



## Evaluating gain functions in foraging bouts using vertical excursions in northern elephant seals



Michelle S. Ferraro<sup>a</sup>, Robin R. Decker<sup>b</sup>, Daniel P. Costa<sup>c</sup>, Patrick W. Robinson<sup>c</sup>,  
Dorian S. Houser<sup>d</sup>, Daniel E. Crocker<sup>a,\*</sup>

<sup>a</sup> Department of Biology, Sonoma State University, Rohnert Park, CA, U.S.A.

<sup>b</sup> Department of Environmental Science and Policy, University of California, Davis, CA, U.S.A.

<sup>c</sup> Department of Biology, University of California, Santa Cruz, CA, U.S.A.

<sup>d</sup> National Marine Mammal Foundation, San Diego, CA, U.S.A.

### ARTICLE INFO

#### Article history:

Received 4 January 2017

Initial acceptance 17 February 2017

Final acceptance 21 April 2017

Available online 4 June 2017

MS. number: A17-00025R2

#### Keywords:

gain function  
marine predator  
optimal foraging  
patch residence  
phocid

The marginal value theorem models patch departure decisions for foraging animals when resources are unevenly distributed. A key component of these models is the decelerating energy gain function used to represent patch depletion. However, the within-patch gain function has rarely been assessed in marine predators. We evaluated the gain functions in foraging bouts of northern elephant seals, *Mirounga angustirostris*, using a long-term data set (2004–2012) that included complete foraging trips from 205 individual female northern elephant seals on 303 migrations as revealed by time–depth recorders and satellite tags (Argos System Inc.). Since the majority of putative prey capture attempts are associated with vertical excursions at the bottom of dives, we used vertical excursions to evaluate patch depletion across foraging bouts as defined using dive shapes. Rates of energy gain were measured using changes in mass and body composition across trips. Decelerating gain functions occurred in 83% of 77 820 foraging bouts, with the remainder showing accelerating functions. Rates of patch depletion strongly influenced patch residence times. Despite wide variation between individual patches, mean deceleration exponents did not vary with year or season, suggesting that average rates of patch depletion were relatively stable across the study period. The mean duration and number of dives in foraging bouts showed little annual or seasonal variation; however, the mean rate of vertical excursions during foraging dives varied and predicted rates of energy gain across migrations. The relative mean consistency of individual diving behaviour despite wide variation in geolocation supports the idea that northern elephant seals have evolved a foraging strategy that buffers against short-term variation in prey abundance and optimizes energy acquisition across the duration of the migration.

© 2017 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Optimal foraging theory predicts the foraging behaviour of animals and contributes to our understanding of the basis of foraging decisions in nature, including risk sensitivity (Barnard & Brown, 1985; Caraco et al., 1990; Cartar, 1991), diet choice (Belovsky, 1978; Koselj, Schnitzler, & Siemers, 2011; Krebs, Erichsen, Webber, & Charnov, 1977; Werner & Hall, 1974), patch departure rules (Goulson, 2000; Tome, 1988) and central place foraging (Lefebvre, Pierre, Outreman, & Pierre, 2007; Lewison & Carter, 2004; Raffel, Smith, Cortright, & Gatz, 2009). Optimal foraging theory assumes animals maximize fitness by optimizing currencies,

such as the long-term average rate of energy intake under constraints specific to the ecology of a given species.

An extension of optimal foraging theory, the marginal value theorem, applies where energy or food is patchily distributed (Charnov, 1976). Assuming that food patches become depleted as an animal forages over time, models of the marginal value theorem have been used to predict when an animal is likely to leave a food patch (Astrom, Lundberg, & Danell, 1990; Boivin, Fauvergue, & Wajnberg, 2004; Cassini, Kacelnik, & Segura, 1990; Laca, Distel, Griggs, Deo, & Demment, 1993; Pyke, 1978; Scrimgeour, Culp, Bothwell, Wrona, & McKee, 1991; Tome, 1988; Wajnberg, Fauvergue, & Pons, 2000). Energy gain over time is assumed to follow a decelerating function that eventually asymptotes (Pyke, 1980), and the rate of deceleration within a food patch is assumed to provide an indication of food patch quality (Mori & Boyd, 2004).

\* Correspondence: D. E. Crocker, Department of Biology, Sonoma State University, 1801 E. Cotati Avenue, Rohnert Park, CA 94928, U.S.A.

E-mail address: [crocker@sonoma.edu](mailto:crocker@sonoma.edu) (D. E. Crocker).

Foragers should increase residence time in patches that take longer to deplete because these patches provide more energy per unit time (McNickle & Cahill, 2009; Shipley & Spalinger, 1995).

Although the marginal value theorem has been successful in qualitative predictions, quantitative predictions have rarely accurately described patch departure times during experimental validation (Jiang & Hudson, 1993; Laca et al., 1993). Difficulties in quantitative predictions may be due to a number of factors, such as limited sample sizes and timescales, unknown constraints and direct validation of the underlying assumptions of the model features within the study system, including the form of the gain function.

A gain function describes the dependency of the change in energy intake rate upon the time spent foraging within a patch. The deceleration exponent ( $\beta$ ), which is derived from the gain function, approximates the reduction in the rate of prey encounter events as prey patch is depleted. As more prey are consumed, the quantity of prey remaining in the patch and the profitability to the predator persisting in the patch both decline. The deceleration exponent has also been used as an index of patch quality; patches that deplete more slowly are considered higher quality than those that deplete more rapidly (Mori & Boyd, 2004). The gain function, together with the time required to locate new patches, ultimately determines the optimal timing for patch departure and is a key assumption of a marginal value theorem model.

Gain functions can take on a variety of shapes described as decelerating (Watanabe, Ito, & Takahashi, 2014), sigmoidal (Ginnett, Dankosky, Deo, & Demment, 1999), linear (Illius & Fryxell, 2002), piece-wise linear (Astrom et al., 1990) and asymptotic (Laca et al., 1993). Previous studies have shown that even slight changes in the shape of the gain function can result in dramatically different calculated patch residence times from marginal value theorem models, resulting in little resemblance to real world conditions (Astrom et al., 1990; Olsson, Brown, & Smith, 2001; Searle, Vandervelde, Hobbs, & Shipley, 2005). This highlights the importance of empirical validation of the form of gain functions prior to attempts to fit marginal value theorem models. Unfortunately, direct characterization of gain functions in free-ranging foragers is difficult and has been rare in previous studies (Halsey, Woakes, & Butler, 2003; Olsson et al., 2001; Searle et al., 2005; Watanabe et al., 2014).

Conceptually, the marine environment provides excellent systems for testing marginal value theorem models. Mesopelagic foraging meets many of the assumptions that are difficult to meet in model terrestrial systems such as foraging over large spatial and temporal scales in a highly patchy and ephemeral environment with low probabilities of patch revisits (Owen, 1981). Logistically, use of the marine environment to test foraging models has been problematic because direct observation of foraging behaviour while at sea is difficult (Robinson, Simmons, Crocker, & Costa, 2010). To appropriately test foraging models, it is critical to be able to define foraging events and delineate patch use from behaviours associated with search and transit. Most problematic is the development of realistic gain functions that accurately reflect rates of patch depletion. Technological advances in satellite tracking and behavioural recording of marine predators have enabled the collection of large-scale data sets of sufficient quality to provide robust tests of foraging models, given the ability to interpret foraging behaviours from available sensor data.

Most investigations of optimal foraging in marine mammals have focused on individual dives, particularly decisions related to time at depth and the allocation of behaviours over the time of the dive cycle. Several models have been proposed to predict optimal depth and time at foraging depth (Carbone & Houston, 1996; Houston & Carbone, 1992; Mori, 1998, 1999, 2002; Thompson & Fedak, 2001). A variety of marine divers, such as grey seals, *Halichoerus grypus*,

southern elephant seals, *Mirounga leonina*, Steller sea lions, *Eumetopias jubatus*, and blue whales, *Balaenoptera musculus*, terminate foraging dives prior to their estimated aerobic limits. This suggests that time spent in the foraging zone is moderated by patch quality, suggesting both individual patch assessment and subsequent adjustment of dive time (Cornick & Horning, 2003; Doniol-Valcroze, Lesage, Giard, & Michaud, 2011; Sparling, Georges, Gallon, Fedak, & Thompson, 2007; Thums, Bradshaw, Sumner, Horsburgh, & Hindell, 2013). In contrast, use of marginal value theorem models to predict multidive use of prey patches and initiation of new patch searches has been rare.

A multidecade research effort on foraging in female northern elephant seals, *Mirounga angustirostris*, provides an extraordinarily large sample size with which to examine patch characteristics over large spatial and temporal scales (Robinson et al., 2012). In addition, deployment and recovery of instrumentation allows direct measures of energy gain while foraging from changes in mass and body composition over trips (Hassrick, Crocker, & Costa, 2013; Robinson et al., 2012). Body reserves accrued at sea during foraging migrations are the primary determinant of reproductive effort in northern elephant seals and thus provide a relevant fitness proxy (Crocker, Williams, Costa, & Le Boeuf, 2001).

