupedal mammals. A) California sea lion (*Zalophus californianus*): large body; short and bent limbs with large manus and pes orientated in the transverse plane. B) Two examples of a cursorial quadruped mammal -- horse (*Equus*) and dog (*Canis*): both with relatively small body long vertical limbs with small manus, and pes orientated in the sagittal plane. C) Two examples of a non-cursorial mammal -- mouse (*Mus*) and mink (*Mustela*): large body; short, bent limbs and relatively large manus and pes orientated in the sagittal plane. (After English, 1976; Williams, 1983)

The kinematics of aquatic and terrestrial locomotion differs among the families of pinnipeds. For aquatic propulsion, phocids use lateral undulations of the body; otariids use vertical undulations of the forelimbs; and the walrus uses a combination of both (English, 1976; Gordon, 1983; Feldkamp, 1987a; Feldkamp, 1987b; Fish et al., 1988; Fish, 1993; Alexander, 2003). For terrestrial propulsion, phocids use anterodorsal undulations of the body and the body is not suspended from the ground; otariids use anteroposterior swings of limbs that suspend the body from the ground; and the walrus uses both these forms of propulsion, with suspension of the body becoming less frequent as individuals approach adult size (English, 1976a; 1976b; Gordon, 1981; Beentjes, 1990). Consequently, otariids are the only pinnipeds to employ quadrupedal terrestrial locomotion through all age classes.

Terrestrial quadrupedal mammals are divided into two groups based on broad morphological differences that reflect differences in locomotion: cursorial (limbs nearly vertical) and non-cursorials (limbs bent, nearly horizontal) (Jenkins, 1971). Cursorial mammals have long limbs, small pedal extremities and swing their limbs in the parasagittal plane. Non-cursorial mammals typically small mammals < 5kg, have short limbs and may move their limbs outside the parasagittal plane. These morphological differences have an effect on the gaits of the animals and that effect shows up in the gait parameters (Jayes and Alexander, 1983; Alexander, 2003).

1.2 Locomotor kinematics of terrestrial quadrupedal mammals

Terrestrial locomotion is achieved by muscle contractions that act against gravity to lift the body (mass) over the legs (struts), while gravity acts to pull the body down.

The mechanical equivalent is an inverted pendulum with the body swinging over fulcra created by the pedal extremity during ground contact (Alexander, 2003). The basic features of terrestrial quadrupedal locomotion are gait type (the spatial pattern of foot placement) and limb phase (the temporal patterns of foot placement) (Hildebrand, 1965). Both change with changes in speed. Speed has two components, stride frequency (the number of strides per unit time) and stride length (the distance traveled in one stride) (Helgund *et al.*, 1974; Alexander, 2003). At slow speeds, stride frequency is the main contributor to increases in speed. As speed increases stride frequency reaches a maximum attributable to a limit in limb swing rate and is represented by a logarithmic relationship with speed (Myers and Steudel 1985; Hutchinson, 2003; Maes *et al.*, 2007). In contrast, stride length increases linearly with speed, and as stride frequency contributes less to speed, stride length becomes the only means to increase speed. Stride length is only limited by how far an animal can reach (Helgund *et al.*, 1974; Alexander, 2003).

Gaits used by terrestrial quadrupedal mammals vary both interspecifically and intraspecifically with changes in speed, body shape and size (Helgund and Taylor, 1988; Alexander, 2003). Hildebrand (1965; 1976) categorized gait types from a combination of two parameters: duty factor (average time of foot contact as a proportion of total stride duration) and relative limb phase (the difference in the moment of ground contact between the left hindlimb and all other limbs expressed as proportion of stride duration). These parameters are measured using high-speed cameras and depicted in gait plots (Fig. 1.2). Duty factor is an indicator of relative speed: the duty factor is >0.5 for walking gaits (each limb is in ground contact for at least half of each stride) and ≤ 0.5 for running gaits (include an aerial duration

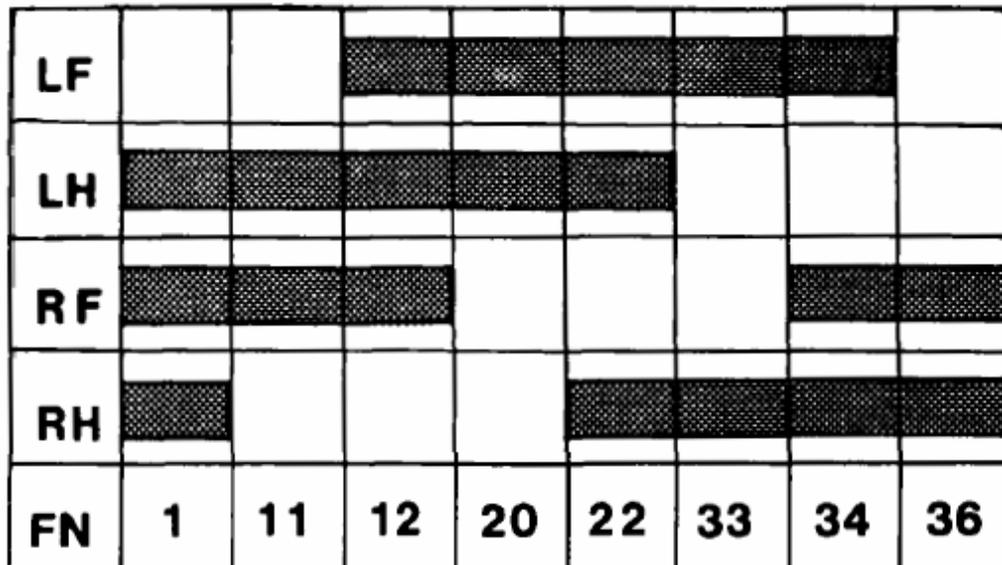


Fig. 1.2. Gait plot for the California sea lion (*Zalophus californianus*) following the Hidebrand (1965) method of presentation. The bars represent the duration that each foot was in contact with the ground quantified as frame number (FN); starting with the left fore (LF), left hind (LH) the foot that designated the start and stop of the stride, the right fore (RF) and right hind (adapted from English, 1976).

with no ground contact with in the stride). Differences in relative limb phase of designates the symmetry of gaits: phase difference between left and right limbs is 50% in symmetrical gaits (walk, pace and trot) and phase differences is more or less than 50% in asymmetrical gaits (gallop and bound) Hildebrand (1965; 1976). The simplicity of depicting gait plots is in marked contrast to complexities in analysis, visualization and comparison between the symmetrical and asymmetrical gaits (Hildebrand, 1976; Abourachid, 2003; Biknevicus and Reilly, 2006; Abourachid et al., 2007). The description of gait plots is hampered by the existence of intermediary gait types that act to blur the distinction between gaits making comparisons more difficult (Biknevicus and Reilly, 2006).

Dimensionless parameters are used in kinematic studies when it is relevant to compare trends among individuals, while eliminating any confounding factors that may arise due to differences in size. Dimensionless parameters are ratios created by dividing a physical variable by a characteristic constant with the same dimensions (thereby canceling each other out), that is easily identified and measured (Hof, 1996; Vogel, 2003). Duty factor used as a dimensionless indicator of speed and an indicator of the walk to run transition has been found to be inaccurate in the case of non-cursorial quadrupeds as well as some birds (Cavagna et al, 1977a, 1977b). The use of duty factor has been superseded by Froude number, $Fr = u^2(gh)^{-1}$, that more accurately defines the underlying kinetics of terrestrial transport; a quantification for transporting a mass acted on by gravity (9.80 ms^{-2}) over a strut (height h , m) at a given speed (u , ms^{-1}) (Alexander and Jayes, 1983; Alexander, 1989; Hoyt, 2006). The height of the strut has been applied to a variety of sites on the body, usually the hip joint (Hof, 1996), but also the shoulder joint (Hutchinson et al., 2006) and the withers

(McMahon, 1975). Theoretically the Froude number for a walk is < 0.5 and ≥ 0.5 for a run but the transition can occur as low as at 0.3 (Alexander, 2003).

Analysis of gaits has been simplified by the creation of the anteroposterior sequence (APS) method that facilitates quantitative rather than qualitative designations of gait types and qualitative comparisons among all gaits (Fig. 1.3). In the APS method the sequence of footfalls in gait plots begins with the lead forelimb (the forelimb that strikes the ground first) instead of the left hindlimb as applied previously (Fig. 1.2, 1.3). The parameters derived from durations of footfalls (duty factor and phase difference) are replaced by three temporal parameters derived from the sequence of footfalls. In contrast to previous analyses of gait, the APS method generates a unique combination of values for parameters for each gait. The APS method also generates spatial parameters that coordinate foot placement in space giving information on the contribution of limb pairs to stride length (Abourachid, 2003).

While it has been known that there are differences in duty factor between the lead and trail forelimbs (Bryant et al., 1987), recently it was found that all limbs differ in force generation and direction (Walter and Carrier, 2007). The APS method utilizes these findings by categorizing the limbs by their actions (lead or trail) within the stride and not by their location on the body. This results in the side of the animal with the lead forelimb labeled as one and the other as two, the limb designations are assigned from there, forelimb one (f1), forelimb two (f2) hindlimb one (h1) and hindlimb two (h2).

In quadrupeds the hindlimb pair and the forelimb pair can be thought of as two independent bipedal locomotors (Cartmill et al., 2002). These two bipedal locomotors

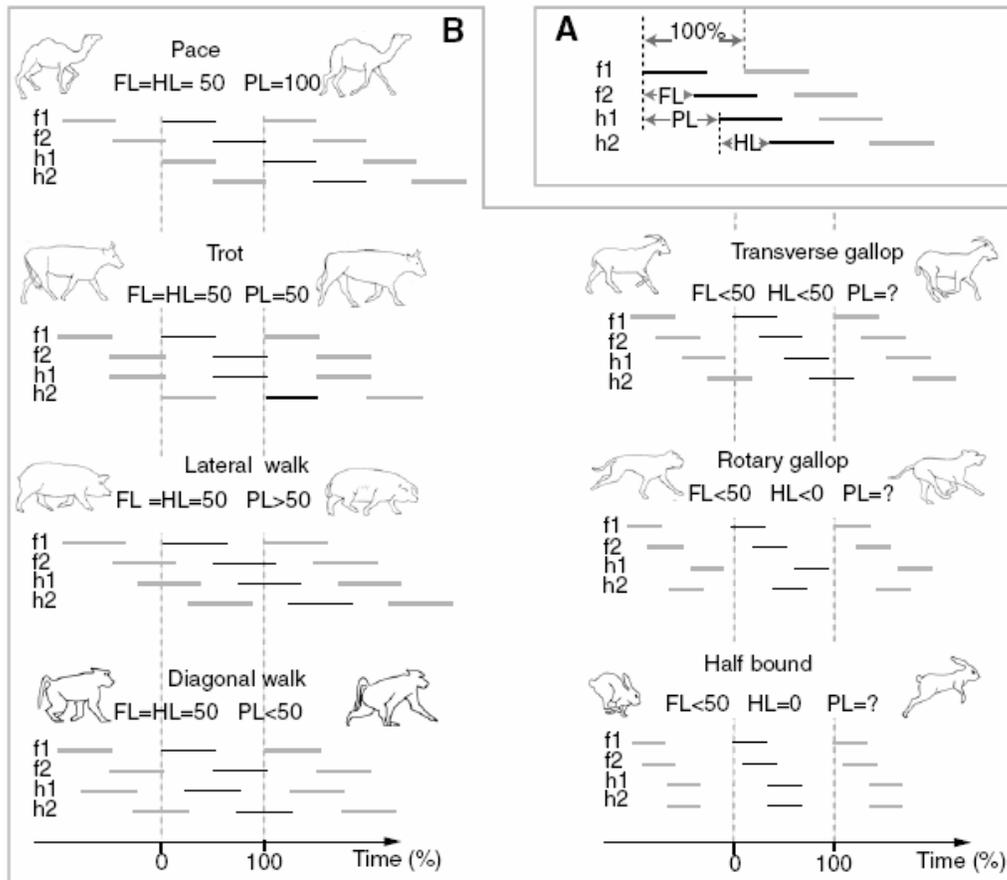


Fig. 1.3. The APS method of gait identification with proportion of stride along the x-axis and the four limb designations along the y-axis; f1 is forelimb one and starts the stride (lead limb), f2 is forelimb two (trail limb), h1 is hindlimb one and is ipsilateral to f1, and h2 is hindlimb 2. Each line represents the time that the corresponding foot is in contact with the ground, dark lines represent the contact times of feet that follow f1 and grey represent the contact times for the preceding and following stride. A) Depictions of lag durations. The fore lag (*FL*) is the duration between the contact of f1 and f2 as a proportion of the total stride, hind lag (*HL*) is the duration between h1 and h2 and pair lag (*PL*) is the duration between f1 and h1. B) Plots of the seven gaits designated by the APS method. In the walking gaits and the symmetrical running gaits *FL* and *HL* are both 50% and the *PL* is used to identify the gait while in the asymmetrical runs it is the *HL* and the *FL* that identify the gait and the *PL* is unused. 2003; Abourachid et al., 2007). Examples of the primary gait types with representative animals and the idealized gait plot below (Figure from Abourachid et al., 2007).

can act differently from each other as reported on for a variety of different quadrupeds over a range of sizes by Biewener (1983). When walking, the duty factor was biased towards the forelimbs for all of the cursorial mammals while the non-cursorial mammals were hindlimb biased. This is attributed to the uneven distribution of the mass of the cursorial mammals with an average 60%:40%, fore to hind ratio (Biewer, 1983). A study of the effects of loading on dogs (*Canis familiaris*) showed that adding a load to the fore or hind section of a dog significantly increased the duty factor of the corresponding limbs (Lee et al, 2004).

In most mammalian predators the spine has been shown to play an important role in locomotion, especially at high speeds (Hildebrand, 1959). The vertical bending of the spine (sagittal flexion) serves two main purposes, it increases stride length and it increases the speed of the limbs (Walter and Carrier, 2007). To increase stride length an animal must increase its limb length or it must increase the angle of the swing of the limbs (Alexander, 2003). Sagittal flexion facilitates for both increases in stride length. First it raises the hips and shoulders at full extension, thereby increasing the angle of the limbs (Hildebrand, 1959). Second, decreasing the distance between the hip and shoulder joints at maximum flexion allows the hindlimbs to be placed further forward than would normally be possible without flexion (Hildebrand, 1959; Alexander et al. 1985; Schilling and Hackert, 2006). The maximum increase in stride length attributable to sagittal flexion by a cursorial mammal is 5% in the cheetah (*Acinonyx jubatus*) (Hildebrand, 1959; English, 1976).

1.3 Terrestrial locomotion of otariids

The otariids are comprised of two subfamilies; the fur seals (Arctocephalinae) and the sea lions (Otariinae), which are morphologically differentiated by the presence of an under fur in the fur seals. Two representative species, the New Zealand (NZ) sea lion (*Phocarctos hookeri*) and the New Zealand (NZ) fur seal (*Arctocephalus forsteri*), were compared by examining skeletal dimensions by Beentjes (1989b) who found they were nearly indistinguishable when factored for scaling. The terrestrial habitats of the NZ fur seal and NZ sea lion differ and these differences are reflected in their gaits (Beentjes, 1990).

NZ fur seals are generally found on exposed and rocky coastlines among boulders and uneven terrain and typically locomote with the bound and half bound (Fig. 1.3) (Beentjes, 1990). The bound and half bound gaits are noted for their use by animals that traverse uneven terrain (Hildebrand, 1977, 1980). NZ sea lions are generally found on flat beaches and they have been reported as far inland as 1 km (Beentjes, 1990). The lateral sequence walking gait employed by the NZ sea lion is noted for its stability and all of the walking gaits for their low cost of transport (Alexander, 2003). Both are desirable attributes for the long journeys undertaken by the NZ sea lion.

English's (1976) paper on the California sea lion (*Zalophus californianus*) is the most comprehensive and complete study on the gait of the Otariids to date. He used a combination of anatomy and locomotion of captive sea lions to make qualitative kinematic observations. He noted the many unusual aspects of the terrestrial locomotion of this species: long duty factors, unusual hip flexion, transverse rotation of all limbs resulting in transverse leverage, lack of an aerial phase, use of spinal

flexion and large lateral oscillations. The hindlimbs were observed to play a relatively small role in sea lions terrestrial locomotion while the use of axial movements and forelimbs were exaggerated. English (1976) concluded that most of these eccentricities were likely the result of morphological compromise between terrestrial and aquatic locomotion. Lastly the gaits of sea lions appeared only superficially similar to their counterparts in terrestrial locomotion(English 1976) as described by Hildebrand (1976).

The Beentjes' (1990) study on the terrestrial locomotion of otariids noted the same characteristics of the gait of California sea lion's gait of the NZ sea lions while noting the difference in gait of the NZ fur seal. Beentjes (1990) attributed the differences in gait to ecological specialization brought on by the need to traverse different terrain. Despite the differences in gait type, both species had long duty factors and the transverse rotation of all limbs necessitated by the large manus and pes of both species.

1.4 New Zealand sea lion

The NZ sea lion is classed as “vulnerable” in the IUCN Red List (IUCN, 2010) but “nationally critical” by the New Zealand Department of Conservation (DOC) in the NZ sea lion species management plan (DOC, 2010). Although the population has been estimated as about 12,000 individuals, the species has a highly restricted breeding range with 86% found on Auckland Islands, 500 km south of South Island, New Zealand, and another 14% found on Campbell Island (Campbell et al., 2006). Recent data indicate the adult population may be lower than 3000 adults (Baker et al., 2010).

Population surveys of pups since 1996 indicate the pup population declined after peaking in 2001 and that this decline has been on the Auckland Island while Campbell has seen an increase (Chilvers et al., 2007). Recent studies indicate that the likely cause of the decline is due to by-catch or competition for resources with the fishing industry (Robertson and Chilvers, 2011). Since 1980 their range has expanded northward to the Otago Peninsula on the southeast coast of the South Island from (McConkey et al, 2002). The typical haul out site at the South Island is sandy beaches generally with access to grass dunes where NZ sea lions will seek shelter on cold days (Beentjes, 1989).

1.5 Aims

Kinematic analyses of quadrupedal locomotion have become more quantitative since the previous studies on sea lions by English (1976) and Beentjes (1990). Notable introductions since 1976 are Froude number, dimensionless parameters and the APS method for gait analysis. The aim of this study was to expand the knowledge of the terrestrial locomotor capabilities of the NZ sea lion using modern quantitative analysis for comparison with terrestrial mammals and detect any changes with individual size. An assessment of their locomotor abilities ashore will contribute towards conservation management by providing information relevant to increasing human interactions as numbers of NZ sea lions increase at South Island locations frequented by people.

Chapter 2: Methods

2.1 Study location and study animals

Video capture was performed between 30 November 2008 and 29 November 2009 at Papanui Beach (45° 51.8' S, 170° 44.4' E) on Otago Peninsula, south-east South Island, New Zealand (Fig. 2.1). The land surrounding and all access to the beach is privately owned and controlled. The 200 m wide flat sandy beach (depicted in Beentjes, 1989a) is the most important haul-out site for male NZ sea lions on Otago Peninsula (Beentjes, 1989a; Lallas et al., 2007) and was an ideal site for this project.

Two permits were acquired for this project, one from the Department of Conservation (DOC, Appendix 1) and a second from the University of Otago Animal Ethics Committee (AEC, Appendix 2). The DOC permit required that the study only involve males and that the project was restricted to Papanui Beach. The AEC permit required that I always have a second person on the beach during filming to ensure my safety. The animals used in this project were all wild, untrained individuals and all filming was done on unrestrained males at Papanui Beach. Individuals were identified by photographic identification following McConkey (1999) and grouped into three age classes; juvenile (1-3 years), sub-adult (4-5 years) and adult (6 years and older) by a combination of body length, body shape, and pelage (McConkey et al., 2002).

2.2 Video trials

Video trials were recorded with a video camera (JVC DV, GR-DVL 9800), set stationary on a tripod with no panning and operated at 100 frames per second (100Hz). A video trial consisted of a single sequence of movement by a sea lion

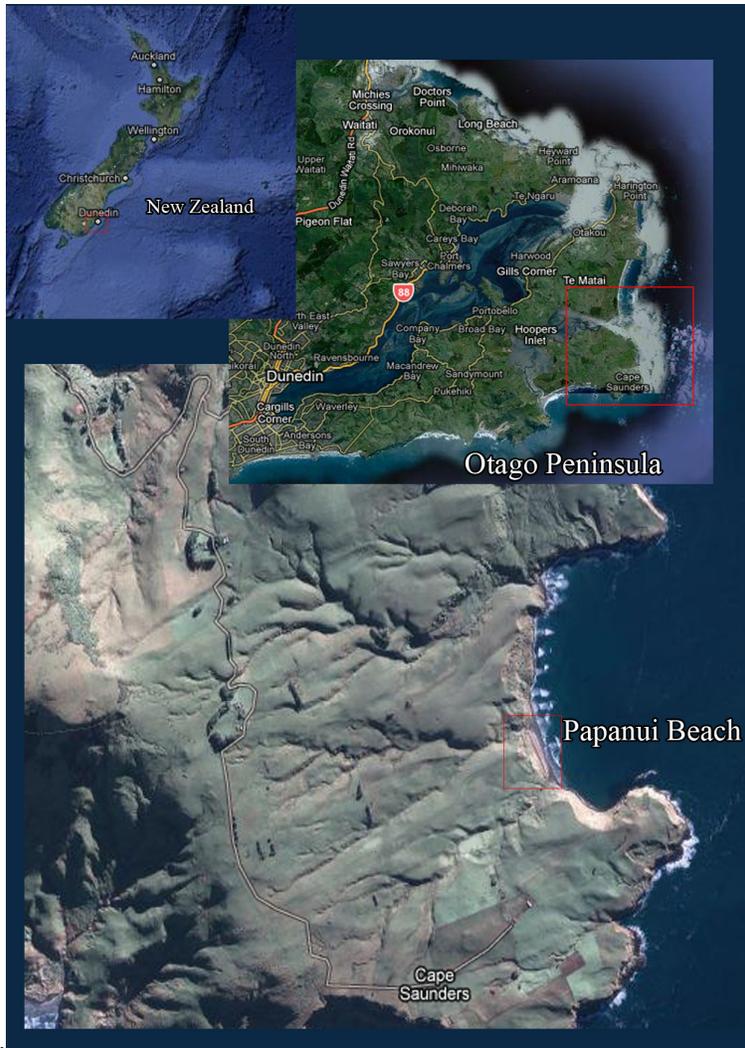


Fig. 2.1 Location of the study site: Papanui Beach, Otago Peninsula, south-east South Island, New Zealand

across the view of the camera resulting in the capture of a single stride with a quality sufficient to measure all parameters. The use of wild animals in an uncontrolled environment led to a large number of unusable trials as well as larger errors than those typically found in a lab-based locomotion study. Each interaction with sea lion was restricted to ≤ 10 minutes in order to reduce disturbance. Video acquisition was preceded by a visual inspection of all sea lions on the beach looking for injuries that could result in anomalies in stride and to determine individual identification.

The first attempts to capture the kinematic movements of NZ sea lions was performed in the standard method of applying paint dots at joints and limb centers (e.g., Hutchinson et al., 2006). Unfortunately, this method had to be abandoned due to inaccuracies and difficulties in consistent application of paint dots. The two main issues were oscillation in the markers during locomotion due to a thick subcutaneous fat layer, and the inherent difficulties in the consistent application of the paint dots on a wild animal. These issues necessitated a simpler approach of using the leading edges of limbs, body and physically-distinct points to capture movement from one frame to the next in a video trial.

Two basic video capturing techniques were employed. The first was an interactive technique to motivate a sea lion to travel in a desired direction. The second was a passive (non-interactive) technique that took advantage of movements by sea lions that were not initiated by human interaction. Instead, sea lions were filmed as they traveled to or from the sea or traveled between groups of sea lions ashore. This technique was less intrusive but did not elicit fast movement or a reliable direction of

travel as the interactive technique did. The two techniques involved different camera setup and initial approach to the sea lion.

For the interactive technique the camera, on a tripod, was placed 2 m in front of a prone sea lion and was pointed perpendicular to the desired line of travel as it was difficult to motivate the animals to move for more than three strides from its chosen site. The camera was set back about 10 m from the line of travel to allow for appropriate framing and zooming to limit parallax issues. The quality of video and available light were both important factors in this study. With this in mind the video camera was set up with consideration to the location of both the sun and the ocean as both could cause glare that led to poor video quality and unusable video trials.

I approached a prone sea lion from the front until he raised himself up on to his forelimbs in a "standing" stance to face me, with his forequarters lifted by the forelimbs and the hindquarters remained prone. I then circled around the sea lion, so that he raised his hindquarters in order to rotate and keep facing me. Once he was raised on all four limbs, I circled back to my original position. The sea lion would circle to keep me in view and we were once again facing in a direction perpendicular to the view of the camera.

I would then slowly approach closer to the sea lion from the front waiting for a response. At this stage the exact procedure was hard to define but the general idea was to encourage the sea lion to chase me. This usually required me to approach to <1 m and then retreat. Retreating too soon would lead to the animal returning to a prone posture, but leaving too late could lead to contact which would cause the sea

lion to stop. Once a sea lion had taken to chasing me the process become much easier as he tended to continue to chase me for 2-3 strides and then return to his original spot until he lost interest. The passive technique took advantage of a tendency for NZ sea lions to travel a few strides and then stop and return to a prone posture for 20-30 seconds. This allowed me to continually move the camera and capture multiple video trials.

Two reference measurements were filmed for every video location, using a 1.3 m scaled rod. While standing on the travel path of the subject, the scaled rod was positioned horizontally and then moved back and forth across the plane perpendicular to the field of view of the camera. This assured that the true parallel would be filmed. Next the scaled rod was placed vertically and then pivoted forward and back to ensure the true perpendicular was recorded. These recordings of known distances on both axes created a vertical and horizontal reference frame that allowed the conversion of pixels to meters. These reference videos were created for each distinct filming location. A new reference was created if the camera was panned, the zoom was altered or with any movement of the tripod or camera.

2.3 Video processing

Video processing included the steps necessary to take a video trial and record all the parameters used to analyze the gait characteristics of the NZ sea lion. The first step in the video processing was to eliminate unusable video trials. While the person operating the camera ensured that the sea lion was properly framed, several other factors that were part of determining good video from unusable could only be distinguished during video processing. The angle of travel was important and the

subtle changes in depth through the stride were difficult to see at the time of filming. The inclusion of a full stride was also important but impossible to see at the time of filming. Obscuring of the pedal extremities by soft sand, poor video quality due to low light levels and obscuring of edges due to cryptic backgrounds were other contributing factors to poor video quality. These types of factors resulted in about 75% of the video trials being unsuitable for the data analysis stage of the project. Those that passed all of the above parameters were cut up into individual frames and saved as a sequence of Joint Photographic Experts Group (jpeg/jpg) files to allow for ease of manipulation.

All temporal measurements were made in frame units and then converted to seconds using the 100 Hz frame rate of the camera. The duration of each limb contact with the ground was determined and used to create a standard foot-fall pattern for each gait. The NZ sea lion larger manus and the loose nature of the substrate (sand) meant foot contact was sometimes difficult to determine. Limb contact was designated as the moment of cessation in forward translation of the pedal extremity, following Hutchinson et al. (2006).

California sea lions used flexion at the manus that lifted the forelimb off the manus and onto the phalanges of the sea lion just before the forelimb was lifted off the ground (English, 1976). Examination of several head-on video sequences of NZ sea lions confirmed that forward translation of the forelimb was restrained until after this flexion in the manus and was consistent with forelimb lift off. Hindlimb ground contact, especially for the trail hindlimb, was most easily recognizable as a visible shock wave (disturbance to the skin and fat) traveling along the hindlimbs or

compression of the hindlimb at touch down. Lift off was more abrupt and less subtle than the forelimbs' translation from manus to phalanges. Movement was easily recognizable due to the movement of sand around the pedal extremity at lift off.

All length measurements were made in pixel units and converted to meter units after the measurement process using the conversion ratio collected for each video location. The stride length was determined by examining the closest forefoot, marking the location of the forelimb at lift off, and again on subsequent contact with the ground. The distance between the contacts of the forelimbs, the hind limbs and between the lead forelimb and the ipsilateral hind foot were also recorded.

Size differences among terrestrial locomotors used in kinematic studies have been adjusted for by standardizing length measurements using the hindlimb length (Alexander, 2003). Most studies have used the hip height (H_h) for scaling between species, but others have used shoulder (H_s) or withers height (H_w) (e.g., McMahon, 1975; Pontzer, 2007; Maes et al., 2008, Fig. 2.2). The positions of the shoulder joint and hip joint were determined by scanning through the stride to locate the fulcrum of limb movement. For this study the withers was designated as the point of flexure along the back in the thoracic region a point easily recognizable in all video trials and through out a stride. Comparing the skeleton of the sea lion with that of a dog, this measured point H_w in NZ sea lions was not at the tallest thoracic vertebrae as defined for a dog or horse (e.g., Davies, 2005), but more posterior of the shoulder joint (Fig. 2.2).

In order to determine a steady-state speed, most kinematic studies employ a means of determining the subjects speed before and after the stride or throughout the stride using known distances marked behind or under the subject, or light triggers (e.g. Williams et al., 2002; Bryant et al., 1987). The field aspects of this study prevented the use of these standard techniques. Instead the locations of the leading edge of the chest and the trailing edge of the hindquarters were recorded for each frame, and then a 6 point running average was applied to consecutive frames to calculate speed at 0.01 s intervals. The two speeds for each frame were averaged and the slope was calculated for a linear regression of speed against time for one stride and compared to the speed derived from dividing the stride length by the duration of the stride. Any strides with a start speed greater or less than 10% of the end speed were rejected. This resulted in a further 30% of digitized video trials being rejected due to speed fluctuations or cryptic backgrounds preventing accurate intra-stride speed determination.

Control studies were performed to quantify intrinsic error in the techniques employed for the data collected. First a high speed clock was filmed to determine the accuracy of the cameras stated 100 Hz, and the actual rates were found to be within 1%. A control for lens distortion was performed at full mechanical zoom. When the camera is fully zoomed light is passing through the flattest part of the lens decreasing vertical and horizontal distortions from parallax deformations (the distortion of lengths due to the bending of light passing through a lens). This test was performed by filming a flat wall with known measurements and comparing them to the ratio of the vertical and horizontal scaled rod measurements which had a ratio of 1.07. No video trial used had a ratio that differed by more than 10% of the 1.07 ratio.

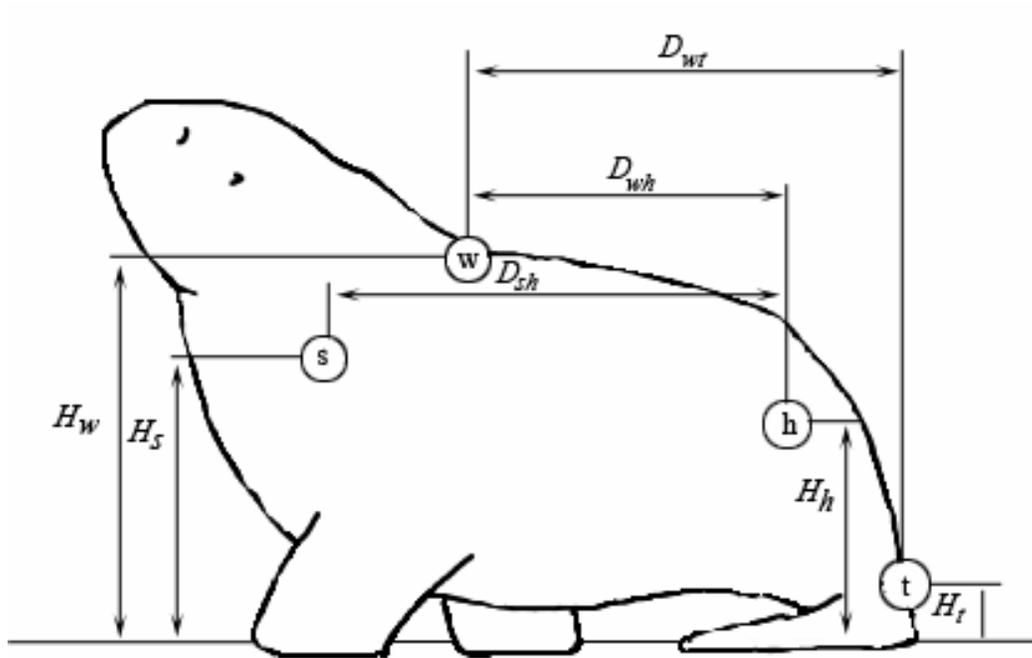


Fig. 2.2. The four reference points (s = shoulder, w = withers, h = hip and t = tail base) four heights (H_w = withers height, H_s = shoulder height, H_h = hip height and H_t = height to tail base) and three lengths (D_{wt} = distance between withers and base of tail, D_{wh} = Distance between withers and hip and D_{sh} = distance between shoulder and hip) measured to quantify locomotor kinematics of New Zealand sea lion.

2.4 Kinematic parameters

The kinematic parameters collected or calculated from the video trials generally conformed to those defined by Hutchinson et al. (2006), but using the APS method (as defined by Abourachid, 2003) to replace the Hildebrand (1976) gait system of gait identification (Table 2.1). Stride duration (t_{sd}) was the time to complete one stride the time from contact of f1 (forelimb one) to just before the second contact of f1, stance time (t_{st}) the average duration of foot contact, and swing time (t_{sw}) the average duration the limbs were not in contact with the ground. Duty factor ($\beta = t_{st}/t_{sd}$) calculated by averaging the t_{st} of each limb and dividing by the t_{sd} . Other related measures were the average duty factor for forelimbs (β_f) and for hindlimbs (β_h) as well as the ratio of the forelimbs to the hindlimb pair ($\beta_{f:h}$) and the individual duty factor for the left forelimb (β_l) and right forelimb (β_r). Stride length (L) was found by measurement from single frames of video, stride frequency ($F = t_{sd}^{-1}$) found by dividing frames per stride by the camera Hz and speed ($u = L \cdot t_{sd}^{-1}$, ms^{-1}) from stride length divided by stride duration. The three temporal gait determinants of the APS method (Abourachid, 2003) are fore lag (FL) designating temporal coordination (the time between the initial contact of f1 and the subsequent contact of f2 [forelimb two], as a percentage of t_{sd}) of the fore legs, hind lag (HL) designating the temporal coordination of the h1 and h2 (hindlimbs one and two) and pair lag (PL) designating the temporal coordination between f1 and h1 (f1 and h1 are ipsilateral by definition, Abourachid, 2007). The three concomitant spatial gait determinants are fore gap (FG) the distance between the contact of f1 and f2, hind gap (HG) the distance between h1 and h2, and pair gap (PG) the distance between f1 and h1. Gaps are ratios of the L but in some instances it is interesting to look at the actual distance, these are called gap distances and given a subscript d in this study for clarity (e.g. FG_d).