Female northern elephant seals perform two extended foraging trips per year to accrue energy reserves for gestation and lactation: once after moulting and once after breeding (Crocker et al., 2001). They feed on mesopelagic prey along oceanic fronts and in meso-scale eddies that occur in distinct patches within the Transition Zone and Subarctic Gyre of the Pacific Ocean (Le Boeuf, Crocker, Costa, et al., 2000; Robinson et al., 2010; Robinson et al., 2012; Simmons et al., 2010). Northern elephant seals display several characteristic dive shapes associated with foraging behaviour (Hassrick et al., 2007), with pelagic foraging dives characterized by a distinctive bottom time with vertical excursions within the water column. Vertical excursions are associated with dramatic changes in swimming speed that are consistent with pursuit of evasive prey (Hassrick et al., 2007). They are easily derived from simple dive traces, are frequently available for entire foraging migrations and can be used to examine large historical databases. Direct measurements of foraging in elephant seals have shown that the vast majority of foraging events occur during vertical excursions that take place at the bottom of dives (Kuhn, Crocker, Tremblay, & Costa, 2009; Naito et al., 2013). Vertical excursions have also been shown to be associated with feeding events in other marine mammal studies (Horsburgh, Morrice, Lea, & Hindell, 2008; Thums, Bradshaw, & Hindell, 2008). As vertical excursions reflect prey capture attempts (Baechler, Beck, & Bowen, 2002; Bost et al., 2007; Gallon et al., 2013; Le Boeuf, Crocker, Costa, et al., 2000; Naito et al., 2013; Thums et al., 2008), it follows that they can be used as a proxy for prey encounter events. However, similar to the use of jaw accelerometers (Naito et al., 2013), the use of vertical excursions as a proxy for foraging success is limited by the inability to confirm the success of foraging attempts; as a result, the use of vertical excursions as a proxy inherently assumes consistent prey capture success.

Northern elephant seals make a series of successive pelagic foraging dives, termed bouts. The temporal structure of bouts of pelagic foraging dives varies with ocean climate, affects foraging success over migrations and is influenced by the age of foraging females (Crocker, Costa, Le Boeuf, Webb, & Houser, 2006; Hassrick et al., 2013; Zeno, Crocker, Hassrick, Allen, & Costa, 2008). In the present study, we considered only large-scale patch departure decisions on the level of dive bouts, including vertical transit to the surface between contiguous foraging dives as 'within patch'. We investigated the bout structure, within-bout gain functions and diving behaviour of female northern elephant seals foraging over a large spatial and temporal scale. The objectives of this study were

to (1) examine within-bout gain functions using vertical excursions as a proxy for prey encounter events, (2) examine variation in foraging bout and gain function characteristics with season, year, geolocation and female age, and (3) examine the relationship of vertical excursions and patch depletion to foraging success.

## METHODS

### *Sample and Instrument Attachment*

The animal use protocol for this research was reviewed and approved by the Institutional Animal Care and Use Committee of the University of California Santa Cruz (Costa1409) and followed the guidelines established by the Canadian Council on Animal Care and the ethics committee of the Society of Marine Mammalogy. Research was carried out under National Marine Fisheries Service permits (786-1463, 87-143 and 14636). We analysed data from 205 individual female northern elephant seals from Año Nuevo State Park (San Mateo County, CA, U.S.A.), which were instrumented during haul-outs between the years 2004 and 2012. Seals were instrumented with 0.5 W Argos satellite transmitters (Wildlife Computers, Bellevue, WA, U.S.A.: SPOT4, SPOT5, MK10-AF; or Sea Mammal Research Unit, St Andrews, U.K.: SRDL-CTD; mass <350 g) transmitting at a 45 s repetition rate, and time–depth recorders (Wildlife Computers MK9, MK10; or Lotek, St John's, NL, Canada: 2310; mass <40 g) sampling at least once every 8 s. Instruments reported geographical location, movement and diving behaviour over the postbreeding and the postmoulting migration foraging trips.

Sampled females ranged from 4 to 17 years of age and were deemed in good health. Out of 303 complete migration records, 249 of the records were from known-age females, whose age was determined from flipper tags applied at weaning. For analysis, known-age females were classified as young (3–5 years old), prime (6–9 years old) and old (10 years or older). Diving behaviour and foraging success in a subset of these females were analysed previously (Robinson et al., 2012).

Females were chemically immobilized with a ~1 mg/kg intramuscular injection of tiletamine hydrochloride and zolazepam hydrochloride (Telazol, Fort Dodge Laboratories, Fort Dodge, IA, U.S.A.). Immobilization was maintained with intravenous injections of 100 mg of ketamine hydrochloride into the extradural vein. Satellite transmitters were attached to the head and time–depth recorders were attached to the dorsal midline using 5 min epoxy and standard procedures described previously (Hassrick et al., 2010; Robinson et al., 2012).

### *Foraging Success*

Body composition of each animal at deployment and recovery was assessed using the truncated cones method (Crocker et al., 2001; Gales & Burton, 1987; Webb, Crocker, Blackwell, Costa, & Boeuf, 1998). Blubber thickness was measured with an ultrasound scanner (Ithaco Scanoprobe, Ithaca, NY, U.S.A.) at 18 locations along the body coupled with eight girth and length measurements. This method has been validated against water isotope measurements of body composition (Webb et al., 1998). Mass was measured using a Dyna-Link scale (capacity 1000 kg, accuracy  $\pm 1$  kg, Dyna-Link MSI-7200, Measurement Systems International, Seattle, WA, U.S.A.) by suspending the seal in a canvas sling attached to a tripod. Mass at return of trip was corrected for time that elapsed between arrival at the rookery and instrument recovery, as well as the time elapsed between instrument deployment and the animal leaving the rookery. Corrections were made using an equation based on serial measurements taken on females over the course of their

haul-outs (Simmons et al., 2010). On average, seals were on shore  $7 \pm 5$  days after deployment and  $5 \pm 4$  days prior to recovery. For postmoulting females, pup mass was added to the estimated weight at arrival with the assumption that pups were 13% adipose tissue (Crocker et al., 2001). We assumed that adipose tissue was 90% lipid and that lean tissue was 27% protein (Crocker et al., 2001). Gross energy content of mass gain during the foraging trip was calculated assuming 37.33 kJ/g and 23.5 kJ/g for lipid and protein, respectively.

### *Track and Diving Analysis*

All tracks were truncated to arrival and departure dates. Tracks were filtered for speed and turning angle and smoothed using a state-space model as described previously (Johnson, London, Lea, & Durban, 2008; Robinson et al., 2012). The IKNOS MatLab dive analysis toolbox (Mathworks, Natick, MA, U.S.A.) was used to zero-offset correct the raw dive data and calculate individual dive summary statistics at sampling intervals of 8 s (Robinson et al., 2012). Dive statistics included information on bottom time, ascent and descent rate, dive duration, maximum dive depth and dive efficiency (bottom time/(dive duration + postdive surface interval)) for each recorded dive. Dives were required to have durations >32 s and depths >15 m to be considered for analysis, thus eliminating variable surface behaviour not associated with foraging.

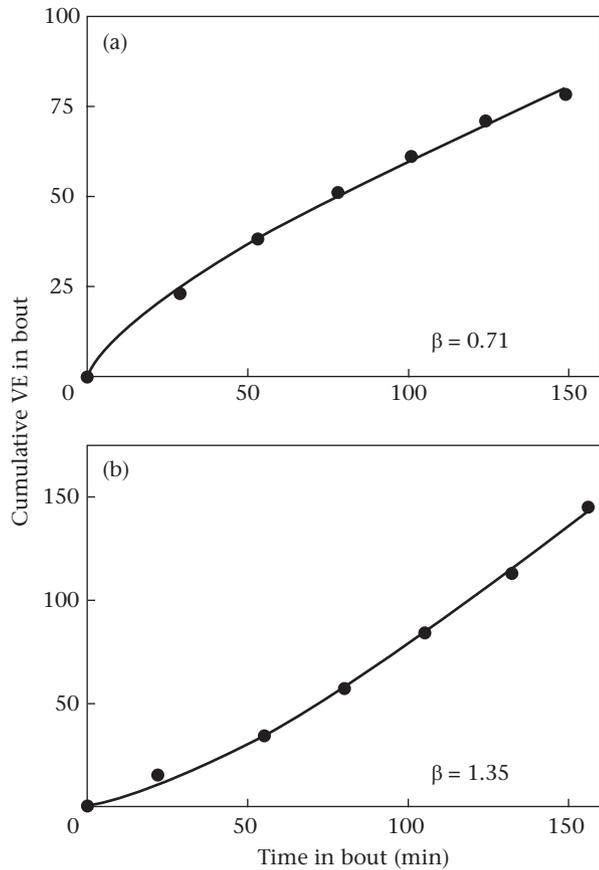
The dives were classified into one of four types based on shape (transit, pelagic foraging, benthic foraging and drift dives) using a hierarchical classification programme to distinguish between individual dives (Robinson et al., 2010) based on the characteristics described in previous investigations (Crocker, Le Boeuf, & Costa, 1997; Hassrick et al., 2007). Pelagic foraging dives were characterized by distinct bottom times with vertical excursions. Vertical excursions were defined by the IKNOS package as a change in vertical direction (i.e. ascent versus descent) at the bottom of a dive over 8 s subsampling periods. We used vertical excursions as a proxy for prey encounter events to calculate the gain functions for northern elephant seals. In previous investigations, log-survivorship analysis generated a minimum bout criterion of two to four dives within individuals (Crocker et al., 2006; Hassrick et al., 2007; Zeno et al., 2008). In this study, we defined a foraging bout as consisting of at least four or more sequential pelagic foraging dives, which were deemed finished when followed by at least two consecutive nonforaging dives (Crocker et al., 2006).