Table 2.1 List of symbols

β	Duty factor $=t_s \cdot t_{sd}^{-1}$
β_f	Duty factor for the forelimbs
β_h	Duty factor for the hindlimb
β_{fl}	Duty factor for the left front forelimb
β_{rf}	Duty factor for the right front forelimb
$B_{f:h}$	Duty factor fore-hind ratio $=\beta_f \cdot \beta_h^{-1}$
D_{wt}	Distance between the withers and the base of the tail
D_{st}	Distance between the shoulder and the base of the tail
D_{ratio}	The ratio of the max distance and min distance between the withers and tail $=(\text{maximum } D_{wt}) (\text{minimum } D_{wt})^{-1}$
f1	Forelimb one, lead forelimb of the stride
f2	Forelimb two, trail forelimb of the stride
F (Hz)	Stride frequency $=t_{sd}^{-1}$
\hat{F}	Relative stride frequency $=F(H_s \cdot g^{-1})^{0.5}$
FG	Fore gap, distance between contact of f ₁ and f ₂
FL	Fore lag, duration between contact of f ₁ and f ₂
Fr	Froude number $=u^2 \cdot (g \cdot H_s)^{-1}$
h1	Hindlimb one, h1 is ipsilateral to f1 by definition in ASP
h2	Hindlimb two, trail ipsilateral to f2 by definition in ASP
H_h (m)	Height from ground to the hip joint
H_s (m)	Height from ground to the shoulder joint
H_w (m)	Height from ground to the withers
H_f (m)	Height from ground to the estimated fission shoulder using otaride forelimb ratio (English, 1977)
HG	Hind gap, distance between contact of h ₁ and h ₂
HL	Hind lag, duration between contact of h ₁ and h ₂ lag
L (m)	Stride length, distance between first and second contact of forelimb 1
L_h	Relative stride length determined by hip height $=L \cdot H_h^{-1}$
\hat{L}_f	Relative stride length determined by fission fore leg ratio $=L \cdot H_f^{-1}$
\hat{L}_s	Relative stride length determined by shoulder height $=L \cdot H_s^{-1}$
\hat{L}_w	Relative stride length determined by withers height $=L \cdot H_w^{-1}$
PG	Pair gap, distance between contact of f ₁ and h ₁
PL	Pair lag, duration between contact of f ₁ and h ₁ lag
t_{sd} (s)	Stride duration, time to complete one stride
t_{st} (s)	Stance time, average stance duration of one stride
t_{sw} (s)	Swing time, average swing phase duration of one stride
u (m/s)	Speed $=L \cdot t_{sd}^{-1}$
\hat{u}	Dimensionless speed $=Fr^{0.5}$

The Froude number ($u^2 g^{-1} H_s^{-1}$, where g is gravitational acceleration, $g=9.81\text{ms}^{-2}$) was calculated for each stride allowing for the calculation of dimensionless speed ($\hat{u} = Fr^{0.5}$), (Hof, 1996). Shoulder height was used to calculate the Froude number for this study, reflecting the more active use of the forelimbs in locomotion in comparison to the hindlimbs (English, 1976), and considering the interchangeability between shoulder height, hip height and withers height found in the literature (e.g. McMahon, 1975; Alexander and Jays, 1983; Alexander, 1996; Williams, 2002; Maes et al., 2008; Pontzer, 2007). Dimensionless, sometimes called relative or normalized in the literature, parameters are all referred to as dimensionless in this study and are designated with a hatted symbols. Dimensionless stride frequency ($\hat{F} = F[H_s \cdot g^{-1}]^{0.5}$) and stride lengths ($\hat{L} = LH_s^{-1}$) were determined (Alexander and Jays, 1983; Gates and Biewener, 1991; Hof, 1996). Several length measurements were made on each subject at the withers to base of tail (D_{wt}), shoulder to base of tail (D_{st}) as well as the heights of all three locations (H_w, H_s, H_h) at two points in the stride for all strides at what was visually determined to be the least and greatest sagittal flexion (Fig. 2.2). One subject (F) was examined over two strides and all measurements ($D_{wb}, D_{sb}, H_w, H_s, H_h$) were made at every frame. This subject was chosen because it provided the only sequence of >1 stride at a constant speed. Lastly a ratio of the minimum D_{wt} to maximum D_{wt} measurement was calculated (D_{ratio}).

2.5 Statistical analysis

All statistical analysis was calculated using the Matlab (r2007) statistical toolbox with u, \hat{u} and H_s as the independent variable and standard stride parameters ($H_s, H_h, H_w, D_{wt}, D_{st}, D_{m:m}, Fr, F, L, \beta, \beta_{rf}, \beta_{f:h}, \beta_h, \beta_f, t_{st}, t_{sw}, t_{sd}, FL, HL, PL, FG, HG, PG$) and two relative stride parameters (\hat{L}, \hat{F}) as the dependent variable. Sample variation was

represented by $\pm 95\%$ confidence intervals (95% CI). The Pearson's least squares coefficient of determination (r^2) was used for all regressions with highest r^2 values designating best fit of linear and curvilinear equations. F-value (f) were calculated for all regression lines, a probability (p) < 0.05 was considered significantly different from $H_0: \rho^2 = 0$ (where $\rho^2 =$ the true population correlation coefficient). The choice of regression models to delineate relationships among stride parameters followed Maes et al. (2008).

Results for adult and sub-adult male NZ sea lions were compared to deduce any significant differences between the two represented age classes across all video trials or across the run video trials. Do to low replication in the walk video trials comparisons solely between walk trials was not possible. The means of parameters for the two age classes were compared through ANOVA analysis. Linear regressions for the age classes were compared through ANCOVA analysis and used to determine significant differences in elevation or slope. In the case of curvilinear (power and logarithmic) relationships the relevant data were natural log transformed in order to perform the ANCOVA analysis. Residuals were examined for even distribution about zero, where a lack of patterns would signify a linear fit.

To determine best fit between predictive models and measured data the coefficient of determination for multiple regressions ($R^2 = 1 - \frac{\sum (y - y_m)^2}{\sum (y - \bar{y})^2}$; y = observed value, y_m = corresponding model value, \bar{y} = mean of observed values; Zar, 1999) was calculated as well as an adjusted coefficient of determination for multiple regression

$$(R_a^2 = 1 - (\frac{n-1}{n-m-1})(1 - R^2)), n = \text{number of trials}, m = \text{number of independent variables};$$

Zar, 1999). The R^2 values can range from negative infinity to 1, with any value <0 signifying a fit worse than applying the mean and 1 being a perfect fit. This particular R^2 is considered the most robust of several variants of R^2 and therefore better for comparing multiple models to measured data (Kvalseth, 1985; Anderson-Sprecher, 1994; Zar, 1999). A Model can only fit the data as well as the data's related r^2 and these are reported along with the R^2 to give a base line.

Chapter 3: Results

3.1 Numbers of individuals and video trials

Photographic identification of individuals was not definitive in all cases and resulted in a possible range of 9-12 individuals. Final analyses were restricted to nine individuals, represented in 55 video trials. Five sub-adults contributed totals of four walk and 32 run video trials and four adult males contributed totals of three walk and 16 run video trials (Table 3.1).

3.2 Gait plot parameters

Gaits used by NZ sea lions were deduced from APS analysis from the relationship between limb lag and speed (Fig. 3.1A). Two gaits were detected, a walk and a run (Fig. 3.1B). The walk was a lateral walk, denoted by fore lag and hind lag equal to 50% and pair lag greater than 50% (Table 3.2). The run gait was a transverse gallop, denoted by fore lag and hind lag less than 50% (Table 3.2). The transverse gallop limbs lift off and touch down are depicted in a photographic sequence in Fig. 3.2.

The means for the hind gaps ($\overline{HG} = 0.36$, $SD = 0.11$) and means for the fore gaps ($\overline{FG} = 0.40$, $SD = 0.08$) for the walk gait were not significantly different ($n = 7$, $p = 0.058$) while the mean gaps ($\overline{HG} = 0.23$, $SD = 0.06$, $\overline{FG} = 0.49$, $SD = 0.15$) for the run gait were significantly different ($n = 48$, $p = 0.000$). The fore gaps in relation to speed for the run gait showed a positive linear correlation ($FG = 0.13 + 0.32u$, $r^2 = 0.545$, $p < 0.001$); the hind gaps had no significant correlation to speed ($r^2 = 0.041$, $p = 0.166$) and appeared constant, $HG = 0.23$ ($SD = 0.08$, Fig. 3.3).

Table 3.1. Measures for the five sub-adult and four adult male New Zealand sea lions used in this study

Individual code	Height (m)			Age class	Length (m)	Walk gait			Run gait		
	Withers H_w	Shoulder H_s	Hip H_h			Video trials n	Range speed u (ms^{-1})	Range Froude number (Fr)	Video trials n	Range speed u (ms^{-1})	Range Froude number (Fr)
A	0.55	0.48	0.33	Sub-adult	1.65	0	-	-	2	1.55-1.69	0.52-0.57
B	0.59	0.47	0.32	Sub-adult	1.66	0	-	-	3	1.18-2.15	0.27-0.93
C	0.57	0.48	0.34	Sub-adult	1.92	2	0.78-0.93	0.14-0.17	7	1.14-1.98	0.27-0.82
D	0.69	0.58	0.41	Sub-adult	1.97	1	0.49	0.04	13	1.54-2.44	0.36-1.01
E	0.66	0.55	0.35	Sub-adult	2.02	1	0.58	0.06	7	1.57-2.41	0.47-1.02
F	0.73	0.56	0.38	Adult	2.05	2	0.38-0.40	0.03-0.03	0	-	-
G	0.80	0.59	0.44	Adult	2.15	0	-	-	6	1.78-2.29	0.52-0.89
H	0.77	0.62	0.42	Adult	2.17	0	-	-	7	1.43-2.37	0.33-0.99
I	0.84	0.67	0.45	Adult	2.29	1	0.65	0.06	3	1.55-2.51	0.36-0.87

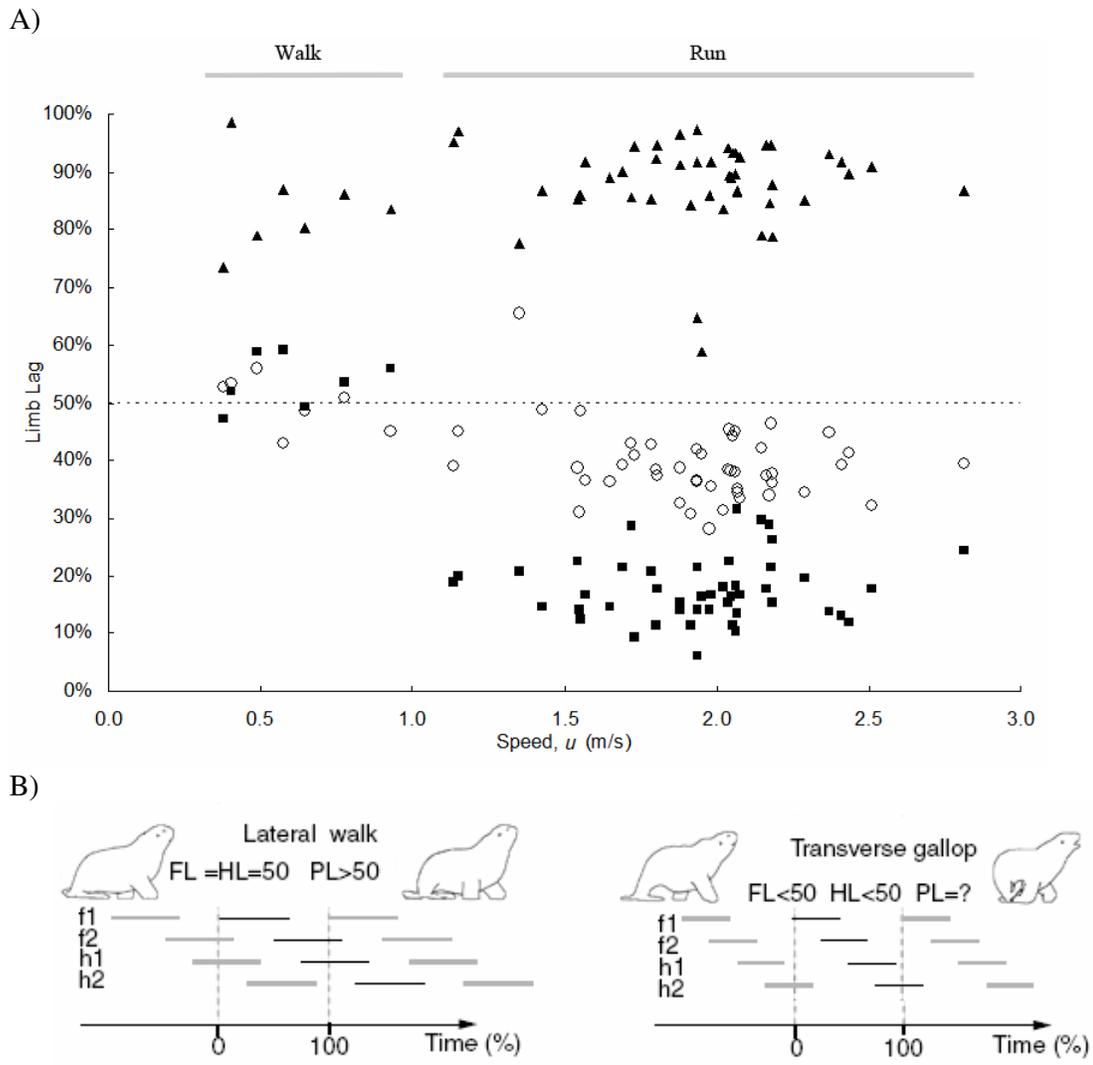


Fig. 3.1. Designation of gaits used by male New Zealand sea lions deduced from APS method. A) Relationship between limb lag and speed. Three categories of limb lag are plotted from 55 video trials: fore lag (FL, open circles) is the duration between the contact of forelimb 1 and the subsequent contact of forelimb 2, hind lag (HL, closed squares) is the duration between hindlimb 1 and hindlimb 2 and pair lag (PL, closed triangles) is the duration between the contact of forelimb 1 and hindlimb 1, plotted against speed. Fore lag and hind lag equal to 50% and a pair lag greater than 50% denotes a lateral walk and a fore lag and hind lag less than 50% denotes a transverse gallop (Abourachid, 2007). B) Gait plots for the two gaits used by the NZ sea lion created by plotting time versus duty factor for each limb (f1=forelimb 1, f2=forelimb 2, h1=hindlimb1, h2=hindlimb 2).

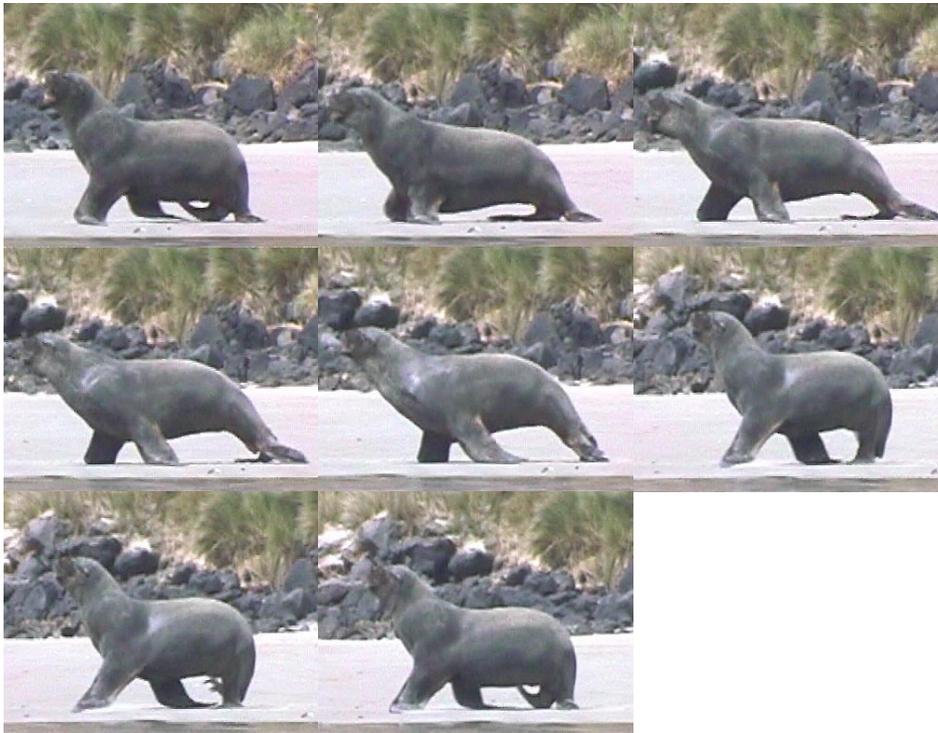


Fig. 3.2. Photographic sequence of a transverse gallop for Subject B. Each sequence is a lift off or touch down of a limb. The sequence starts with touch down of forelimb 1, lift off of hindlimb 1, touch down of forelimb 2, lift off of forelimb 1, lift off of hindlimb 2, touch down of hindlimb 1, lift off of forelimb 2 and the final image is the touch down of hindlimb 2.

Table 3.2. Comparisons of measured limb lag against 50%, the value that delineates gait type in the APS method. *HL* = hind lag, *FL* = fore lag and *PL* = pair lag.

Limb lag and gait type	<i>n</i>	Mean	SD	95% CI	ANOVA F-value	p-value	Outcome
<i>HL</i> walk	7	0.54	0.047	0.1	4.41	0.058	same
<i>FL</i> walk	7	0.50	0.047	0.04	0.00	1.000	same
<i>PL</i> walk	7	0.84	0.080	0.05	129.23	< 0.001	higher
<i>FL</i> run	48	0.39	0.02	0.04	154	< 0.001	lower
<i>HL</i> run	48	0.17	0.02	0.04	1592.85	< 0.001	lower

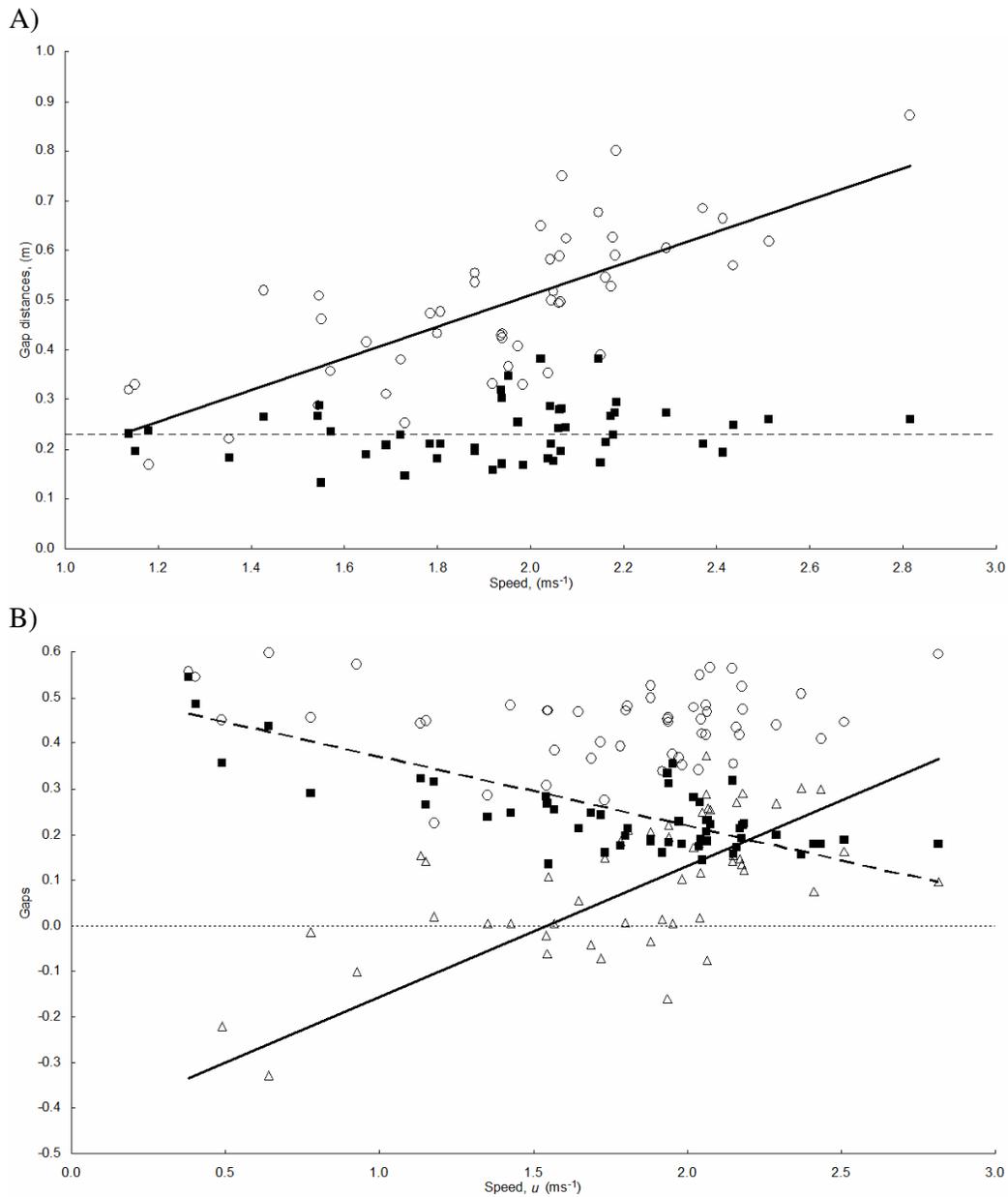


Fig. 3.3. Gap distances and gaps used to quantify spatial coordination in the APS method for 48 run gait video trials. A) Distance between forelimb contacts (open circles) and speed showing a positive linear regression (solid line). Hindlimb contacts (closed squares) plotted against speed as a constant (dashed line). B) Hind gap (closed squares) showed a linear decrease with speed (dashed line) while fore gap (open circles) appeared constant. Pair gap (closed triangles) increases linearly with speed (solid line).

3.3 Stride length and stride frequency

The run gait video trials analyzed for eight individuals (Table 3.1) included three parameters with dimensionized and dimensionless counterparts: speed, stride length and stride frequency. Running speed ($u = 0.59 + 1.92H_w$, $r^2 = 0.776$, $p = 0.004$; Fig. 3.4A) and stride length ($L = 0.11 + 1.42H_w$, $r^2 = 0.844$, $p = 0.001$; Fig. 3.4B) each showed linear increases with size. Stride frequency was not significantly correlated to withers height ($r^2 = 0.485$, $p = 0.055$) and appeared constant, $F = 1.78$ ($SD = 0.11$, Fig. 3.4C). None of the dimensionless counterparts were correlated to the size of the individuals (Fig. 3.4).

Stride frequency (F) increased in a logarithmic curve with speed (Fig. 3.5A) with a diminished effect of speed on F beyond 1.5 m/s at which point F appeared constant $F(u > 1.5) = 1.82$ ($n = 43$, $SD = 0.17$, Fig. 3.3). Stride length had a positive linear relationship with speed (Fig. 3.5, Table 3.3). Dimensionless stride length (\hat{L}) had a positive linear relationship to dimensionless speed (\hat{u}) and dimensionless stride frequency (\hat{F}) had a positive logarithmic relationship to \hat{u} (Fig. 3.5) as with L and F (Table 3.3). \hat{F} also shows a decrease in the effect of \hat{u} on \hat{F} at a $\hat{u} > 0.7$ at which point \hat{F} appeared constant $\hat{F}(\hat{u} > 0.7) = 0.44$ ($n = 40$, $SD = 0.03$).

The ANOVA analysis of the means of the adult and sub-adult age class for L showed they were significantly different from each other (Table 3.4). ANCOVA analysis of L by age class showed that for both groups correlation to speed and the x-intercept were significantly different while the slopes were not significantly different (Fig. 3.6A).

For F the ANOVA test of the means by age class were also significantly different.

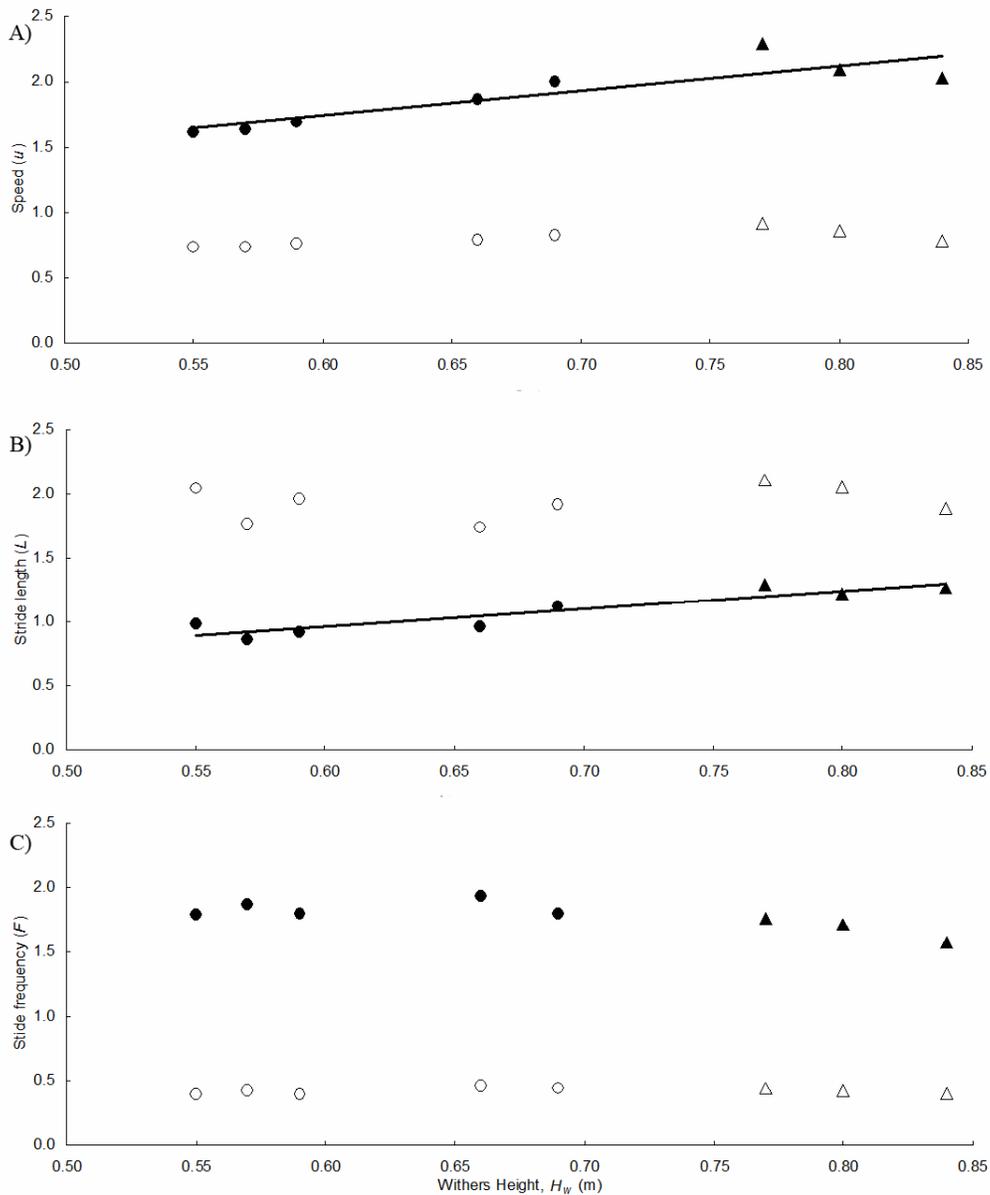
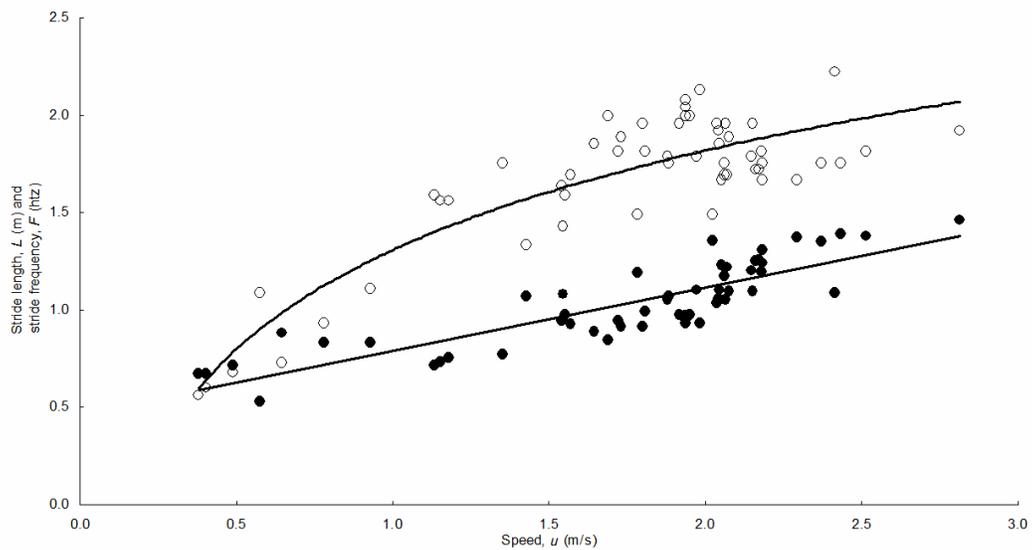


Fig. 3.4. Comparison of averaged parameters for the eight New Zealand sea lions with ≥ 1 run video trial plotted against the withers height as an indicator of size. Dimensionalized parameters are closed symbols and dimensionless parameters are open symbols, circles represent five sub-adults and triangles represent three adults. A) Speed for each subject for both dimensionless speed (\hat{u}) and speed (u) showing a positive correlation for u and no correlation for \hat{u} . B) Stride length (L) with a positive correlation to size and relative stride length (\hat{L}) showing no correlation. C) Stride frequency (F) and dimensionless stride frequency (\hat{F}) has no correlation to size.

A)



B)

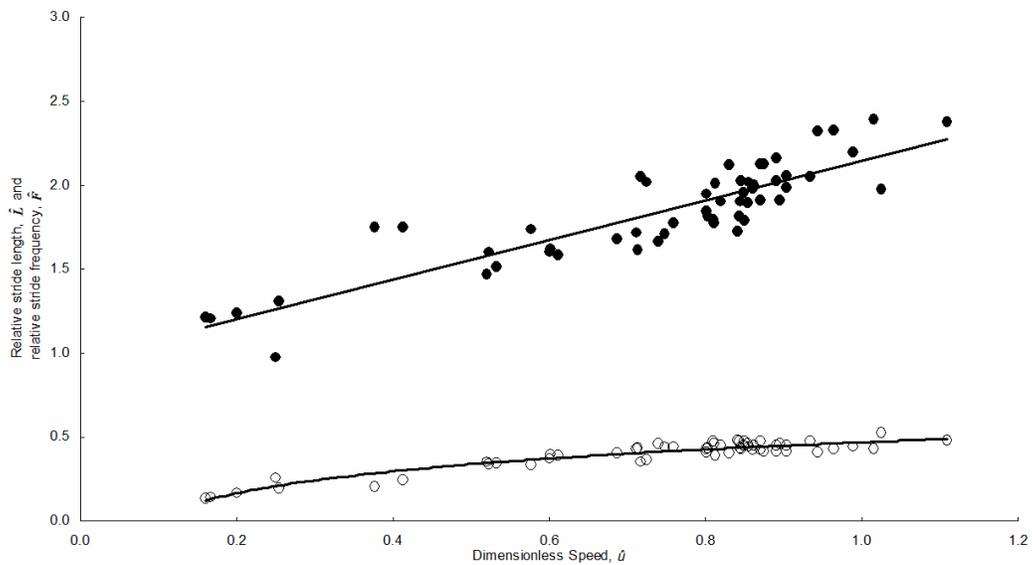


Fig. 3.5. The two components of speed, stride frequency and stride length, dimensionized and dimensionless for all 55 video trials from New Zealand sea lions. A) Stride frequency, (open circles, logarithmic curve) and stride length, (closed circles, straight line) plotted against speed. B) Dimensionless stride frequency (open circles, logarithmic curve) and dimensionless stride length (closed circles, straight line), plotted against dimensionless speed.

Table 3.3. Least squares best fit regression equations for all parameters from all 55 run and walk video trials of New Zealand sea lions.

Dependent	Independent	a (95% C.I.)	b (95% CI)	r^2	Curve fit type
Walk and run video trials					
F (Hz)	u (55)	1.31 (0.07)	0.74 (0.11)	0.786	Logarithmic
L (m)	u (55)	0.47 (0.10)	0.32 (0.05)	0.728	Linear
\hat{F}	\hat{u} (55)	0.47 (0.01)	0.19 (0.02)	0.889	Logarithmic
\hat{L}_s	\hat{u} (55)	0.98 (0.14)	1.17 (0.18)	0.766	Linear
t_{st} (s)	\hat{u} (55)	0.26 (0.01)	-0.86 (0.04)	0.958	Power
t_{sw} (s)	\hat{u} (55)	0.24 (0.01)	-0.30 (0.07)	0.489	Power
β	\hat{u} (55)	0.77 (0.03)	-0.26 (0.04)	0.742	Linear
β_f	\hat{u} (55)	0.56 (0.01)	-0.12 (0.02)	0.723	Linear
β_h	\hat{u} (55)	0.49 (0.02)	-0.16 (0.04)	0.622	Linear
D_{ratio}	\hat{u} (55)	0.56 (0.03)	-0.21 (0.05)	0.597	Linear

a and b values for the equations; linear: $y=a+bx$, Logarithmic: $y=a+b(\ln(x))$, power: $y=ax^b$. $\ln =$ natural log

Table. 3.4. ANOVA results for comparisons parameters between adult and sub-adult New Zealand sea lions.

Stride Parameter	<i>n</i>	Mean	0.95 CI	ANOVA <i>F</i> -value	<i>p</i> -value
Stride length					
Adult	19	1.17	0.10	14.49	0.000
Sub-adult	36	0.97	0.06		
Stride frequency					
Adult	19	1.52	0.19	4.73	0.034
Sub-adults	36	1.74	0.11		
Dimensionless stride length					
Adult	19	1.90	0.16	1.35	0.250
Sub-adult	36	1.80	0.09		
Dimensionless stride frequency					
Adult	19	0.38	0.05	1.1	0.299
Sub-adult	36	0.41	0.03		
Swing duration					
Adult	19	0.31	0.02	11.49	0.001
Sub-adult	36	0.25	0.02		
Stance duration					
Adult	19	0.47	0.15	2.29	0.136
Sub-adult	36	0.37	0.05		
Duty factor					
Adult	19	0.56	0.04	1.09	0.301
Sub-adult	36	0.58	0.02		
Average duration					
Stance	8	0.32	0.01	27.84	0.000
Swing	8	0.26	0.02		
Average $\beta f:h$					
Walking	5	1.06	0.05	2.67	0.130
Running	8	1.11	0.05		

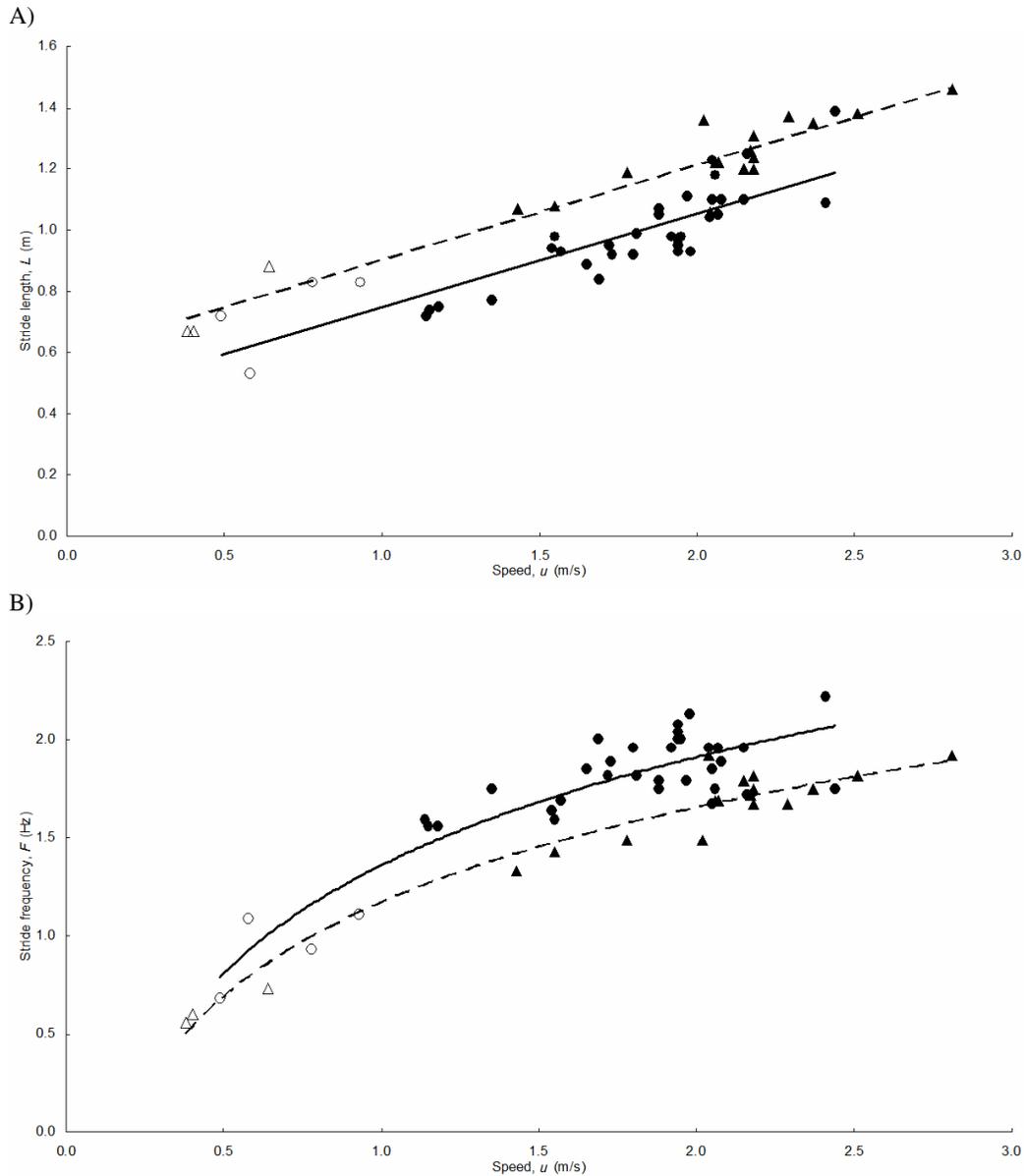


Fig. 3.6. Relationship of stride length and stride frequency for adults (walk = open triangles, run = closed triangles) and sub-adults (walk = open circles, run = closed circles) age classes versus speed (u). A) Stride length (L): age classes as a variable had a significant effect on the correlation L versus u , the elevations were significantly different and the slopes were not significantly different. B) Stride frequency (F): age class as a variable had a significant effect on the correlation of F versus u , the elevations were significantly different and the slopes were not significantly different.