### *Gain Function Analysis*

We fitted a power function ( $y = \alpha \times x^\beta$ ) to each bout using least squares minimization, where  $y$  indicates the total number of prey capture attempts,  $x$  represents time in minutes since the start of a foraging bout,  $\alpha$  is the coefficient parameter estimate that is linked to the initial number of vertical excursions, and  $\beta$  is the exponent parameter estimate representing change in prey encounter rates over a foraging bout. When  $\beta$  was less than 1, a bout was classified as decelerating, as rate of vertical excursions declined with time in the bout. When  $\beta$  exceeded 1, a bout was classified as accelerating, as the rate of vertical excursions increased with time in the bout (Fig. 1).

### *Statistical Analysis*

We analysed variation in power function parameters with season, year, age class, geolocation and dive depth using linear mixed effects models with individual seal as a random effect. When significant effects of categorical variables were present, post hoc



**Figure 1.** Example of (a) a decelerating gain function fit from seal 2004005 and (b) an accelerating gain function from seal 2004004 using time within a bout and cumulative number of vertical excursions (VE) within a bout.

comparisons were made using a Student's *t* test to compare least square means from the mixed model. Model residuals were assessed for approximate normality and homoscedasticity. A mixed model logistic function was fitted to the relationship between

number of dives in a bout and the deceleration exponent,  $\beta$ . Because of the extremely large sample size, we filtered significant model effects based on effect size. Effect size was calculated for statistically significant fixed effects using a mixed model  $R^2$  (Edwards, Muller, Wolfinger, Qaqish, & Schabenberger, 2008). Only effects with  $R^2$  greater than 0.10 are presented and discussed. We used linear regression to examine the relationship between the mean rate of vertical excursions over entire dives or bottom time and the mean energy gain rate for each annual migration. We used mixed model regression to examine this relationship for individual females.

We calculated mean bout and dive characteristics for all individual records and calculated a grand mean by season and year, including the number of dives in a bout, bout duration, dive depth, vertical excursions/bout, vertical excursions/dive, vertical excursions/min, vertical excursions/min of bottom time, total vertical distance covered during vertical excursions for each dive, vertical depth range covered by vertical excursions during each dive and dive efficiency (bottom time/(dive duration + surface interval)). All statistical analyses were performed in JMP 12.0 or SAS 9.3 (SAS Institute, Cary, NC, U.S.A.), unless otherwise noted.

## RESULTS

### Diving Behaviour

In total, we analysed 77 820 foraging bouts over 303 different migration trips. The mean number of foraging bouts per migration was 2.3 times higher during the gestational postmoulting trip than during the postbreeding trip (Table 1). This difference was strongly influenced by the increased mean duration of the postmoulting migration (2.9 times greater; mean of 220 days versus 76 days). Within seasons, the number of bouts per trip did not vary annually. The number of dives per foraging bout did not vary by season or year, although this parameter had much greater variance among individuals during the postmolt migration (Table 1). Mean bout duration, dive depth and dive duration were invariant between seasons and years, indicating stable dive behaviour over large spatial and temporal scales (Table 1).

**Table 1**  
Mean dive statistics for all records averaged by year and season

Season	Year	Females	Bouts analysed	Bouts/trip		Dives/bout		Bout duration (min)		Dive depth (m)		Dive duration (min)	
				Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Postbreeding	2004	4	651	162.8	49.2	13.5	7.0	285.0	154.4	460	66	20.7	2.1
	2005	15	3587	163.8	35.1	14.3	4.2	330.2	113.3	545	61	22.5	2.0
	2006	18	3819	170.9	38.8	15.5	4.8	332.3	100.1	520	56	21.4	1.6
	2007	15	4206	190.5	25.3	11.9	3.8	261.6	89.3	563	34	21.4	1.3
	2008	20	5229	190.6	26.1	11.6	4.7	253.5	109.7	553	33	21.6	1.5
	2009	14	2748	168.6	32.6	11.9	4.2	279.9	122.3	550	38	22.7	1.7
	2010	20	4282	170.2	23.9	13.4	3.6	305.3	74.4	568	42	22.7	2.5
	2011	18	3431	190.6	43.1	14.0	4.7	331.4	86.4	539	33	23.5	2.5
	2012	19	3314	177.2	38.1	13.0	4.4	298.1	96.5	550	48	22.6	2.7
	Mean	–	–	176.1 <sup>a</sup>		13.2		297.4		539		22.1 <sup>a</sup>	
Postmoulting	2004	21	11 622	422.0	95.0	12.5	11.1	292.9	77.2	520	45	23.5	2.3
	2005	24	10 930	410.2	87.4	13.1	11.9	305.1	104.3	528	47	22.7	2.7
	2006	19	9206	378.6	131.3	11.7	10.8	259.6	83.7	526	27	22.0	2.5
	2007	18	9563	398.9	103.0	12.5	10.6	295.9	91.4	535	47	23.7	2.7
	2008	13	6618	402.7	99.2	14.2	11.6	362.1	115.7	546	25	25.2	2.5
	2009	10	3070	371.9	107.4	12.3	10.6	299.6	93.2	545	39	24.1	2.2
	2010	18	7002	398.7	109.9	12.9	10.5	316.9	55.2	550	43	25.0	2.3
	2011	14	6778	484.1	134.1	13.7	11.2	333.2	78.1	539	29	24.3	1.6
	Mean	–	–	408.4 <sup>a</sup>		12.9		304.6		536		23.8 <sup>a</sup>	

A minimum criterion for a foraging bout was defined as three consecutive foraging dives. A mean was calculated for each individual seal's foraging trip, and grand means and SDs are presented for all years and seasons.

<sup>a</sup> Denotes significant differences between seasons.

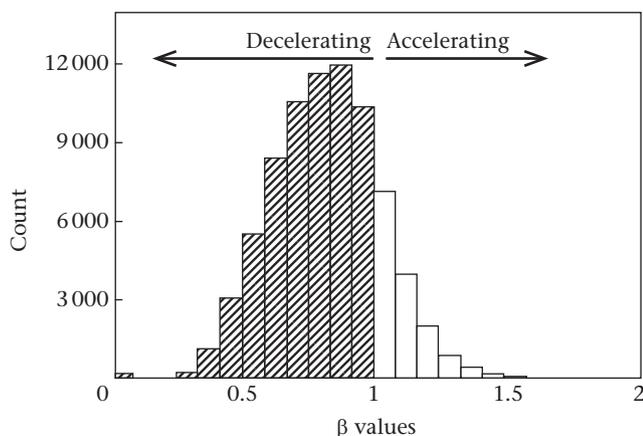
**Table 2**

Grand mean and SD for vertical excursions (VE) on the bottom of dives, total vertical distance covered during VE for each dive (TVD), the vertical depth range covered by VE for each dive (bottom range), and the ratio of bottom time to dive cycle duration (efficiency) averaged for each female by season and year