The natural-log-transformed dependent and independent variables for F run through the ANCOVA analysis found the age classes had significantly different correlations from speed and significantly different elevations while the slope was not significantly different (Fig. 3.6B). ANOVA and ANCOVA analysis of adult and sub-adult age classes for \hat{L} and \hat{F} showed no significant difference among means, age class correlation to \hat{u} , elevation or slope for combined walk and run gaits or just run gaits. (Table 3.5)

3.4 Swing and stance duration

The stance (t_{st}) and the swing times (t_{sw}) both decreased in a power relationship with \hat{u} (Fig 3.7A). When the walk and run gaits were analyzed separately, the t_{st} and the t_{sw} of the walk gaits were both significantly correlated with \hat{u} by a power regression (Fig. 3.7B). For the run gait, the relationship between t_{st} and \hat{u} was best delineated by a power regression; t_{sw} did not show any significant change with \hat{u} so was delineated by a mean $t_{sw} = 0.32$ ($n = 48$, $SD = 0.05$) (Table 3.3).

ANOVA showed the swing duration by age class means to be significantly different. When examining the mean of stance duration by age class the ANOVA test showed no significant difference (Table 3.5). When stance and swing duration were related to withers height (H_w) as a representation of size, only swing duration had a significant correlation. When swing duration is examined by the hindlimb and forelimb pairs both appear to have a positive correlation but only the hindlimb swing is significant (hind $t_{sw} = 0.05 + 0.32H_w$, $r^2 = 0.778$, $n = 8$, $p = 0.004$) (Fig. 3.8).

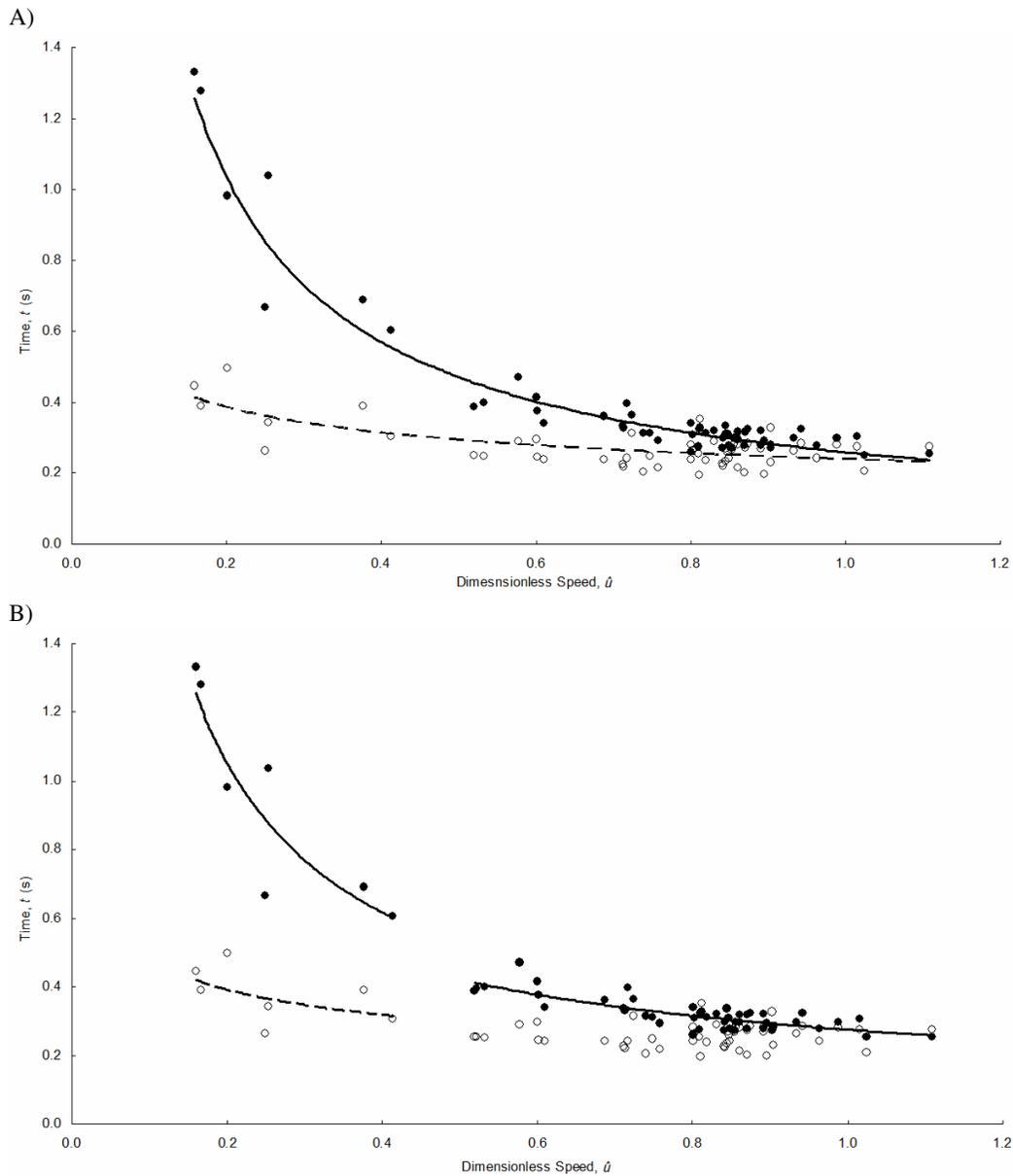


Fig. 3.7. Stance duration (closed circles) and swing duration (open circles) plotted against dimensionless speed for the seven walk (speed < 0.45 m/s) and 48 run (speed > 0.45 m/s) video trials. A) Power regression of best fit across all 55 video trials B) Separate analysis for walk and run gait. For the walk gait, both delineated by a power regression. For the run gait, the relationship for stance duration is delineated by a power regression and for the swing duration by the recorded mean as no significant relationship was found.

Table 3.5. Least squares best fit regression equations for 19 adult and 36 sub-adult parameters for both walk and run video trials

Dependent	Independent(<i>n</i>)	a (95% CI)	b (95% CI)	r^2	Curve fit type
Adult subjects run and walk video trials					
L (m)	u (19)	0.59 (0.10)	0.31 (0.05)	0.912	Linear
F (Hz)	u (19)	1.17 (0.06)	0.70 (0.08)	0.950	Logarithmic
\hat{L}_s	\hat{u} (19)	0.99 (0.13)	1.22 (0.16)	0.936	Linear
\hat{F}	\hat{u} (19)	0.45 (0.01)	0.18 (0.02)	0.952	Logarithmic
t_{st} (s)	\hat{u} (19)	0.28 (0.02)	-0.87 (0.04)	0.989	Power
t_{sw} (s)	\hat{u} (19)	0.27 (0.02)	-0.22 (0.06)	0.717	Power
β	\hat{u} (19)	0.84 (0.04)	-0.32 (0.05)	0.903	Linear
Sub-adult subjects walk and run trials					
L (m)	u (36)	0.44 (0.11)	0.31 (0.06)	0.736	Linear
F (Hz)	u (36)	1.36 (0.08)	0.80 (0.14)	0.802	Logarithmic
\hat{L}_s	\hat{u} (36)	0.97 (0.21)	1.13 (0.27)	0.678	Linear
\hat{F}	\hat{u} (36)	0.48 (0.02)	0.20 (0.03)	0.835	Logarithmic
t_{st} (s)	\hat{u} (36)	0.26 (0.02)	-0.79 (0.07)	0.917	Power
t_{sw} (s)	\hat{u} (36)	0.22 (0.02)	-0.39 (0.04)	0.522	Power
β	\hat{u} (36)	0.73 (0.04)	-0.20 (0.06)	0.606	Linear
a and b values for the equations; linear: $y=a+bx$, Logarithmic: $y=a+b(\ln(x))$, power: $y=ax^b$. ln = natural log					

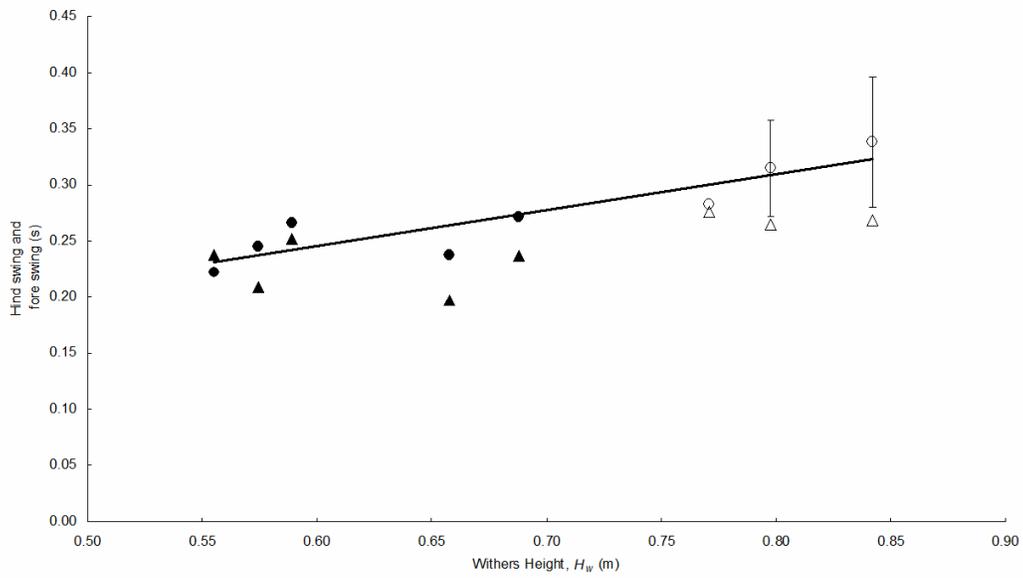


Fig. 3.8. Hind swing (circles) and fore swing (triangles) durations plotted against withers height as an indicator of size. Only the average hind swing time (t_{sw}) has a significant linear relationship (solid line). Each point represents an individual NZ sea lion, closed symbols represent sub-adults and open symbols are adults.

3.5 Duty factor

Duty factor (β) has a negative linear correlation with \hat{u} (Fig. 3.9). The recorded aerial phases all occurred close to a duty factor of 50% (45-57%) but were restricted to a \hat{u} of 0.75-0.90 within a range in \hat{u} of 0.16-1.11 and so there was no minimum duty factor after which all or most trials recorded an aerial phase.

The ANOVA test of the fore duty factor (β_f) and hind duty factor (β_h) showed the means were significantly different for the walk and run gaits combined and for the run gait alone but not significantly different for the walk gait alone (Table 3.6). When the fore and hind limb duty factor was plotted against speed both had a linear relationship with dimensionless speed. The ANCOVA analysis showed that for both groups' hind and fore limb duty factor had a significantly different effect on the correlation and the slopes were significantly different (Fig. 3.10).

The mean of the ratio of fore to hind limb duty factor ($B_{f:h}$) mean $B_{f:h} = 1.11$ ($n = 55$, $SD = 0.10$) and was significantly different from 1.00 ($p < 0.001$), where a $B_{f:h} = 1.00$ represented an even distribution between fore and hind duty factors (Fig 3.11). ANOVA tests of the duty factors of the forelimbs as designated for the APS method on lead (f1) or trail (f2) showed a significant difference in means while forelimbs designated as left or right showed no significant difference (Table 3.6).

When the $\beta_{f:h}$ was split into adult and sub-adult the ANOVA shows the means were not significantly different and the ANCOVA shows the adult and sub-adult age class did not have a significantly different correlation to \hat{u} . When comparing the subject average $\beta_{f:h}$ to the subjects H_w , a strong positive linear correlation emerged for the run

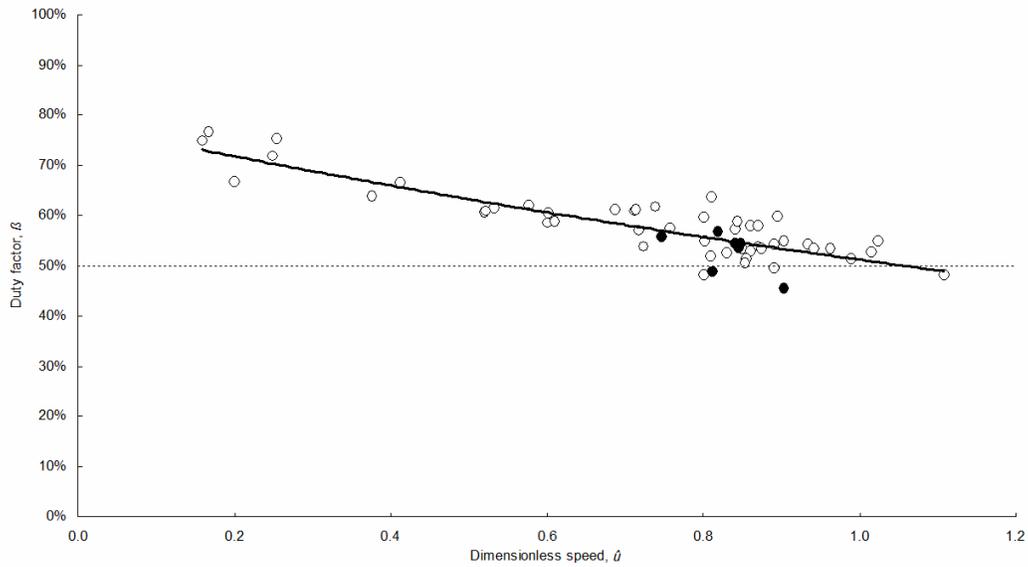


Fig 3.9. The relationship between duty factor (the ratio of average limb contact duration and stride duration) and dimensionless speed for all 55 video trials for New Zealand sea lions delineated by a linear regression of best fit (solid line). Seven trials included aerial phases with all four limbs simultaneously off the ground (closed circles). Delimitation between walk and run gaits theoretically occurs at a duty factor = 50% (horizontal dotted line) or a Dimensionless speed > 1.00

Table 3.6. ANOVA results for comparisons of parameters between duty factor for limbs and limb pairs

Stride Parameter	n	Mean	0.95 C.I	F-value	p-value
Walk gait and run gait					
β_{fl}	55	0.60	0.02	18.42	0.000
β_{hl}	55	0.55	0.02		
Walk gait					
β_f	7	0.73	0.05	2.18	0.165
β_h	7	0.69	0.04		
Run gait					
β_f	48	0.59	0.01	38.27	0.000
β_h	48	0.61	0.02		
Run gait					
β_{f1}	48	0.60	0.01	5.55	0.021
β_{f2}	48	0.57	0.01		
β_{rf}	48	0.57	0.01	3.34	0.066
β_{rl}	48	0.59	0.01		

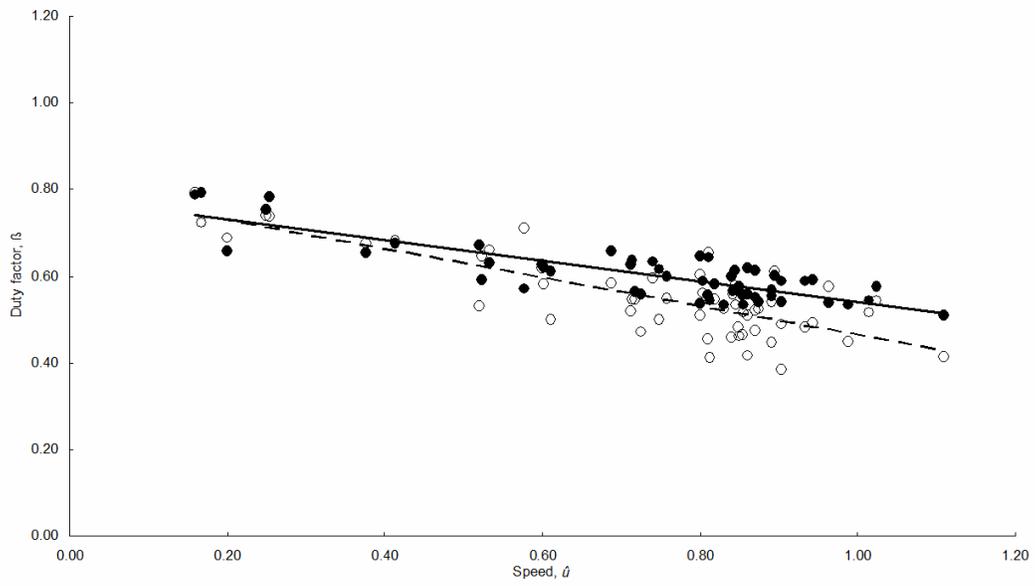


Fig. 3.10. Relationship between fore duty factor (solid circles, solid line) and hind duty factor (open circles, dashed line) and speed, delineated by linear regression of best fit showing a negative correlation.