Season	Year	VE/bout		VE/dive		VE/min		VE/bottom time		TVD (m)		Bottom range (m)		Efficiency	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Postbreeding	2004	257	287	14.1 <sup>a</sup>	1.6	0.66 <sup>a</sup>	0.11	1.56 <sup>a</sup>	0.22	273 <sup>a</sup>	31	87 <sup>a</sup>	11	0.43	0.02
	2005	226	247	15.9 <sup>a,b</sup>	1.9	0.71 <sup>a</sup>	0.08	1.72 <sup>a</sup>	0.24	288 <sup>a</sup>	28	98 <sup>a</sup>	14	0.41	0.02
	2006	256	275	15.6 <sup>a</sup>	2.2	0.70 <sup>a</sup>	0.09	1.72 <sup>a</sup>	0.26	286 <sup>a</sup>	30	93 <sup>a</sup>	15	0.41	0.03
	2007	182	191	16.2 <sup>b</sup>	2.1	0.73 <sup>a,b</sup>	0.06	1.81 <sup>b</sup>	0.15	285 <sup>a</sup>	35	100 <sup>a</sup>	23	0.40	0.02
	2008	176	193	15.9 <sup>b</sup>	1.0	0.73 <sup>a,b</sup>	0.04	1.79 <sup>b</sup>	0.26	290 <sup>a</sup>	29	101 <sup>a</sup>	9	0.40	0.02
	2009	182	193	18.9 <sup>c</sup>	1.3	0.85 <sup>b</sup>	0.06	2.04 <sup>b</sup>	0.21	290 <sup>a</sup>	34	100 <sup>a</sup>	14	0.39	0.03
	2010	214	227	18.7 <sup>c</sup>	1.5	0.80 <sup>b</sup>	0.04	2.01 <sup>b</sup>	0.25	320 <sup>a</sup>	45	116 <sup>b</sup>	26	0.39	0.03
	2011	236	238	18.3 <sup>c</sup>	1.6	0.78 <sup>b</sup>	0.07	1.85 <sup>b</sup>	0.19	374 <sup>b</sup>	53	143 <sup>c</sup>	22	0.42	0.03
	2012	216	206	18.2 <sup>c</sup>	1.6	0.80 <sup>b</sup>	0.08	1.83 <sup>b</sup>	0.13	379 <sup>b</sup>	52	142 <sup>c</sup>	22	0.44	0.03
	Mean	216		16.9		0.75		1.81		322		110		0.41	
Postmoulting	2004	211	200	16.7	1.9	0.70	0.07	1.57 <sup>a,b</sup>	0.36	312 <sup>a</sup>	27	97 <sup>a</sup>	13	0.41 <sup>a</sup>	0.03
	2005	223	219	17.2	1.9	0.74	0.06	1.69 <sup>a</sup>	0.37	311 <sup>a</sup>	45	99 <sup>a</sup>	10	0.41 <sup>a</sup>	0.03
	2006	194	186	15.9	1.6	0.73	0.09	1.74 <sup>a</sup>	0.34	287 <sup>a</sup>	46	92 <sup>a</sup>	11	0.38 <sup>a</sup>	0.03
	2007	175	188	16.3	1.7	0.71	0.04	1.77 <sup>a</sup>	0.35	327 <sup>a</sup>	50	98 <sup>a</sup>	11	0.40 <sup>a</sup>	0.02
	2008	242	310	17.1	1.0	0.71	0.03	1.71 <sup>a</sup>	0.34	329 <sup>a</sup>	28	99 <sup>a</sup>	7	0.41 <sup>a</sup>	0.02
	2009	217	197	18.3	1.4	0.74	0.04	1.75 <sup>a</sup>	0.33	334 <sup>a</sup>	46	109 <sup>a</sup>	19	0.41 <sup>a</sup>	0.03
	2010	231	201	16.9	1.5	0.68	0.05	1.44 <sup>b</sup>	0.33	391 <sup>b</sup>	59	139 <sup>b</sup>	25	0.46 <sup>a</sup>	0.02
	2011	241	216	17.1	1.0	0.69	0.05	1.42 <sup>b</sup>	0.17	417 <sup>b</sup>	47	146 <sup>b</sup>	18	0.46 <sup>b</sup>	0.02
	2012	217	216	16.9	1.0	0.71	0.05	1.64	0.17	417 <sup>b</sup>	47	146 <sup>b</sup>	18	0.46 <sup>b</sup>	0.02
	Mean	217		16.9		0.71		1.64		327		110		0.42	

Different superscripts denote significant differences between years within a season.

Mean prey encounter behaviour over bouts was also consistent across seasons and years but showed marked variation at the level of individual bouts and dives. Vertical excursions per bout were highly variable in individual bouts but did not vary significantly between years or seasons (Table 2). In contrast, the number of vertical excursions per dive steadily increased over the duration of the study during the postbreeding migration but was consistent in the postmoulting migration (Table 2). Similarly, the rate of vertical excursions during the entire dive varied between years during the postbreeding migration but remained the same in the postmoulting season. The rate of vertical excursions during bottom time varied annually in both foraging migrations; rates of vertical excursions during the bottom of dives increased across years during the postbreeding migration and decreased across years during the postmoulting migration (Table 2). Both the bottom range and the total vertical distance covered during vertical excursions for each dive increased across years for both migrations. For example, the range of depths covered during vertical excursions increased 63% over the study period in postbreeding females and 51% in postmoulting females. Dive efficiency was relatively consistent across seasons and years, except for an increase in efficiency during 2010 and 2011 in postmoulting females (Table 2).



**Figure 2.** The number of bouts associated with  $\beta$  values in the power function. Decelerating bout counts are shaded while accelerating are blank.

### Gain Functions

The fit of the power function to cumulative vertical excursions calculated across individual dive bouts yielded an  $r^2 \geq 0.99$  in 96.4% of bouts analysed, suggesting that the power function was an appropriate model for patch depletion in northern elephant seals. The majority of bouts (83%) were classified as decelerating, with the remaining 17% yielding accelerating rates of vertical excursions (Fig. 2). The percentage of bouts classified as accelerating or decelerating was consistent across postmoulting and postbreeding migrations and across age classes (Table 3). Similarly, the mean coefficient  $\alpha$ , which varies with the initial number of vertical excursions per bout, did not vary between seasons or years. Thus, when used as an index of patch quality, the model suggested consistent overall patch depletion characteristics across years and seasons (see Table 4).

**Table 3**

Mean energy gain rate, deceleration exponent ( $\beta$ ) and coefficient ( $\alpha$ ), which varies with the initial number of vertical excursions, for all records by year and season

Season	Year	Energy gain (MJ/day)		$\beta$		$\alpha$	
		Mean	SD	Mean	SD	Mean	SD
Postbreeding	2004	12.8 <sup>a</sup>	7.2	0.813	0.053	2.98	0.95
	2005	14.1 <sup>a</sup>	7.0	0.821	0.038	2.55	0.54
	2006	14.5 <sup>a</sup>	7.5	0.808	0.059	2.73	0.68
	2007	19.6 <sup>a,b</sup>	7.5	0.801	0.033	2.65	0.56
	2008	16.7 <sup>a,b</sup>	7.3	0.799	0.045	2.77	0.47
	2009	23.6 <sup>b</sup>	9.8	0.807	0.040	2.55	0.41
	2010	22.3 <sup>b</sup>	8.1	0.813	0.036	2.57	0.39
	2011	18.3 <sup>a,b</sup>	7.4	0.802	0.033	2.66	0.31
	2012	19.5 <sup>a,b</sup>	6.9	0.776	0.101	2.86	0.65
	Mean	17.9		0.804		2.70	
Postmoulting	2004	19.5	2.9	0.818	0.037	2.47	0.32
	2005	19.2	3.3	0.817	0.039	2.65	0.55
	2006	15.7	3.2	0.804	0.041	2.70	0.45
	2007	15.2	4.5	0.807	0.046	2.66	0.49
	2008	17.5	3.5	0.843	0.026	2.54	0.83
	2009	21.8	5.5	0.826	0.029	2.39	0.24
	2010	16.3	3.5	0.832	0.035	2.52	0.35
	2011	18.4	2.6	0.811	0.022	2.78	0.51
	2012	18.4	2.6	0.811	0.022	2.78	0.51
	Mean	18.0		0.820		2.59	

A minimum criterion for a foraging bout was defined as four consecutive foraging dives. Different superscripts denote significant differences between years.

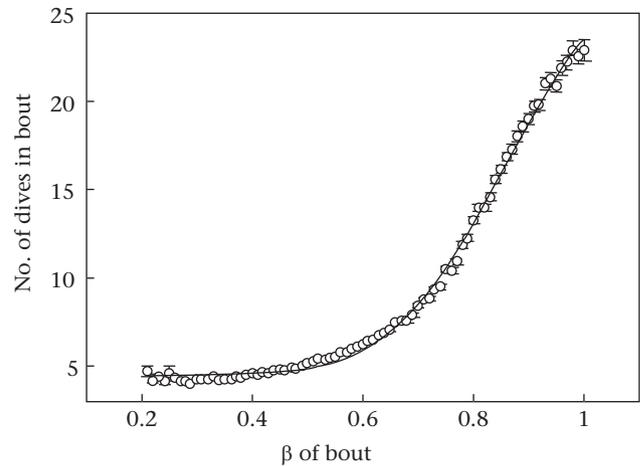
**Table 4**

Relative percentages of accelerating and decelerating patches during postmoulting and postbreeding seasons, for young, prime and old age classes, and for all migrations

	% Decelerating	% Accelerating
Postmoulting	81.0±5.7	19.0±5.7
Postbreeding	84.2±5.8	15.8±5.8
Young (3–5 years)	84.6±5.1	15.4±5.1
Prime (6–9 years)	81.8±5.4	18.2±5.4
Old (10+ years)	83.4±5.3	16.6±5.3
All migrations	82.8±6.0	17.2±6.0

Patch depletion coefficients ( $\beta$ ) and initial coefficients ( $\alpha$ ) exhibited statistically significant but biologically insignificant linear or quadratic associations with latitude and longitude ( $R^2 = 0.001–0.05$ ,  $P < 0.05$ ) across both migrations. This indicates that there were no important relationships between geoposition and patch depletion characteristics or the initial number of prey capture attempts. The lack of a relationship was consistent with visual inspection of the occurrence of decelerating or accelerating bouts along tracks, which revealed no distinct pattern to the location of decelerating or accelerating bouts (Fig. 3). Similarly,  $\beta$  and  $\alpha$  had statistically significant but weak relationships to dive depth and duration ( $R^2 = 0.01–0.03$ ,  $P < 0.0001$ ).