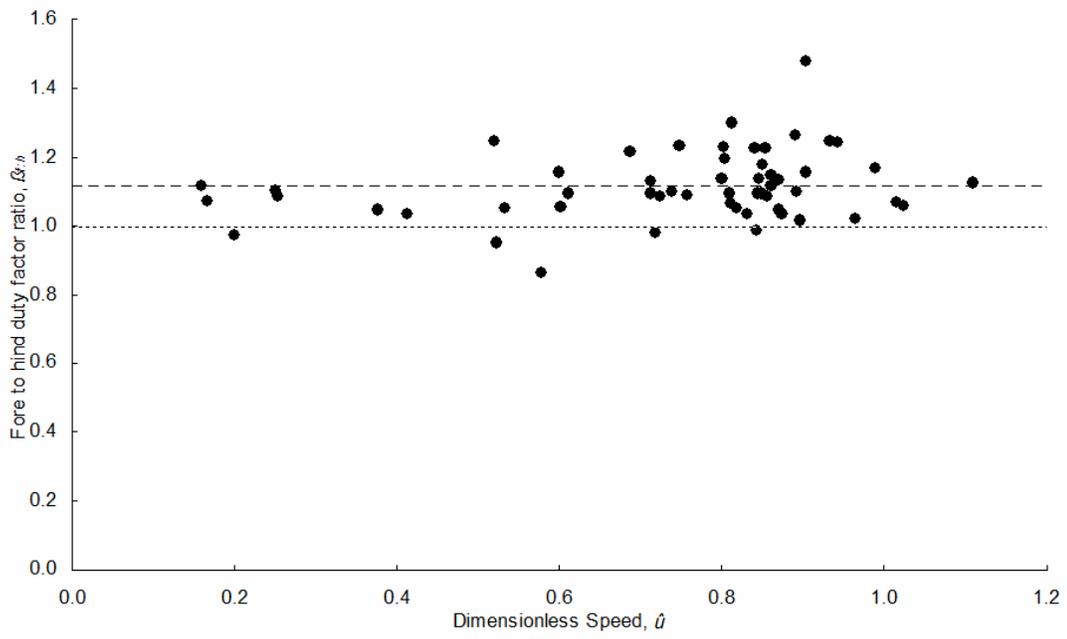


Fig. 3.11. Forelimb to hindlimb duty factor ratio ($\beta_{f:h}$) plotted against dimensionless speed (\hat{u}) with a mean equal to 1.11 (dashed line) and standard deviation of 0.10 and an even distribution of duty factor at 1.00 (dotted line).

gait while the walk gait had no correlation (Fig. 3.12). The ANOVA of the walk and run gait means showed no significant difference between the two gait type's means. ANCOVA analysis revealed no significant effect of the gaits on \hat{u} or their slope or their intercept.

3.6 Sagittal flexion

The flexion minimum to maximum ratio D_{ratio} showed a negative logarithmic correlation to \hat{u} (Fig. 3.13, Table 3.3). When divided into adults and sub-adults groups the ANOVA of the groups mean showed no significant difference and the ANCOVA regression analysis showed the groups correlation to \hat{u} were not significantly different. A comparison of the distance between withers and base of tail with height of withers, shoulder, hip and tail base all in relationship to time and the foot contact pattern over two strides is shown in Fig. 3.14. Here the graph shows that the flexion is at its greatest at the transition from the trail forelimb (f2) to the lead forelimb (f1) and at its least at the transition from the lead (f1) to trail (f2) forelimb. Lastly a comparison of the average D_{ratio} in relationship to withers height as a representation of subject size can be made for both walk and run (Fig 3.15). The run gait has a significant negative linear correlation between D_{ratio} while the walk gait correlation is not significant. ANOVA analysis shows the means to be significantly different and the ANCOVA shows the age class has a significant effect on the correlation to \hat{u} and the elevation and the slopes are not significantly different.

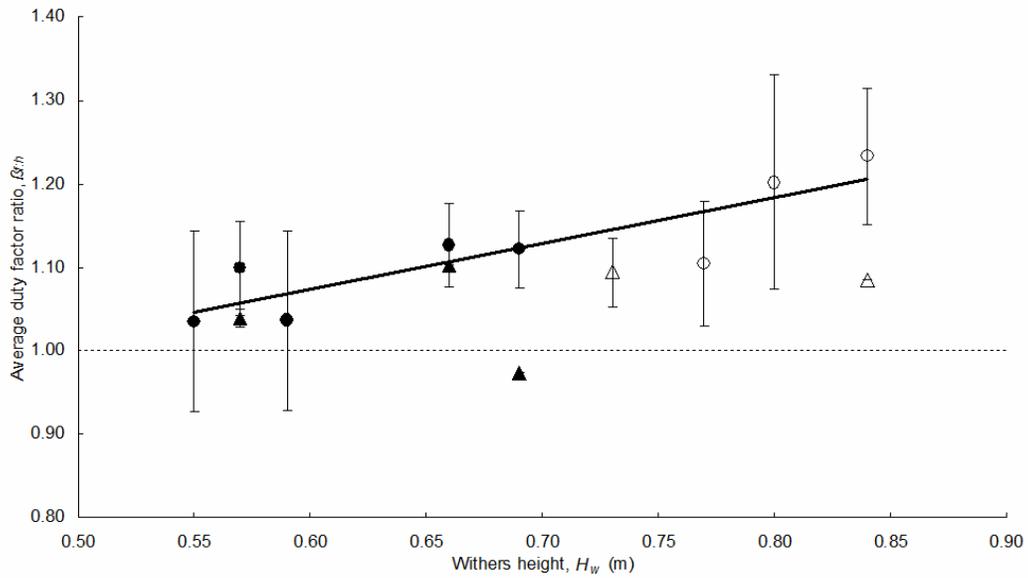


Fig. 3.12. Relationship between forelimb to hindlimb duty factor ratio ($\beta_{f:h}$) and withers height of male New Zealand sea lions. Each point represents one subject's (n=9) ratio averaged for all run gaits (circles, 48 runs) and walk gaits (triangles, 7 walks). Error bars represent 95% CI for each individuals video trials, closed symbols are sub-adults and open symbols are adults. Solid line represents least squares best fit for the run trials, the walk trials showed no significant correlation. Withers height is used to represent size change. Dotted line represents an even ratio of forelimb to hindlimb duty factor.

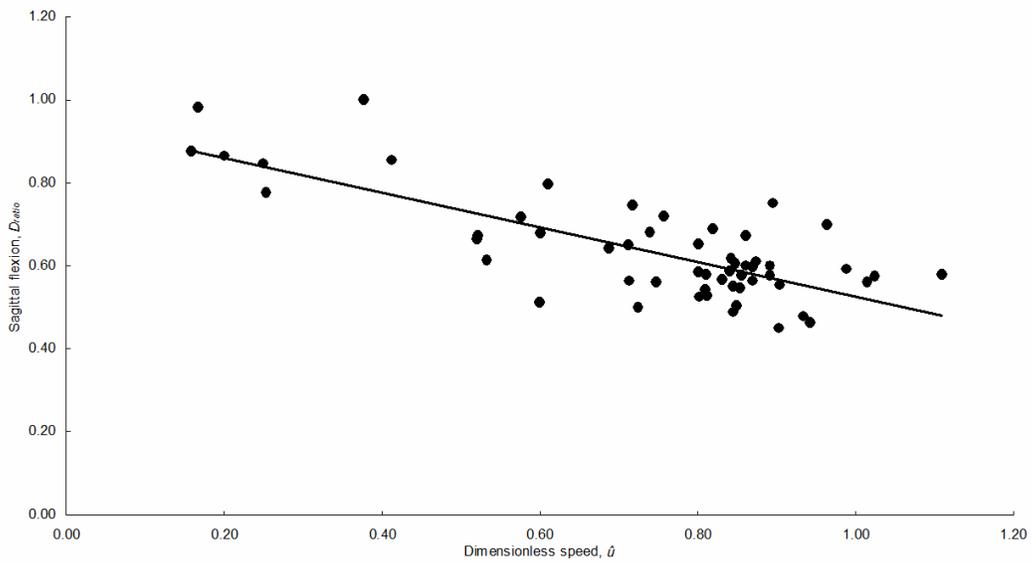


Fig. 3.13. The relationship between sagittal flexion and dimensionless speed with the least squares best fit delineated by the solid line showing a negative correlation.

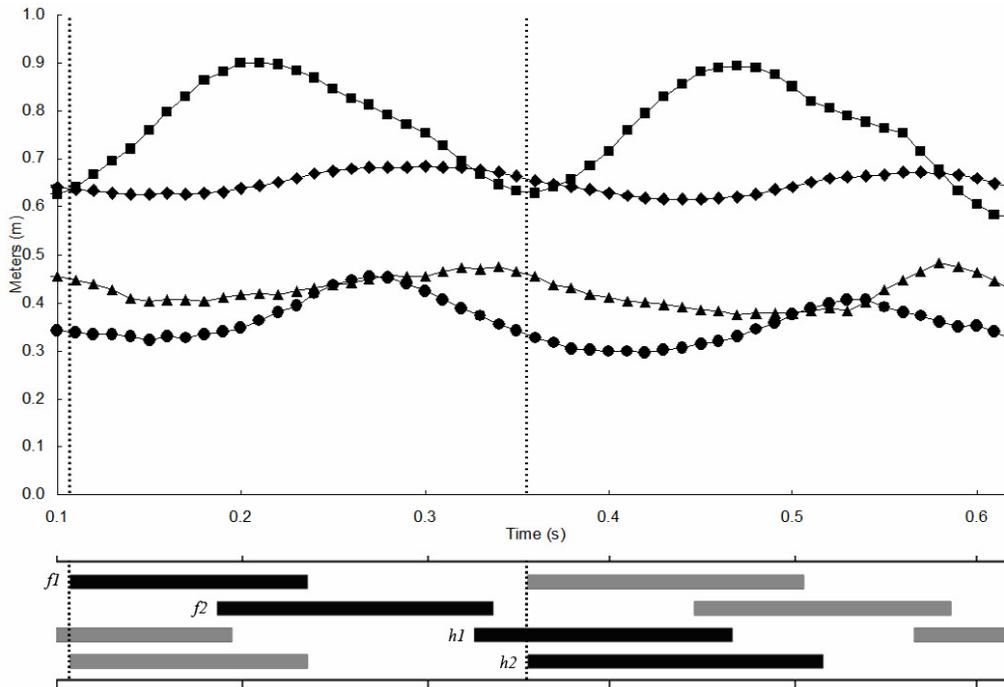


Fig. 3.14. Comparison of body movements to foot fall pattern for one video trial encompassing two strides of subject A (Table 3.1). A) Relationship of body movement to action of the feet over two strides the distance between the withers and the tail (squares, D_{wt}) along with wither height (diamonds, H_w) shoulder height (circles, H_s) and hip height (triangles, H_h) to foot placement B) Black bars are the progression of one stride by APS definition; vertical dotted line represents one stride length. Each bar represents the duration of a pedal extremity in contact with the ground, top bar is forelimb 1 (f1), second is forelimb 2 (f2), third is hindlimb 1 (h1) and fourth is hindlimb 2 (h2), f1 and h2 are ipsilateral by definition. Flexion is greatest at the f2 to f1 transition and at its least at the f1 to f2 transition. All data represent 0.05 s running averages.

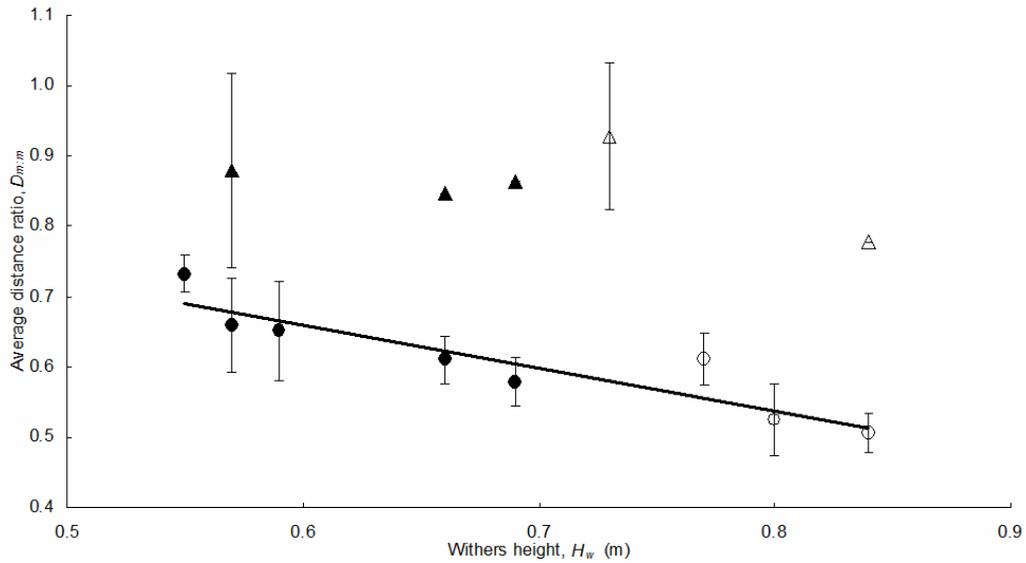


Fig. 3.15. Average withers to tail distance (D_{wt}) ratio with the shortest distance as a ratio of the longest distance ($D_{m:m} = \min D_{wt} / \max D_{wt}$) versus withers height (H_w) used as an indication of relative size. Circles represent runs with closed circles for subadults and open for adults, triangles represent walk gaits with closed triangles for subadults and open for adults. Smaller withers to tail flexion ratio indicate greater flexion. Solid line is the least square linear fit for the run gaits with a negative linear correlation to size. The walk did not have a significant correlation to size. An ANOVA analysis of the walk to run means found them to be significantly different. Error bars represent 95% confidence intervals for the trials of each subject.

Chapter 4: Discussion

4.1 Overview

When traversing a terrestrial environment NZ sea lion employ typical energy-saving strategies but at lower speeds than their fully-terrestrial counterparts. Their strategies include gait changes, increased stride length and stride frequency, reduced duty factor, and the use of sagittal flexion (Hildebrand, 1976; Alexander and Jayes, 1983; Alexander, 1989; Alexander, 2003). Stride length, associated gaps, stride frequency, stance and swing duration all follow normal patterns of terrestrial locomotors but occur and maintain at lower speeds. Duty factor is reduced as speeds increase but again at overall lower speeds than a similar terrestrial locomotor. The fore-to-hind duty factor ratio increases with the size of individuals, as do fore gap distances and swing duration. Sagittal flexion is employed, with greater flexion at both higher speeds and in larger individuals. These factors combined to allowed one NZ sea lion in this study to achieve a moderate top speed of 2.8 ms^{-1} or about 75% of expected maximum speed using Alexander and Jayes (1983) model, (but both the mass and the lengths of NZ sea lions used for maximum speed calculation were unproven estimation techniques).

4.2 Morphological constraints and sagittal flexion

There are a few morphological constraints that the NZ sea lion must contend with in order to locomote on land. All limbs are reduced in length and the proximal elements (i.e. humerus in the fore limb) are enclosed within the torso, with both changes being more pronounced in the hind quarters (Beentjes, 1990). The hindlimbs are effectively constrained to one another down to the pes, while the forelimbs are only moderately constrained in the torso. The increase in the size of the forelimb manus is impressive

and adds mass to the limb, especially at the apex of the forelimbs, where it costs more energy to accelerate (Alexander, 2003). Added mass in the form of fat stores and a movement of the center of mass forward, closer to the forelimbs only adds to instability (English, 1976). All of these various influences impede the terrestrial effectiveness of the NZ sea lion.

The effect of the morphological constraints on the hindlimbs is illustrated in the gap parameters. The gap parameters give an indication of the contribution of hindlimb and forelimb pairs to the stride length as well as the coordination between limb pairs. It is immediately noticeable from the gap figure that the hind gap distance (HG_d) shows the hindlimbs are restrained to a set distance and hence contribute less to the over all stride length with increased speed as shown in the hind gap ratio (HG).

When gap distance parameters of NZ sea lions are compared to those recorded for dogs, the fore gap (FG) are similar while the pair gap (PG) is higher than the dogs' at speeds $> 1 \text{ ms}^{-1}$ (Fig. 4.1), while hindgap (HG) contributes less as speed increases. HG_d measures the distance between the contact of h1 and h2 so any difference between HG_d and FG_d must be made up in the contact distance of h2 to h1 or the hindlimbs will end up being dragged. The swing measurements can illustrate this made-up distance, though swing duration is static in relation to speed the mean of hind swing duration is greater than the mean of fore swing duration.