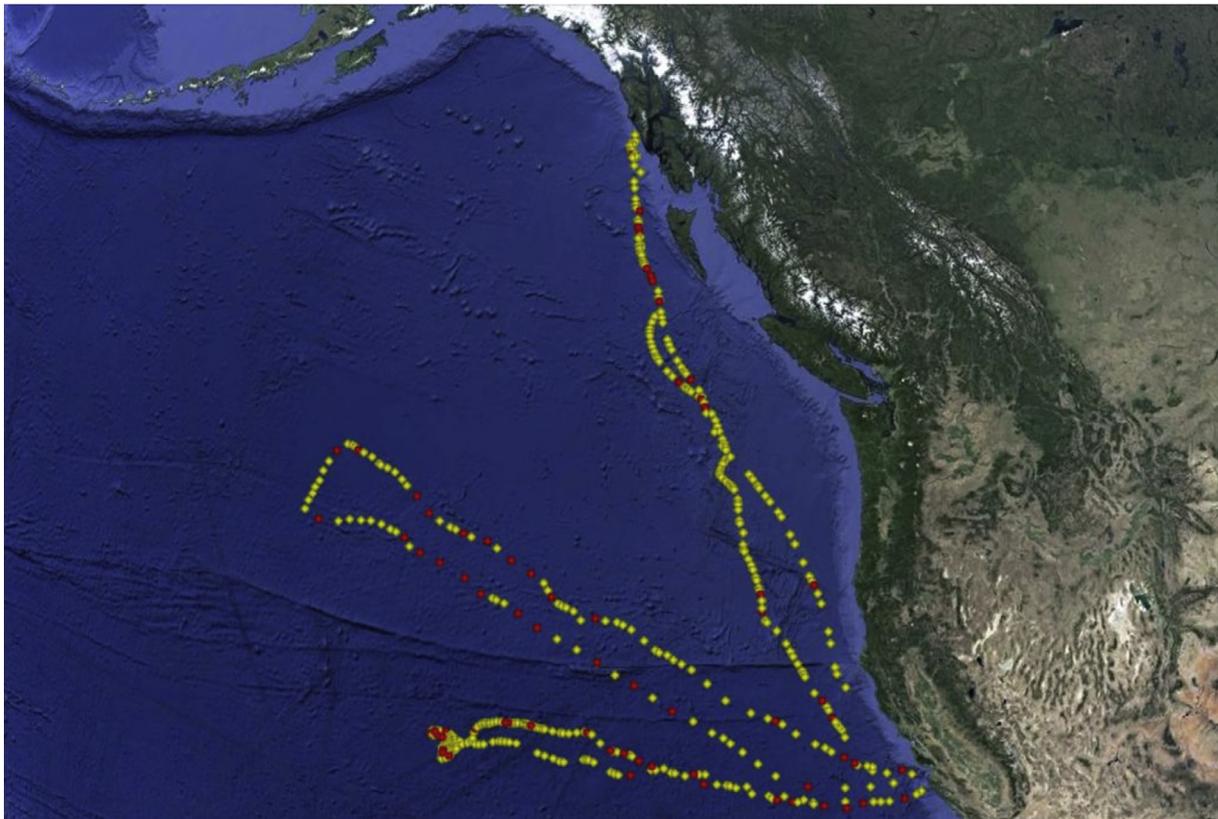
There were no significant effects of season or year on either  $\beta$  or  $\alpha$ , regardless of whether all bouts were combined or separated into decelerating and accelerating types. Deceleration coefficients had strong and consistent impacts on the number of dives within a foraging bout. The mean number of dives in a foraging bout increased exponentially as rates of patch depletion declined for both foraging migrations ( $r^2 = 0.99$ ,  $F_{1,160} = 3771$ ,  $P < 0.0001$ ; Fig. 4).



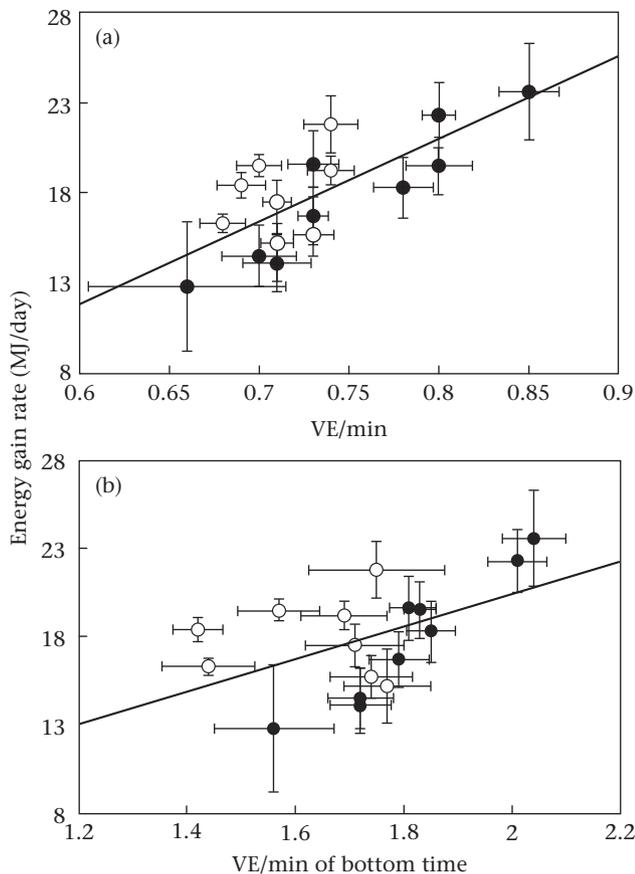
**Figure 4.** When a power function was fitted to the cumulative number of vertical excursions in a foraging bout, the power exponent,  $\beta$ , predicted the mean number of dives in decelerating bouts. Curve fit is a four-parameter logistic function.

#### Foraging Success

Foraging success over the entire migration was not affected by any bout or diving variable except the long-term mean rate of vertical excursions. When grouped by year and migration season (e.g. postmoult, 2005), the mean rate of energy gain increased with the rate of vertical excursions per minute of dive time ( $R^2 = 0.56$ ,  $F_{1,15} = 19.4$ ,  $P < 0.001$ ; Fig. 5a) and with the rate of vertical excursions per minute of bottom time ( $R^2 = 0.26$ ,  $F_{1,15} = 5.4$ ,  $P = 0.03$ ; Fig. 5b). Across individual trips, the rate of vertical excursions per

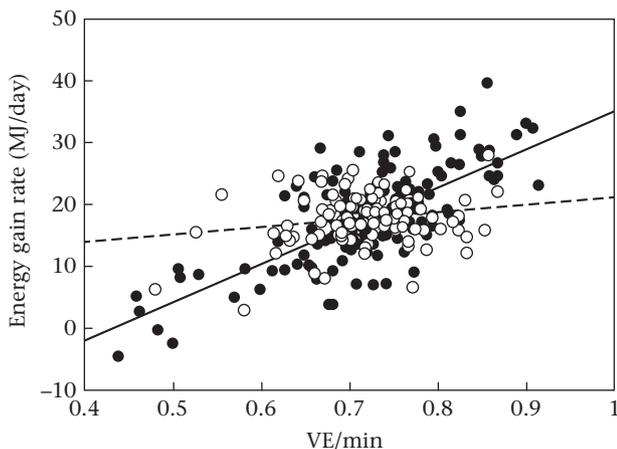


**Figure 3.** Individual patches along the tracks of three different seals: 2009008, 2009014 and 2012010. Red positions indicate accelerating patches while yellow indicate decelerating patches. Geoposition shows no relationship with patch type.



**Figure 5.** Daily energy gain rate relative to the (a) mean rate of vertical excursions (VE) during an entire dive and (b) number of VE per minute of bottom time. Each point represents the grand mean for all females in a migration season. Error bars are SEs of the grand mean.

minute of dive time was also a significant predictor of individual energy gain rate ( $R^2 = 0.34$ ,  $F_{1,270} = 140.7$ ,  $P < 0.0001$ ; Fig. 6). However, the slope of the relationship was significantly greater in postbreeding migrations ( $F_{1,268} = 36.6$ ,  $P < 0.0001$ ; Fig. 6). Individual seal accounted for 12.6% of the variance in energy gain rate. The depth range of vertical excursions and the total vertical



**Figure 6.** Changes in energy gain rate of entire foraging migrations with the mean rate of vertical excursions (VE) during dives. Open circles and dashed line are means for individual postmoult females. Closed circles and solid line are means for individual postbreeding females.

distance covered during vertical excursions showed no association with foraging success ( $P > 0.05$ ).

## DISCUSSION

Consistent with marginal value theorem assumptions, female northern elephant seals exhibited decelerating gain functions in the majority of foraging patches. This suggests utility of the northern elephant seal system to test marginal value theorem models of patch departure during pelagic foraging migrations and provides an empirical basis for describing rates of patch depletion. The deceleration exponent, derived from fitting a power function to cumulative vertical excursions in a foraging bout, indicated that patch depletion characteristics influenced patch departure decisions. Thus, foraging female northern elephant seals appear to follow the qualitative predictions of the marginal value theorem by modifying the number of dives in a bout in response to prey patch quality and spending more time in higher-quality patches that take longer to deplete.

The proportion of patches with decelerating gain functions was consistent across years, seasons and female age. This was reflected in similar mean foraging bout characteristics; there were similar numbers of dives and putative prey encounter events within a foraging bout over seasons and years. The mean patch deceleration exponent and the mean number of prey encounters on the initial dives in foraging bouts were also similar across seasons and years. The stability of these features over nearly a decade of sampling suggests that female northern elephant seals have the potential to develop consistent, long-term strategies to maximize energy gain over long timescales. This foraging strategy may help to buffer against short-term reductions in prey availability and support a capital breeding life-history strategy that prioritizes success across the entire foraging migration. This hypothesis is supported by the striking similarity in mean diving behaviour across the large data set (Table 1) and the weakened influence of the rate of prey encounter events on foraging success during longer foraging trips. However, we note that the study period did not include a strong El Niño event and only one event was considered ‘moderate’ in intensity (2009–2010). Application of consistent foraging behaviour during major changes in prey distribution may have contributed to the foraging difficulties exhibited during the strong 1997–1998 El Niño (Crocker et al., 2006).

A subset of the gain functions were found to be accelerating (17%), highlighting the need to quantify gain functions when implementing marginal value theorem models (Searle et al., 2005). The existence of patches with accelerating gain functions may reflect use of varied prey resources by northern elephant seals (e.g. the pattern might result from encountering high-quality prey that satiate the seal before patch resources are depleted). Accelerating patches may also result from prey that aggregate more closely in response to the presence of a predator, or are less evasive, thus leading to higher encounter rates later in the bout. Alternatively, varied mesoscale oceanographic features that lead to the aggregation of prey (Simmons et al., 2010) may limit the dispersal of prey fields and alter rates of prey encounter events. However, there was no clear geospatial pattern to accelerating type patches; they occurred intermittently across most foraging tracks, with decelerating patches sometimes occurring during the same day. Nevertheless, prey patches with accelerating gain functions occurred in all records and might contribute significantly to energy acquisition across the migration.

The similarity of mean within-bout dive behaviour (e.g. mean seasonal dive durations and depths) across the study period, despite widely varying characteristics of individual bouts and changes in physiological features that can influence breath-hold

ability (Hassrick et al., 2010; Maresh et al., 2015), further support the potential for a consistent long-term foraging strategy that serves to maximize energy acquisition across the migration. In contrast, mean vertical excursions per minute of dive time changed markedly across the years studied and appeared to strongly affect foraging success (as measured by body reserves when seals came on shore). Mean energy gain rates for annual and seasonal foraging migrations varied positively with vertical excursions per minute of dive time. Although less strong, this relationship was also evident at the level of individual female migrations. Collectively, these results support the use of vertical excursions as a proxy for prey encounter events in female northern elephant seals, which is consistent with previous studies on foraging seals (Baechler et al., 2002; Bost et al., 2007; Gallon et al., 2013; Le Boeuf, Crocker, Costa, et al., 2000; Naito et al., 2013; Thums et al., 2008).

Mean numbers of prey encounter events over bouts and rates of prey encounter events during dives were more variable during postbreeding migrations than during postmoult migrations, which was reflected in the more variable rates of energy gain among postbreeding individuals. Similarly, the relationship of vertical excursions to energy gain (i.e. the slope of the regression) was significantly greater during the shorter postbreeding migration. The lower variability in mean prey encounter events and the stability in foraging success over the gestational postmoult migration may reflect the seal's ability to buffer against short-term variation in prey availability over the longer migration. However, it may also reflect differences in habitat use between the two migrations. During both migrations, many females appear to exploit the gyre–gyre boundary when foraging, as evidenced by slower transit rates and greater area-restricted searching (Robinson et al., 2012, 2010; Simmons et al., 2010). However, the increased duration of the postmoult migration allows females to cover a significantly greater range of longitudes and may allow access to different prey resources than during the postbreeding migration. Previous investigations have shown the duration of the postbreeding migration to be more variable in response to ocean climate (Crocker et al., 2006). This may suggest flexibility that is necessary to compensate for more variable rates of foraging success while recovering from the endogenous nutrient loss of the preceding lactation period and allow sufficient recovery of body reserves before implantation occurs. In contrast, the postmoult trip duration is constrained by gestational progress and females must initiate return to the breeding colony in time for parturition.

In contrast to the consistent number of vertical excursions per bout and patch depletion characteristics, annual differences were evident in the characteristics of individual vertical excursions. There was a strong increase in the vertical depth range (bottom range) and the total vertical distance covered by vertical excursions in a dive during both foraging migrations in 2010–2012, suggesting increased foraging effort during the bottom of dives that was not reflected in our proxy for prey encounter events. A change in foraging effort may be due to a number of factors, including changes in prey type, prey behaviours or physical forcing of oceanographic characteristics. Notably, dive efficiency, defined as the proportion of the dive in the foraging zone, increased in postmoult females in those same years and exhibited a similar trend during the postbreeding migration. The increase in efficiency may reflect increased aerobic breath-hold ability through metabolic and behavioural adjustments (Hassrick et al., 2013; Maresh et al., 2015). While the source of the change is not known, the magnitude of the change and its consistency across years suggests an important alteration in predator/prey dynamics with changes in ocean climate.

Previous marginal value theorem studies have shown that many marine mammals optimize their average rate of energy intake on the level of dives by moderating their time at depth in relation to

patch quality. Southern elephant seals showed increased bottom durations on dives where they encountered prey and when more prey capture attempts occurred (Gallon et al., 2013; Jouma'a et al., 2016), aligning with predictions from the marginal value theorem. Studies in sea lions and grey seals demonstrate a direct but asymptotic relationship between the bottom duration of dives and prey encounter rates, suggesting potential constraints on dive times due to limitations in oxygen carrying capacity (Cornick & Horning, 2003; Sparling et al., 2007). Similar results have been found in Australian fur seals, *Arctocephalus pusillus* (Foo et al., 2016). Collectively, evidence suggests marine divers spend more time at depth in response to increasing patch quality, but within the constraints of available oxygen stores. At the level of the foraging dive bout, our results also conformed to predictions of the marginal value theorem; divers performed more sequential dives in patches that depleted more slowly, a characteristic that is suggestive of patch quality. Together these results suggest that foraging decisions for marine divers are complex and reflect hierarchical decisions where divers optimize behaviour at different levels (e.g. single dive versus dive bout) relative to patch characteristics. Recent investigations in elephant seals suggest that there is a hierarchical structure to the vertical component of elephant seal diving that links diving angles and search behaviour at the bottom of dives to prey encounter rates (Adachi et al., 2017; Le Bras, Jouma'a, Picard, & Guinet, 2016). Additional hierarchical decisions occur at the level of patch distribution; for example, decisions about whether to return to previously exploited patches on subsequent dives, or to invest in horizontal transit (Hassrick et al., 2007) to search for new, unexploited patches.

The value of using vertical excursion-derived gain functions to test marginal value theorem models depends on several assumptions linking vertical excursions to prey encounter events and subsequent rates of energy gain. The dramatic changes in swimming speeds during vertical excursions (Hassrick et al., 2009) and evidence that the great majority of jaw openings (Naito et al., 2013) and prey acquisition events (Kuhn et al., 2009) occur during vertical excursions suggest strongly that vertical excursions at the bottom of dives represent the primary hunting behaviour in elephant seals. However, other specialized modes of hunting are possible, including benthic foraging when on the continental margin or on seamounts (Maxwell et al., 2012), or single foraging events at the bottom of extremely deep dives without distinct bottom times (Naito et al., 2013).

Using vertical excursion-derived prey encounter events to explicitly estimate energy gain functions assumes consistent average rates of capture success and similar prey energy contents across capture attempts. Direct measures of prey consumption using stomach temperature in elephant seals could not identify individual prey captures during feeding events, but suggested foraging success on 18–24% of foraging dives. However, these data were mostly acquired during the initial week of the foraging migration and prior to the occurrence of bout feeding (Kuhn et al., 2009). In contrast, during bout feeding, successful captures occurred on most dives. Based on repeated deployments on females, ~13% of the variation in foraging success was due to individual quality. This component of foraging success may include individual differences in hunting ability and capture success. Despite these caveats, the association of prey encounter event rates with a direct measure of foraging success (energy gain) and the strong impacts of prey encounter events' decay functions on bout duration suggest utility in using vertical excursions to describe energy gain functions.

A major criticism of the marginal value theorem is that predators are implicitly assumed to know the total prey capture rates in the environment, including information on the distribution of prey

patches. The wide variation in individual patch quality, as indicated by rates of patch depletion, and strong impacts of this variation on bout duration suggests that a rate-maximizing forager would exhibit differing optimal patch departure times for a given search time between patches. Maximizing a marginal value theorem model for individual bouts that incorporates the rate of patch depletion may provide insight into whether elephant seals have some knowledge of the prior distribution of patches in the foraging trip and what temporal scale of prior experience influences current foraging decisions.