Any imbalance in the swing and stance time should appear in the duty factor and this can be seen in the forelimb to hindlimb duty factor ratio (β_{ratio}) in relation to speed. Biewener (1983) tested the duty factor ratio of several different mammals over three

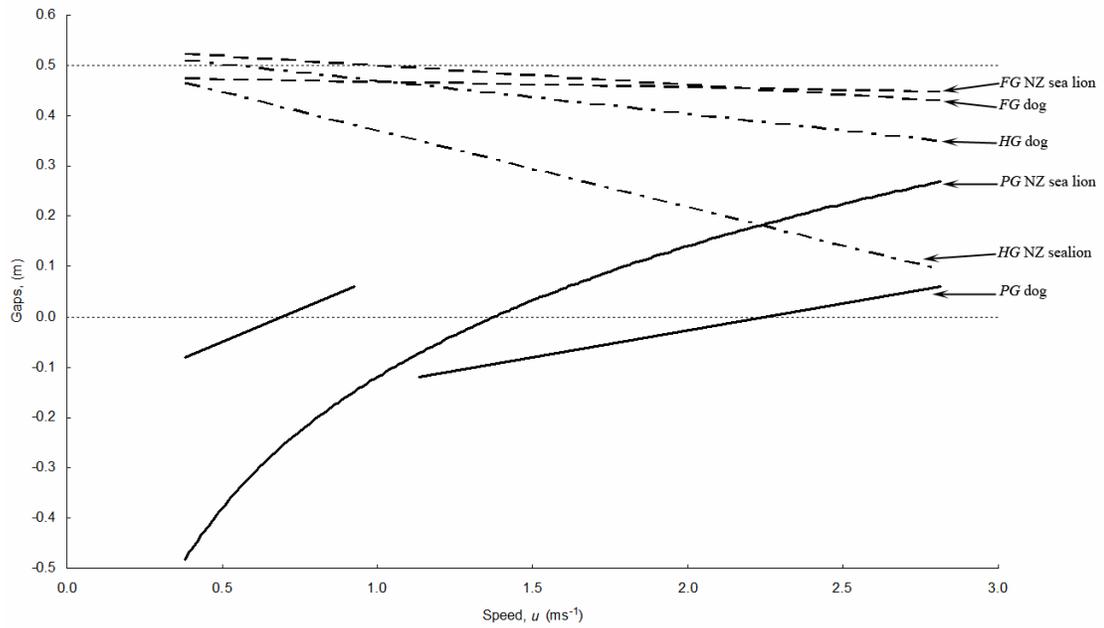


Fig 4.1. Measured gaps for the NZ sea lion least squares best fit are graphed alongside the calculated models for dogs from Maes (2007). Solid line is pair gap (PG), dotted line is fore gap (FG) and dashed dotted is hind gap (HG).

gaits, the walk, trot and run. To this a dog (*Canis familiaris*; Maes 2007) and a bat (*Desmodus rotundus*; Riskin et al. 2006) were added along with an average of the adults and sub-adults for comparison (table 4.1) and the trot factors were removed. While all the cursorials have a duty factor ratio with a forelimb bias only the sea lion and the bat increase that ratio in the run gait. The simple explanation for the high β_{ratio} is the added mass at the forelimbs, but this does not address the further increase of the ratio when utilizing the run gait. Nor does it explain why the fore hind ratio shows an increase with the size of the individual. Lastly it ignores the similar morphological constraints on the hindlimbs of both bats and sea lions. For either hydrodynamic or aerodynamic reasons the results are the same, a reduction in size and a decrease in independent hindlimb mobility.

Sagittal flexion offers an alternate explanation to the HG_d FG_d gap issue while explaining the β_{ratio} . Flexing the back effectively increases the hip height allowing for a greater distance of forward limb swing this allows the hind limbs to strike the ground further forward than it normally would. The flexion has the added benefit of decreasing the distance between the shoulder and hips, combined these allow the sea lion to place its shortened hindlimbs past the lift off point of the forelimbs, increasing the stride length. The sagittal flexion resulted in a flexed to extended ratio of 60% (CI = 0.02) for the NZ sea lion compared to the horse with 87% and the cheetah with 67%, and even more impressive if just using the adult age class with a ratio of 57%.

The sagittal flexion also overcomes the disadvantage of the decreased hip height and the hindlimbs limited HG_d . The cross over of hindlimb pes contact to forelimb manus

Table 4.1. The ratio of fore to hind duty factor for the walk and run gait of 13 species ranging from a mass of 0.01 to 270 kg, (adapted from Biewener, 1983).

	Mass (kg)	Walks			Run				
		n_w	F:H	SD	n_r	F:H	SD	Fore L:T	Hind L:T
Mouse	0.01	1	0.82		4	0.77	0.05		
Bat	0.02	28	1.16		21	1.55			
Mouse	0.03	5	0.87	0.03	6	0.90	0.04		
Chipmunk	0.09	1	0.97		6	0.95	0.02		
Squirrel	0.15	1	0.96		13	0.95	0.03	0.98	0.99
Small dog	1.80	1	1.07		10	1.12	0.08	0.89	0.98
Large dog	27.0	5	0.99	0.01	9	0.96	0.04	0.98	0.95
Pony 1	110.0	4	1.00	0.01	6	0.96	0.02	0.96	0.97
Pony 2	140.0	1	1.02		6	0.93	0.04	0.96	0.91
SA NZSL	170.0	4	1.04	0.05	32	1.11	0.08	1.03	0.95
A NZSL	238.0	3	1.09	0.02	16	1.15	0.14	1.00	0.99
NZSL	188.0	7	1.06	0.05	48	1.12	0.12	1.02	0.97
Horse	270.0	4	1.08	0.02	7	0.95	0.03	0.97	0.98

F:H= to the fore to hind duty factor for the specified gait type. Fore and hind L:T is the duty factor ratio between the lead and trail limb for the specified limb pair. SA NZSL is the average of the sub-adult NZ sea lions with 5 individuals, A NZSL is the average of the adult NZ sea lions with 4 individuals and NZSL is the overall average for all 9 individuals. Some individual sea lions lacked a walk or a run video trial leading to discrepancies between total number and numbers for walks or runs

lift off is shown in positive numbers for the PG parameter. The effects are seen in the hindlimb swing durations increasing in relation to withers height (size) which has the added effect of lowering hindlimb duty factor and hence increasing β_{ratio} . The benefits of the sagittal flexion can be seen in other aspects of the gait parameters as well. The larger adult NZ sea lions are using a lower F at any given speed than the smaller sub-adults. Alexander (1977) showed that larger animals typically have slower F . If we take the logarithmic relationship of F to u to suggest that F is contributing less to speed, and a logistic curve suggests this is the case

$$(F = \frac{1.88}{(1 + e^{-2.69(x-0.69)})}, r^2 = 0.817, \text{ where the numerator is the asymptote}), \text{ then the}$$

stride length is the only means of increasing speed above 2.17 ms^{-1} . This trade off is seen as the adult NZ sea lions are using larger L at any given speed in comparison to the smaller sub-adults. The size increase of adult males alone could allow for an increased L , with longer limbs and a longer body. The problem is as HG_d only moderately increases in relation to the size of the sea lion it becomes a limiting factor on increased L . Sagittal flexion increases with both speed and size and as shown above may help to compensate for the limits of HG_d .

4.3 Cursorial versus non-cursorial modeled parameters

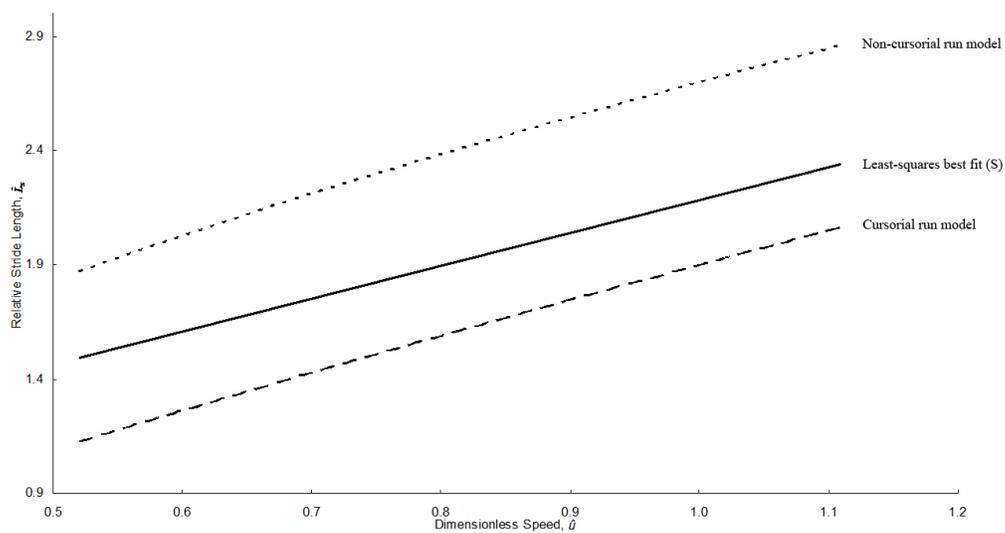
The dimensionless stride length (\hat{L}) should allow the comparison of any terrestrial runner regardless of size. The problem is two models exist: one for cursorial and one for non-cursorial animals (Alexander and Jayes, 1983). Deciding which the sea lion fits into is not straightforward. The ancestors of the sea lion could well be the mustelids (Sato et al., 2006; Rybczynski et al., 2009) which are non-cursorial. The hindlimbs are certainly bent but the forelimbs while not straight are essentially fixed

in height and are more prominently used in locomotion. The sheer size of the sea lion suggests cursorial. Comparing the NZ sea lions \hat{L} to the two models doesn't give a satisfying answer either as it trends right between the two models with the cursorial ($R^2 = -1.215, r^2 = 0.703$) being slightly closer than the non-cursorial ($R^2 = -3.962, r^2 = 0.703$) but neither model is a better fit than just applying the mean (as seen with the negative R^2 's (Fig. 4.2A).

When comparing the \hat{L} of the sea lion (Fig. 4.2B [S]) to the cursorial model the NZ sea lion appears to be using a higher \hat{L} than expected and hence using a larger stride length than expected for its shoulder height. The morphologically reduced hip height and the expected limb length for a fissioned are used to illustrate the effects of differing conversion factors on the \hat{L} . The hip height (Fig. 4.2B [H]; $R^2 = -30.977, r^2 = 0.682$), which is comparable to a small dog, would give the impression that the NZ sea lion is using L well above expected at a given speed. The fissioned ratio (Fig. 4.2B, [F]; $R^2 = -11.643, r^2 = 0.701$) gives an idea of what the L of a mammal of a similar length to the NZ sea lion would have in comparison showing the NZ sea lion is actually underperforming for its size.

At a given speed the non-cursorials and the sea lion are achieving a higher stride length to shoulder height ratio than the cursorials. Non-cursorials can typically increase their stride length by extending their bent limbs so the effective hip height underestimates their L compared to a cursorial mammal. Sea lions are likely using their longer body length in relation to shoulder height to achieve a greater \hat{L} in comparison to the expected \hat{L} for a cursorial mammals. The added length is not

A)



B)

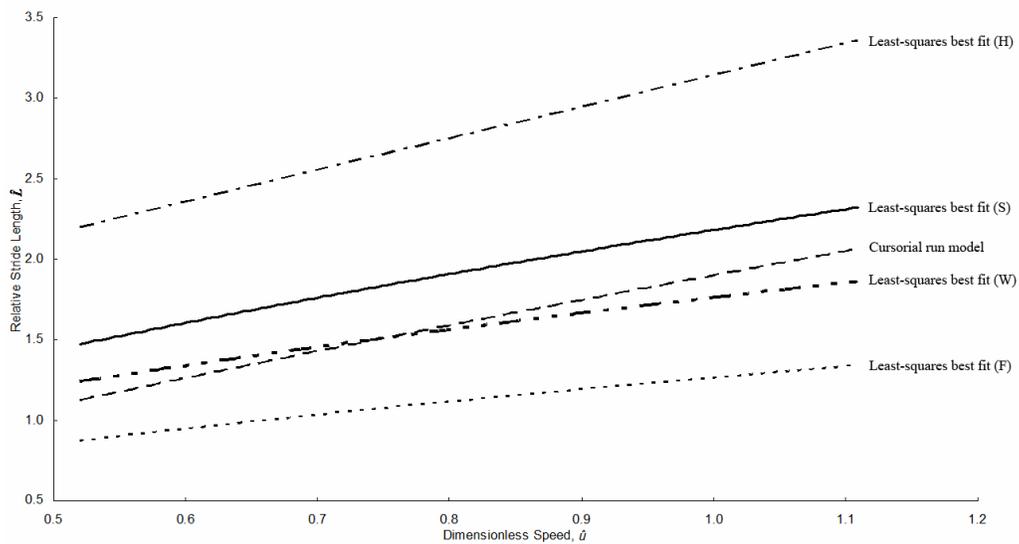


Fig 4.2. A) Dimensionless stride length (\hat{L}) versus dimensionless speed (\hat{u}) with the expected \hat{L} for cursorial and non-cursorial models. B) Model comparisons to measured data normalized using a variety of factors, (H) = hip height, (S) = shoulder height, (W) = withers height and (F) = is the expected forelimb length using a ratio of measured sea lion and fur seal forelimb length to the measured fissioned forelimb length equalized by body length (English, 1976b). \hat{L} calculated using a variety of constants used in the literature in comparison to the cursorial run model (solid line) developed by Alexander and Jayes (1983).

enough to make up for there shortened limbs when compared to that expected for its size (Fig. 4.2B [F]).

Stride frequency (F) is the second component of speed and dimensionless stride frequency (\hat{F}) allow for comparisons regardless of size. Using the small dog and otter (*Lontra canadensis*) shoulder height and stride frequency-to-speed equations from Williams et al., (2002) allows for a dimensionless comparison to the NZ sea lion. When the dog (cursorial) \hat{F} model is applied to NZ sea lion \hat{F} the fit is worse than the mean ($R^2 = -0.694$, $r^2 = 0.888$) while the otter (non-cursorial) \hat{F} model gives a pretty good fit to the data ($R^2 = 0.766$, $r^2 = 0.888$) it is clear that the sea lion \hat{F} is closer to the otter than the dog (Fig. 4.3).

As β is a dimensionless parameter we can compare the NZ sea lions duty factor to the expected for cursorial and non-cursorial mammals from another Alexander and Jayes (1983) model. In the walk gait the NZ sea lions consistently have a lower duty factor than expected for a cursorial or a non-cursorial (Fig. 4.4) and the hind and fore duty factors are almost indistinguishable. In the run gait the forelimbs are close to the non-cursorial model ($R^2 = 0.166$, $r^2 = 0.340$) and the cursorial is worse than fitting the mean ($R^2 = -0.877$, $r^2 = 0.340$) while the hind limbs are much lower than either of the models or the forelimbs.

That differences exist between cursorials and non-cursorials is apparent but a clear delineated transition is less obvious. Stien and Casinos (1997) approach the delineation problem by presenting a simple definition of cursorial runners. Using that

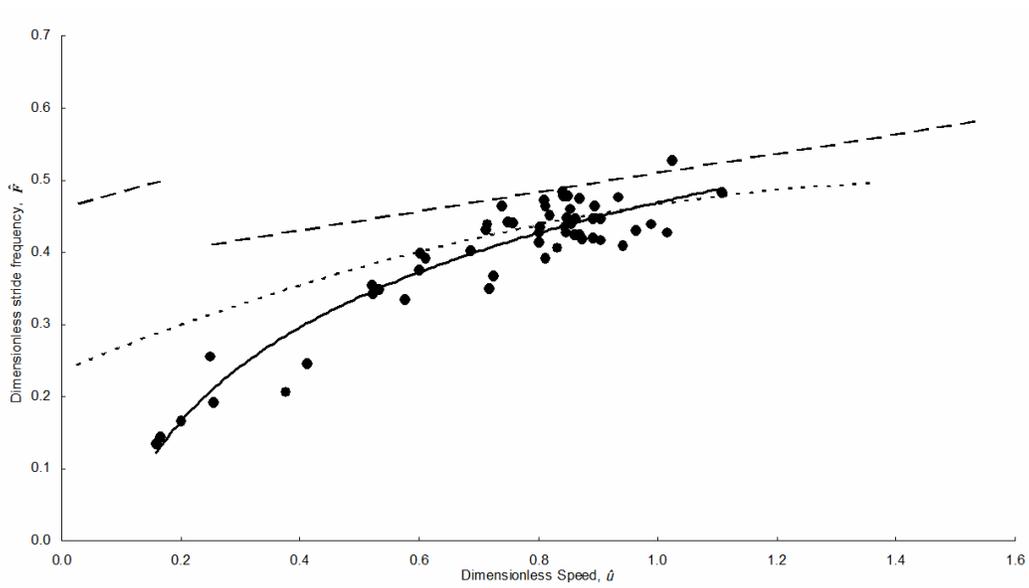


Fig. 4.3. Dimensionless stride frequency (\hat{F}) plotted against dimensionless speed with best fit linear regression (solid line), the expected \hat{F} for a cursorial mammal (dashed line) and \hat{F} for a non-cursorial mammal.

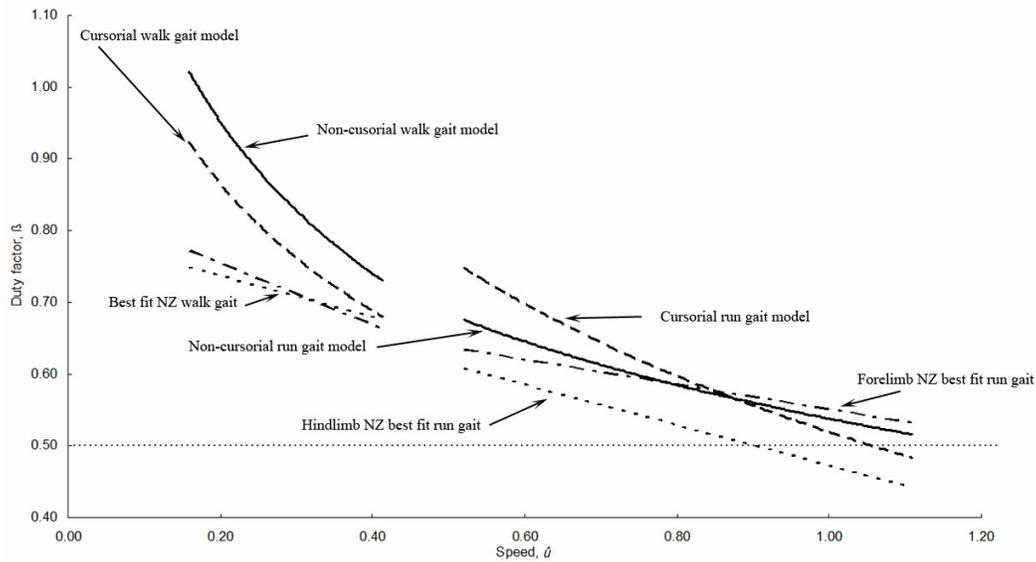


Fig. 4.4. A comparison of the relationship of speed on duty factor between the cursorial and non-cursorial and those measured for the NZ sea lion. The models for the walk duty factor from Alexander and Jayes (1983) show a higher β at any given speed. The run gait for the non-cursorial model is a better fit than the cursorial model, to the forelimb duty factor of the NZ sea lion. Neither fit accounts for the NZ sea lion hindlimb duty factor. The model also implies that the NZ sea lion should not be attaining an aerial phase until speeds greater than those recorded for this study.

definition of cursorial the answer is straight forward; the sea lion violates the parasagittal plane rule as both the hindlimbs and the forelimbs move in the transverse plane and the sea lion, and is therefore non-cursorial. Raichlen (2006) asks whether the differences in stride parameters are simply a strategy of an animal with more distally distributed limb mass. The study used infant baboons (*Papio cynocephalus*) with greater distal limb masses to show they have parameters similar to non-cursorials and the adult baboon with proximally concentrated limb masses have more cursorial parameters. (Raichlen, 2006).

The river otters from Williams et al. (2002) do show some distal distribution in their limbs when compared to the dogs. If, however, one considers sagittal flexion as part of the stride frequency then the swinging of the fore and hind trunk would undoubtedly count as distally distributed masses. The flexion of the river otter results in a 20.5% decrease in the axial length (measured from the hip to shoulder) while the NZ sea lion shows a 34% decrease. The NZ sea lions use a transverse rotation of the hips to further increase its stride length so the above measurements cannot be considered an exact comparison. It does illustrate that the NZ sea lion, like the river otter, is swinging a lot of distally distributed mass back and forth in the act of a single stride. Add to this the NZ sea lion's large manus and pes and it is not surprising that the sea lion acts to minimize that cost with lower F and higher L as other non-cursorials seem to.

4.4 Running gait definition

The NZ sea lion has an ungainly form of locomotion when running and walking. It does however fit into the typical gait pattern of more adept runners. The NZ sea lion

uses the lateral walk (Beentjes, 1989), a gait known to reduce interference between fore and hind limbs (Hildebrand, 1965) and employed by the California sea lion as well (English, 1976). When the duty factor of the lateral walk is low enough, it becomes the transverse gallop used by both the NZ sea lion and the California as well (Hildebrand, 1965; English 1976; Beentjes, 1989).

The gallop of the California sea lion did not include an aerial phase leading English (1976) to question its validity. While the NZ sea lions did have some aerial phases they were inconsistent and not related to speed, duty factor or Froude number. Of the other definitions of a run, the NZ sea lion did archive speeds greater than one Froude number (Alexander and Jayes, 1983), a duty factor less than 50% (Hildebrand, 1976) and a distinct change in stride parameters (Alexander, 1989). The gait pattern is the most convincing evidence the sea lion is galloping, but with the forelimb lags (*FL*) centered on 39% they are different to the dogs with both HL and FL centered on 25% while galloping (Maes et al., 2007).

Most, if not all, terrestrial quadrupedal mammals use coordinated footfall patterns between hind and fore limb pairs. The footfall patterns of the NZ sea lion highlight the clear differences between the forelimb stance duration and the hindlimbs stance duration. Using the footfall patterns defined by the APS method the forelimbs appear closer to the walk gaits than the transverse gallop, with a duty factor of 54%. The hindlimbs on the other hand more closely resemble the forelimbs of the half bound than the transverse gallop. This observation is not surprising considering the restrictions on the independent movement of the hindlimbs and the small *HL* in the half-bound.

The comparison of the footfall patterns with the height of the withers, shoulder and hip and the flexion of the back offer some insight into the running gait of the NZ sea lion (Fig 3.12). First, the highest points for all three height measurements are at the same moment in the stride, when forelimb 2 (f2) is solely in contact with the ground. At this point in the stride the other three limbs are passing under the body before being placed back down at the transitions from f2 to forelimb 1 (f1). While it is impossible to say for sure this is likely the highest point of the center of mass. As the limb is still in contact with the ground the sea lion in this APS defined run could still be using walking kinetics.

Looking at this from another angle: what separates the hindlimbs of a quadruped to that of the human limb and foot? Ignoring the obvious two limbs to one; when a person walks, and sometimes when running, foot contact starts with the heel and ends with the toe. The distance between the two is a translation that lowers the curve traveled by the center of mass when traveling a given distance forward (Lee and Farley, 1998). In the case of a dog running, the hind quarters act in unison until the lead leg touches down. Then the trail limb separates until it too contacts the ground. It does not seem a far stretch to call this a translation as well that allows the hindquarters center of mass to travel forward with less of a vertical displacement. Using this definition then the hindlimbs of the sea lion are not behaving much different from those of the dog.

4.5 Conservation implications

This study offers some insight into the walking and running performance of the NZ sea lion while on land. This type of information is useful in conservation where it allows for a greater understanding of the locomotor capabilities of the NZ sea lion, allowing for safer interactions for conservation staff and assessing safety protocols for the public. With increasing numbers of NZ sea lions on the mainland South Island and the inevitable increase in interactions between animals and the public, the availability of reliable locomotor information can only help in setting and defining safety measures for public interactions. It also offers a basis for more encompassing energetic studies helpful in making conservation assessments and impacts of projects and laws. This study also serves as a base for comparison in a more in-depth kinematic study in the future that includes juveniles and females.

The study records a top speed of 2.8 ms^{-1} for the NZ sea lion, a speed slower than the average 4 ms^{-1} of a typical person. This could be mistakenly interpreted to mean that it is safe to get close to NZ sea lion; this is not the case. Tests of human speeds are on hard running surfaces, while the NZ sea lion was recorded on sand. Nothing in this study suggests that the top speed of the NZ sea lion was recorded, especially since all running was voluntary. Thus, on sand and when taken by surprise, a person can easily be outrun by a NZ sea lion. Currently recommended approach distances of 10 m seem sufficient though further kinematic studies of both humans on sand and sea lions on a hard substrate would seem pertinent as interactions on and off the beach will become more frequent as NZ sea lion populations increase.

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Appendix I

Least-squares regression equations for kinematic parameters with dimensionless velocity (\hat{u}) and withers height (H_w) for seven walk trial and 48 run trials

Dependent	Independent (n)	a (\pm 95% C.I.)	b (\pm 95% C.I.)	r^2 (r^2 -adj. r^2)	Curve fit type
Walk and run trials					
β	\hat{u} (55)	0.53 (0.17)	-0.13 (0.02)	0.742 (0.083)	Logarithmic
β_f	\hat{u} (55)	0.56 (0.01)	-0.12 (0.02)	0.723 (0.005)	Logarithmic
β_h	\hat{u} (55)	0.49 (0.02)	-0.16 (0.04)	0.622 (0.007)	Logarithmic
t_{st} (s)	\hat{u} (55)	0.26 (0.01)	-0.86 (0.04)	0.958 (0.001)	Power
t_{sw} (s)	\hat{u} (55)	0.24 (0.01)	-0.30 (0.07)	0.489 (0.010)	Power
L (m)	u (55)	0.47 (0.10)	0.32 (0.05)	0.728 (0.005)	Linear
L_a (m)	u (19)	0.59 (0.10)	0.31 (0.05)	0.912 (0.005)	Linear
L_{sa} (m)	u (36)	0.44 (0.11)	0.31 (0.06)	0.736 (0.008)	Linear
\hat{L}_s	\hat{u} (55)	0.98 (0.14)	1.17 (0.18)	0.766 (0.004)	Linear
F (Hz)	u (55)	1.31 (0.07)	0.74 (0.11)	0.786 (0.004)	Logarithmic
F_a (Hz)	u (19)	1.17 (0.06)	0.70 (0.08)	0.949 (0.003)	Logarithmic
F_{sa} (Hz)	u (36)	1.37 (0.08)	0.80 (0.14)	0.802 (0.005)	Logarithmic
\hat{F}	\hat{u} (55)	0.47 (0.01)	0.19 (0.02)	0.889 (0.002)	Logarithmic
$D_{m:m}$	\hat{u} (55)	0.56 (0.03)	-0.21 (0.05)	0.597 (0.008)	Logarithmic
Run trials					
u (m/s)	H_w (8)	0.59 (0.71)	1.92 (1.03)	0.776 (0.037)	Linear
L (m)	H_w (8)	0.11 (0.42)	1.42 (0.61)	0.844 (0.026)	Linear
F (Hz)	H_w (8)	2.24 (0.48)	-0.67 (0.68)	0.485 (0.086)	Linear
\hat{L}_h	\hat{u} (48)	1.44 (0.18)	1.66 (0.23)	0.802 (0.004)	Linear
\hat{L}_s	\hat{u} (48)	0.75 (0.23)	1.43 (0.28)	0.704 (0.006)	Linear
\hat{L}_w	\hat{u} (48)	0.70 (0.18)	1.07 (0.22)	0.672 (0.007)	Linear
\hat{L}_F	\hat{u} (48)	0.44 (0.13)	0.84 (0.16)	0.705 (0.006)	Linear
t_{st} (s)	\hat{u} (48)	0.28(0.01)	-0.63(0.13)	0.643 (0.008)	Power
Subject averaged run trials					
$D_{w:t}$	H_w (8)	1.01 (0.18)	-0.59 (0.26)	0.836 (0.027)	Linear
$\beta_{h:f}$	H_w (8)	0.75 (0.22)	0.54 (0.32)	0.740 (0.043)	Linear
Adult subjects run and walk trials					
t_{st} (s)	\hat{u} (19)	0.28 (0.02)	-0.87 (0.04)	0.989 (0.001)	Power
t_{sw} (s)	\hat{u} (19)	0.27 (0.02)	-0.22 (0.06)	0.717 (0.017)	Power
β	\hat{u} (19)	0.84 (0.04)	-0.32 (0.05)	0.903 (0.006)	Linear
L (m)	u (19)	0.59 (0.10)	0.31 (0.05)	0.912 (0.005)	Linear
F (Hz)	u (19)	1.17 (0.06)	0.70 (0.08)	0.950 (0.003)	Logarithmic
$\ln(F)$ (Hz)	$\ln(u)$ (19)	0.04 (0.04)	0.64 (0.10)	0.979 (0.001)	Linear
\hat{L}_s	\hat{u} (19)	0.99 (0.13)	1.22 (0.16)	0.936 (0.004)	Linear
Dependent	Independent (n)	a (\pm 95% confidence)	b (\pm 95% confidence)	r^2 (r^2 -adj. r^2)	Curve fit type
\hat{F}	\hat{u} (19)	0.45 (0.01)	0.18 (0.02)	0.952 (0.003)	Logarithmic
$\ln(\hat{F})$	$\ln(u)$ (19)	-0.75 (0.04)	0.66 (0.05)	0.976 (0.001)	Linear

t_{sr} (s)	\hat{u} (36)	0.26 (0.02)	-0.79 (0.07)	0.917 (0.002)	Power
t_{sw} (s)	\hat{u} (36)	0.22 (0.02)	-0.39 (0.04)	0.522 (0.014)	Power
Sub-adult subjects walk and run trials					
β	\hat{u} (36)	0.73 (0.04)	-0.20 (0.06)	0.606 (0.012)	Linear
L (m)	u (36)	0.44 (0.11)	0.31 (0.06)	0.736 (0.008)	Linear
F (Hz)	u (36)	1.36 (0.08)	0.80 (0.14)	0.802 (0.006)	Logarithmic
$\ln(F)$ (Hz)	$\ln(u)$ (36)	0.25 (0.06)	0.59 (0.10)	0.820 (0.005)	Linear
\hat{L}_s	\hat{u} (36)	0.97 (0.21)	1.13 (0.27)	0.678 (0.010)	Linear
\hat{F}	\hat{u} (36)	0.48 (0.02)	0.20 (0.03)	0.835 (0.005)	Logarithmic
$\ln(\hat{F})$	$\ln(\hat{u})$ (36)	-0.70 (0.05)	0.66 (0.05)	0.853 (0.004)	Linear

a and b values for the equations; linear: $y=a+bx$, Logarithmic: $y=a+b(\ln(x))$, power: $y=ax^b$. \ln stands for the natural log and is applied to those variables it is found with in order to straighten lines for ANOCOVA analysis and adj. stands for adjusted used in the context of adjusted r^2 values. Parameters defined in table 2

Appendix II

Comparisons between fore and hind limb duty factors, between f1 and f2 etc, between walk gait and run gait flexion and limb heights

Stride Parameter	n	Mean	± 0.95 C. I.	F-statistic	p-value
Walk gait and run gait					
β_{fl}	55	0.60	0.02	18.42	0.000
β_{hl}	55	0.55	0.02		
Walk gait					
β_f	7	0.73	0.05	2.18	0.165
β_h	7	0.69	0.04		
Run gait					
β_f	48	0.59	0.01	38.27	0.000
β_h	48	0.61	0.02		
Run gait					
β f1	48	0.60	0.01	5.55	0.021
β f2	48	0.57	0.01		
β_{fj}	48	0.57	0.01	3.34	0.066
β_{rf}	48	0.59	0.01		
Average $\beta_{f:h}$					
Walking	5	1.06	0.05	2.67	0.130
Running	8	1.11	0.05		
Flexion (Average $D_{w:t}$)					
Walking	5	0.86	0.05	44.44	0.000
Running	8	0.61	0.05		
Heights					
H_h (m)	55	0.39	0.01	336.87	0.000
H_s (m)	55	0.56	0.02		
H_h (m) for run gait	48	0.40	0.01	2.17	0.147
H_h (m) for walk gait	7	0.36	0.04		
Stride length					
Adult	19	1.17	0.10	14.49	0.000
Sub-adult	36	0.97	0.06		
Dimensionless stride length					
Adult	19	1.90	0.16	1.35	0.250
Sub-adult	36	1.80	0.09		
Stride frequency					
Adult	19	1.52	0.19	4.73	0.034
Sub-adults	36	1.74	0.11		
Dimensionless stride frequency					
Adult	19	0.38	0.05	1.1	0.299
Sub-adult	36	0.41	0.03		
Stance duration					
Adult	19	0.47	0.15	2.29	0.136
Sub-adult	36	0.37	0.05		
Stance duration for run gait only					
Adult	16	0.32	0.01	0.14	0.711
Sub-adult	32	0.32	0.01		
Swing duration					
Adult	19	0.31	0.02	11.49	0.001
Sub-adult	36	0.25	0.02		

Stride Parameter	n	Mean	± 0.95 C. I.	F	p-value
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Swing duration for run gait

only						
	Adult	16	0.29	0.01	41.30	0.000
	Sub-adult	32	0.24	0.01		
Duty factor						
	Adult	19	0.56	0.04	1.09	0.301
	Sub-adult	36	0.58	0.02		
Lags						
	HL walk	7	0.50	0.03	2.22	0.162
	FL walk	7	0.54	0.03		
	PL walk	7	0.88	0.84	96.22	0.000
	HL walk	7	0.54	0.03		
	FL runs	48	0.39	0.02	154	0.000
	Lag=50%	48	0.50	0.00		
	HL runs	48	0.17	0.02	1592.85	0.000
	Lag=50%	48	0.50	0.00		

In the APS system f1 is the lead forelimb and f2 is the trail forelimb by definition regardless of right or left. Parameters defined in table 7.

Appendix III

Otago University Animal Ethics Committee Permit

Otago University Animal Ethics Committee

Hunter Centre
C/o Faculty Office
Medical School

15 May 2009

Dr C Lalas
Marine Science
University of Otago

Dear Dr Lalas

Application No. 36/09

I have to advise you that at its meeting on 13 May 2009 the Animal Ethics Committee deferred your application for use of live animals in the programme/project entitled '*Running mechanics of the New Zealand Sea Lion (Phocarctos hookeri) through three life stages; juvenile, adolescent and adult*'. The Committee was concerned that a number of personal health and safety issues related to the student had not been addressed. If these are resolved, the Committee is prepared to consider interim approval before the next meeting, to allow the project to continue. As well as providing further information as requested below, please contact the University's Director of Animal Welfare to discuss these issues in more detail.

- a) in # 3.3.1: please revisit and answer in terms of the potential hazards to the student, eg what would happen if he lost his footing while being chased? Are there other helpers/staff present to provide assistance in case of injury?
- b) in # 3.3.5: please revisit and answer as per (a). Will any protective clothing be worn? How would the student call for assistance if something unforeseen happened?
- c) how would you avoid using the same animal twice or multiple times if the poster paint washes off readily?
- d) have you considered the possibility that the project will predispose certain sea lions to be more aggressive in the future towards members of the public? Please comment.
- e) in # 4.1: the Committee recommends that the animals be recorded in invasiveness grade A.

Yours sincerely

Barbara Lee
Secretary
Otago University Animal Ethics Committee

cc Assoc Prof K Probert

Appendix IV

MARINE MAMMALS PROTECTION ACT 1978

PERMIT TO TAKE MARINE MAMMALS

PURSUANT TO section 6 of the Marine Mammals Protection Act 1978:

Chris Lalas and Will Heyward (the Permittees)

are hereby authorised by the Minister of Conservation to approach male NZ sea lions (*Phocarctos hookeri*) in the Otago coastal area to within 1m for the purpose of marking and filming them to analyse the mechanics of their terrestrial locomotion.

Subject to the following conditions:

1. The Permittee will take care not to cause unnecessary harassment when working in close proximity to sea lions. No more than ten dots of paint (each less than 2 cm in diameter) will be applied while the sea lion is resting or sleeping.
2. No animal is to be permanently harmed as a result of the activities carried out by the authority of this permit.
3. Contact with any animal, or groups of animals, will be broken off if indications of undue stress are displayed.
4. The area of operation for marking sea lions under this permit will be Papanui Beach, and the Permittees will take responsibility for arranging access to this site at suitable times with the land owner and tour operators.
5. The area of operation for filming under this permit includes all beaches of Otago Peninsula, provided access arrangements are made with appropriate land owners.
6. This permit is to be carried during its exercise, and presented to any member of the public who expresses concern about the activities carried out by the authority of the permit.
7. Directly after its completion, the Permittee shall send a copy of any research findings, reports and published papers resulting from the research to the Coastal/Marine Ranger Coastal Otago Area Office.
8. This permit is not transferable without the prior written approval of the Conservator, and is valid for a period of 1 year from the date of issue unless sooner suspended, amended or revoked.

Dated at Dunedin this day of 2008

Signed for and on behalf of the Minister of Conservation by Jeff Connell, Conservator, Otago Conservancy, pursuant to a delegation given to him by the Director-General of Conservation and dated the 29th day of October, 1997.