## Conclusion

As capital breeders, northern elephant seals maximize reproductive effort and success by optimizing their average long-term rate of energy gain during foraging migrations and over their life span. The long-duration migrations and decelerating patch characteristics of preferred prey form the basis for an optimized patch departure strategy that enables the breeding strategy of northern elephant seals. Rates of patch depletion, as measured by putative prey encounter events, strongly influenced patch residence times, and rates of prey encounter were a major driver of foraging success. Consistent mean rates of patch depletion over seasons and years were associated with consistent mean diving behaviour and bout durations. These findings provide insight into the advantages that select for capital breeding strategies, their association with foraging over wide spatial and temporal scales, and the ability to buffer reproductive success over short-term variations in prey availability.

## Acknowledgments

We thank Gitte McDonald, Carey Kuhn, Jason Hassrick, Sam Simmons, Melinda Fowler, Sarah Peterson, Luis Huckstadt, Sarah Maxwell, Jen Maresh, Stella Villegas-Amtmann and many others for assistance with field work. We thank Año Nuevo State Park and the University of California Natural Reserve System for logistical support. This research was part of the TOPP - Tagging of Pacific Predators programme supported by grants from the Moore, Packard and Sloan Foundations and from the Office of Naval Research (N00014-13-1-0134 and N00014-10-1-0356), and contract number JIP 22 07-23 from the E&P Sound & Marine Life Joint Industry Programme of the International Association of Oil & Gas Producers (IAGOP).

## References

- Adachi, T., Costa, D. P., Robinson, P. W., Peterson, S. H., Yamamichi, M., Naito, Y., et al. (2017). Searching for prey in a three-dimensional environment: Hierarchical movements enhance foraging success in northern elephant seals. *Functional Ecology*, *31*(2), 361–369.
- Astrom, M., Lundberg, P., & Danell, K. (1990). Partial prey consumption by browsers: Trees as patches. *Journal of Animal Ecology*, *59*(1), 287–300.
- Baechler, J., Beck, C. A., & Bowen, W. D. (2002). Dive shapes reveal temporal changes in the foraging behaviour of different age and sex classes of harbour seals (*Phoca vitulina*). *Canadian Journal of Zoology*, *80*(9), 1569–1577. <http://dx.doi.org/10.1139/z02-150>.
- Barnard, C., & Brown, C. (1985). Risk-sensitive foraging in common shrews (*Sorex araneus* L.). *Behavioral Ecology and Sociobiology*, *16*(2), 161–164.
- Belovsky, G. E. (1978). Diet optimization in a generalist herbivore: The mouse. *Theoretical Population Biology*, *14*(1), 105–134.
- Boivin, G., Fauvergue, X., & Wajnberg, E. (2004). Optimal patch residence time in egg parasitoids: Innate versus learned estimate of patch quality. *Oecologia*, *138*(4), 640–647.
- Bost, C. A., Handrich, Y., Butler, P. J., Fahlman, A., Halsey, L. G., Woakes, A. J., et al. (2007). Changes in dive profiles as an indicator of feeding success in king and Adélie penguins. *Deep Sea Research Part II: Topical Studies in Oceanography*, *54*(3–4), 248–255. <http://dx.doi.org/10.1016/j.dsr2.2006.11.007>.
- Caraco, T., Blanckenhorn, W. U., Gregory, G. M., Newman, J. A., Recer, G. M., & Zwicker, S. M. (1990). Risk-sensitivity: Ambient temperature affects foraging choice. *Animal Behaviour*, *39*, 338–345.
- Carbone, C., & Houston, A. (1996). The optimal allocation of time over the dive cycle: An approach based on aerobic and anaerobic respiration. *Animal Behaviour*, *51*, 1247–1255.
- Carter, R. V. (1991). A test of risk-sensitive foraging in wild bumble bees. *Ecology*, *72*(3), 888–895.
- Cassini, M. H., Kacelnik, A., & Segura, E. T. (1990). The tale of the screaming hairy armadillo, the guinea pig and the marginal value theorem. *Animal Behaviour*, *39*, 1030–1050.
- Charnov, E. L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology*, *9*(2), 129–136.
- Cornick, L. A., & Horning, M. (2003). A test of hypotheses based on optimal foraging considerations for a diving mammal using a novel experimental approach. *Canadian Journal of Zoology*, *81*(11), 1799–1807. <http://dx.doi.org/10.1139/z03-179>.
- Crocker, D. E., Costa, D. P., Le Boeuf, B. J., Webb, P. M., & Houser, D. S. (2006). Impact of El Niño on the foraging behavior of female northern elephant seals. *Marine Ecology-Progress Series*, *309*, 1–10.
- Crocker, D. E., Le Boeuf, B. J., & Costa, D. P. (1997). Drift diving in female northern elephant seals: Implications for food processing. *Canadian Journal of Zoology*, *75*, 27–39.
- Crocker, D. E., Williams, J. D., Costa, D. P., & Le Boeuf, B. J. (2001). Maternal traits and reproductive effort in northern elephant seals. *Ecology*, *82*(12), 3541–3555.
- Doniol-Valcroze, T., Lesage, V., Giard, J., & Michaud, R. (2011). Optimal foraging theory predicts diving and feeding strategies of the largest marine predator. *Behavioral Ecology*, *22*(4), 880–888. <http://dx.doi.org/10.1093/beheco/arr038>.
- Edwards, L. J., Muller, K. E., Wolfinger, R. D., Qaqish, B. F., & Schabenberger, O. (2008). An  $R^2$  statistic for fixed effects in the linear mixed model. *Statistics in Medicine*, *27*(29), 6137–6157.
- Foo, D., Semmens, J. M., Arnould, J. P., Dorville, N., Hoskins, A. J., Abernathy, K., et al. (2016). Testing optimal foraging theory models on benthic divers. *Animal Behaviour*, *112*, 127–138.
- Gales, N., & Burton, H. (1987). Ultrasonic measurement of blubber thickness of the southern elephant seal, *Mirounga leonina* (Linn). *Australian Journal of Zoology*, *35*(3), 207–217.
- Gallon, S., Bailleul, F., Charrassin, J. B., Guinet, C., Bost, C. A., Handrich, Y., et al. (2013). Identifying foraging events in deep diving southern elephant seals, *Mirounga leonina*, using acceleration data loggers. *Deep Sea Research Part II: Topical Studies in Oceanography*, *88–89*, 14–22. <http://dx.doi.org/10.1016/j.dsr2.2012.09.002>.
- Ginnett, T., Dankosky, J., Deo, G., & Demment, M. (1999). Patch depression in grazers: The roles of biomass distribution and residual stems. *Functional Ecology*, *13*(1), 37–44.
- Goulson, D. (2000). Why do pollinators visit proportionally fewer flowers in large patches? *Oikos*, *91*(3), 485–492.
- Halsey, L., Woakes, A., & Butler, P. (2003). Testing optimal foraging models for air-breathing divers. *Animal Behaviour*, *65*, 641–653. <http://dx.doi.org/10.1006/anbe.2003.2090>.
- Hassrick, J. L., Crocker, D. E., & Costa, D. P. (2013). Effects of maternal age and mass on foraging behaviour and foraging success in the northern elephant seal. *Functional Ecology*, *27*, 1055–1063.
- Hassrick, J. L., Crocker, D. E., Teutschel, N. M., McDonald, B. I., Robinson, P. W., Simmons, S. E., et al. (2010). Condition and mass impact oxygen stores and dive duration in adult female northern elephant seals. *Journal of Experimental Biology*, *213*, 585–592. <http://dx.doi.org/10.1242/jeb.037168>.
- Hassrick, J. L., Crocker, D. E., Zeno, R. L., Blackwell, S. B., Costa, D. P., & Le Boeuf, B. J. (2007). Swimming speed and foraging strategies of northern elephant seals. *Deep Sea Research Part II: Topical Studies in Oceanography*, *54*(3), 369–383.
- Horsburgh, J. M., Morrice, M., Lea, M.-A., & Hindell, M. A. (2008). Determining feeding events and prey encounter rates in a southern elephant seal: A method using swim speed and stomach temperature. *Marine Mammal Science*, *24*(1), 207–217. <http://dx.doi.org/10.1111/j.1748-7692.2007.00156.x>.
- Houston, A. I., & Carbone, C. (1992). The optimal allocation of time during the diving cycle. *Behavioral Ecology*, *3*, 255–265.
- Illius, A. W., & Fryxell, J. M. (2002). Methodological problems with estimating patch depression during resource depletion. *Oikos*, *98*(3), 558–559.
- Jiang, Z., & Hudson, R. J. (1993). Optimal grazing of wapiti (*Cervus elaphus*) on grassland: Patch and feeding station departure rules. *Evolutionary Ecology*, *7*(5), 488–498.
- Johnson, D. S., London, J. M., Lea, M.-A., & Durban, J. W. (2008). Continuous-time correlated random walk model for animal telemetry data. *Ecology*, *89*(5), 1208–1215.
- Jouma'a, J., Le Bras, Y., Richard, G., Vacquière-García, J., Picard, B., El Kasbi, N., et al. (2016). Adjustment of diving behaviour with prey encounters and body condition in a deep diving predator: The southern elephant seal. *Functional Ecology*, *30*(4), 636–648.
- Kosefj, K., Schnitzler, H.-U., & Siemers, B. M. (2011). Horseshoe bats make adaptive prey-selection decisions, informed by echo cues. *Proceedings of the Royal Society B: Biological Sciences*, *278*(1721), 3034–3041.
- Krebs, J. R., Erichsen, J. T., Webber, M. I., & Charnov, E. L. (1977). Optimal prey selection in the great tit (*Parus major*). *Animal Behaviour*, *25*, 30–38.
- Kuhn, C. E., Crocker, D. E., Tremblay, Y., & Costa, D. P. (2009). Time to eat: Measurements of feeding behaviour in a large marine predator, the northern elephant seal *Mirounga angustirostris*. *Journal of Animal Ecology*, *78*(3), 513–523. <http://dx.doi.org/10.1111/j.1365-2656.2008.01509.x>.
- Laca, E., Distel, R., Griggs, T., Deo, G., & Demment, M. (1993). Field test of optimal foraging with cattle: The marginal value theorem successfully predicts patch

- selection and utilisation. In *Proceedings of the 17th International Grassland Congress, 8–21 February 1993, New Zealand and Queensland* (pp. 709–710). Palmerston North, New Zealand: New Zealand Grassland Association.
- Le Boeuf, B. J., Crocker, D. E., Costa, D. P., Blackwell, S. B., Webb, P. M., & Houser, D. S. (2000). Foraging ecology of northern elephant seals. *Ecological Monographs*, *70*(3), 353–382.
- Le Bras, Y., Jouma'a, J., Picard, B., & Guinet, C. (2016). How elephant seals (*Mirounga leonina*) adjust their fine scale horizontal movement and diving behaviour in relation to prey encounter rate. *PLoS One*, *11*(12), e0167226.
- Lefebvre, D., Pierre, J., Outreman, Y., & Pierre, J.-S. (2007). Patch departure rules in bumblebees: Evidence of a decremental motivational mechanism. *Behavioral Ecology and Sociobiology*, *61*(11), 1707–1715.
- Lewison, R. L., & Carter, J. (2004). Exploring behavior of an unusual megaherbivore: A spatially explicit foraging model of the hippopotamus. *Ecological Modelling*, *171*(1), 127–138.
- Maresh, J., Adachi, T., Takahashi, A., Naito, Y., Crocker, D. E., Horning, M., et al. (2015). Summing the strokes: Energy economy in northern elephant seals during large-scale foraging migrations. *Movement Ecology*, *3*, 1–16.
- Maxwell, S. M., Frank, J. J., Breed, G. A., Robinson, P. W., Simmons, S. E., Crocker, D. E., et al. (2012). Benthic foraging on seamounts: A specialized foraging behavior in a deep-diving pinniped. *Marine Mammal Science*, *28*(3), E333–E344.
- McNickle, G. G., & Cahill, J. F. (2009). Plant root growth and the marginal value theorem. *Proceedings of the National Academy of Sciences of the United States of America*, *106*(12), 4747–4751.
- Mori, Y. (1998). The optimal patch use in divers: Optimal time budget and the number of dive cycles during bout. *Journal of Theoretical Biology*, *190*(2), 187–199.
- Mori, Y. (1999). The optimal allocation of time and respiratory metabolism over the dive cycle. *Behavioral Ecology*, *10*(2), 155–160.
- Mori, Y. (2002). Optimal diving behaviour for foraging in relation to body size. *Journal of Evolutionary Biology*, *15*(2), 269–276.
- Mori, Y., & Boyd, I. L. (2004). The behavioral basis for nonlinear functional responses and optimal foraging in Antarctic fur seals. *Ecology*, *85*(2), 398–410.
- Naito, Y., Costa, D. P., Adachi, T., Robinson, P. W., Fowler, M., & Takahashi, A. (2013). Unravelling the mysteries of a mesopelagic diet: A large apex predator specializes on small prey. *Functional Ecology*, *27*(3), 710–717.
- Olsson, O., Brown, J. S., & Smith, H. (2001). Gain curves in depletable food patches: A test of five models with European starlings. *Evolutionary Ecology Research*, *3*(3), 285–310.
- Owen, R. W. (1981). Fronts and eddies in the sea: Mechanisms, interactions and biological effects. In A. R. Longhurst (Ed.), *Analysis of marine ecosystems* (pp. 197–233). London, U.K.: Academic Press.
- Pyke, G. H. (1978). Optimal foraging in hummingbirds: Testing the marginal value theorem. *American Zoologist*, *18*(4), 739–752. <http://dx.doi.org/10.1093/icb/18.4.739>.
- Pyke, G. H. (1980). Optimal foraging in bumblebees: Calculation of net rate of energy intake and optimal patch choice. *Theoretical Population Biology*, *17*(2), 232–246.
- Raffel, T. R., Smith, N., Cortright, C., & Gatz, A. J. (2009). Central place foraging by beavers (*Castor canadensis*) in a complex lake habitat. *American Midland Naturalist*, *162*(1), 62–73.
- Robinson, P. W., Costa, D. P., Crocker, D. E., Gallo-Reynoso, J. P., Champagne, C. D., Fowler, M. A., et al. (2012). Foraging behavior and success of a mesopelagic predator in the northeast Pacific Ocean: Insights from a data-rich species, the northern elephant seal. *PLoS One*, *7*(5), e36728. <http://dx.doi.org/10.1371/journal.pone.0036728>.
- Robinson, P. W., Simmons, S. E., Crocker, D. E., & Costa, D. P. (2010). Measurements of foraging success in a highly pelagic marine predator, the northern elephant seal. *Journal of Animal Ecology*, *79*(6), 1146–1156.
- Scrimgeour, G. J., Culp, J. M., Bothwell, M. L., Wrona, F. J., & McKee, M. H. (1991). Mechanisms of algal patch depletion: Importance of consumptive and non-consumptive losses in mayfly–diatom systems. *Oecologia*, *85*(3), 343–348.
- Searle, K. R., Vanderveelde, T., Hobbs, N. T., & Shipley, L. A. (2005). Gain functions for large herbivores: Tests of alternative models. *Journal of Animal Ecology*, *74*(1), 181–189.
- Shipley, L. A., & Spalinger, D. E. (1995). Influence of size and density of browse patches on intake rates and foraging decisions of young moose and white-tailed deer. *Oecologia*, *104*(1), 112–121.
- Simmons, S. E., Crocker, D. E., Hassrick, J. L., Kuhn, C. E., Robinson, P. W., Tremblay, Y., et al. (2010). Climate-scale hydrographic features related to foraging success in a capital breeder, the northern elephant seal *Mirounga angustirostris*. *Endangered Species Research*, *10*, 233–243. <http://dx.doi.org/10.3354/esr00254>.
- Sparling, C. E., Georges, J.-Y., Gallon, S. L., Fedak, M., & Thompson, D. (2007). How long does a dive last? Foraging decisions by breath-hold divers in a patchy environment: A test of a simple model. *Animal Behaviour*, *74*, 207–218. <http://dx.doi.org/10.1016/j.anbehav.2006.06.022>.
- Thompson, D., & Fedak, M. A. (2001). How long should a dive last? A simple model of foraging decisions by breath-hold divers in a patchy environment. *Animal Behaviour*, *61*, 287–296. <http://dx.doi.org/10.1006/anbe.2000.1539>.
- Thums, M., Bradshaw, C. J., & Hindell, M. A. (2008). A validated approach for supervised dive classification in diving vertebrates. *Journal of Experimental Marine Biology and Ecology*, *363*(1), 75–83.
- Thums, M., Bradshaw, C. J., Sumner, M. D., Horsburgh, J. M., & Hindell, M. A. (2013). Depletion of deep marine food patches forces divers to give up early. *Journal of Animal Ecology*, *82*(1), 72–83. <http://dx.doi.org/10.1111/j.1365-2656.2012.02021.x>.
- Tome, M. W. (1988). Optimal foraging: Food patch depletion by ruddy ducks. *Oecologia*, *76*(1), 27–36.
- Wajnberg, E., Fauvergue, X., & Pons, O. (2000). Patch leaving decision rules and the marginal value theorem: An experimental analysis and a simulation model. *Behavioral Ecology*, *11*(6), 577–586.
- Watanabe, Y. Y., Ito, M., & Takahashi, A. (2014). Testing optimal foraging theory in a penguin–krill system. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1779), 20132376.
- Webb, P., Crocker, D., Blackwell, S., Costa, D., & Boeuf, B. (1998). Effects of buoyancy on the diving behavior of northern elephant seals. *Journal of Experimental Biology*, *201*(16), 2349–2358.
- Werner, E. E., & Hall, D. J. (1974). Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology*, *55*(5), 1042–1052.
- Zeno, R., Crocker, D. E., Hassrick, J. S., Allen, S. A., & Costa, D. P. (2008). Development of foraging behavior in juvenile northern elephant seals. *Journal of Zoology*, *274*, 180–187.