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ARTICLE

Testing predictions of optimal diving theory using animal-borne video from harbour seals (*Phoca vitulina concolor*)

Susan G. Heaslip, W. Don Bowen, and Sara J. Iverson

Abstract: Optimal diving theory predicts that animals make decisions that maximize their foraging profitability subject to the constraint of oxygen stores. We examined the temporal pattern of prey encounters within a dive from concurrently collected dive data and animal-borne video from a free-ranging pinniped to test predictions of optimal diving theory. CRITTERCAMS were deployed on 32 adult male harbour seals (*Phoca vitulina concolor* De Kay, 1842) at Sable Island, Nova Scotia, Canada, for 3 days each. Deployments resulted in approximately 3 h of video per seal and a total of 2275 capture attempts for 1474 prey encounter events recorded. We found support for seven of the nine selected predictions of optimal diving theory. As predicted, prey encounters increased with bottom duration; dive duration increased with dive depth; and travel duration, bottom duration, and percent bottom duration decreased over a wide range of travel durations. Descent duration did increase with dive depth, and seals terminated dives earlier when no prey were encountered and when prey were encountered later in a dive. Contrary to prediction, bottom duration did not increase and then decrease for short travel durations and dives were not terminated earlier when travel durations were short and prey encounter rate was low.

Key words: optimal diving theory, optimal foraging theory, harbour seal, *Phoca vitulina concolor*, animal-borne camera, CRITTERCAM.

Résumé : La théorie de la plongée optimale prédit que les animaux prennent des décisions qui maximisent la profitabilité de l'activité d'alimentation au vu de leurs réserves d'oxygène. Nous avons examiné la distribution temporelle des rencontres de proie durant une plongée à partir de données de plongée et de vidéos prises par des caméras montées sur des animaux recueillies simultanément afin de vérifier les prédictions de la théorie de la plongée optimale pour un pinnipède en liberté. Des caméras CRITTERCAM ont été déployées pendant 3 jours sur 32 phoques communs (*Phoca vitulina concolor* De Kay, 1842) mâles adultes à l'île de Sable (Nouvelle-Écosse, Canada). Ces déploiements ont produit environ 3 h de vidéo par phoque et un total de 2275 tentatives de capture pour 1474 évènements de rencontre de proie enregistrés. Les données recueillies appuient sept des neuf prédictions sélectionnées de la théorie de la plongée optimale. Comme prévu, le nombre de rencontres de proie augmentait de pair avec la durée au fond; la durée de la plongée augmentait de pair avec la profondeur de la plongée; et la durée de déplacement, la durée au fond et le pourcentage de cette dernière diminuaient pour une grande fourchette de durées de déplacement. La durée de la descente augmentait avec la profondeur de la plongée, et les phoques terminaient leurs plongées plus tôt quand ils ne rencontraient aucune proie ou quand ces rencontres avaient lieu plus tardivement durant la plongée. Contrairement aux prédictions, la durée au fond n'augmentait pas pour ensuite diminuer pour de courtes durées de déplacement et les plongées ne se terminaient pas plus tôt pour de courtes durées de déplacement et de faibles fréquences de rencontres de proie. [Traduit par la Rédaction]

Mots-clés : théorie de la plongée optimale, théorie de l'alimentation optimale, phoque commun, *Phoca vitulina concolor*, caméra montée sur l'animal, CRITTERCAM.

Introduction

Animals are expected to balance the benefits and costs of foraging decisions to maximize their probability of survival and reproductive success. Foraging theory aims to predict how foragers should optimize energy intake over time (predictions 6–9, Table 1; Emlen 1966; MacArthur and Pianka 1966; Charnov 1976), and optimal diving theory (ODT) is nested within foraging theory with the additional constraints that diving imposes on air-breathing predators that forage aquatically at depth. One of the main physiological constraints imposed on diving animals is a rise in blood lactate concentrations once all of the usable oxygen stores have been exhausted during a dive, which is termed an animal's aerobic dive limit (Kooyman 1985). Animals diving beyond their aerobic dive limit pay a penalty of requiring increased time at the surface to clear the accumulated lactic acid. This increased surface duration reduces the time available to forage. Theoretical models of optimal diving predict the optimal allocation of time between foraging at depth and obtaining oxygen at the surface, with the assumption that divers maximize their time spent underwater with dive durations equal to or less than the aerobic dive limit and that prey capture does not result in termination of a dive (Kramer 1988; Houston and Carbone 1992; Carbone and Houston 1994, 1996).

Optimal diving models predict that resource gain should increase linearly with time spent at depth and assume that swimming speed and therefore the rate of oxygen consumption is

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Table 1. Tested predictions of optimal diving theory from harbour seals (*Phoca vitulina concolor*), including the response variable and covariates used for statistical analysis (for each prediction or model).

Prediction	Response variable	Covariate(s)	References
1. Resource gain (no. of prey encountered) increases linearly with search time spent at depth	Prey encountered	Bottom duration	Kramer 1988
2. Dive duration increases with dive depth and (or) travel duration	Dive duration	Dive depth and travel duration	Kramer 1988; Houston and Carbone 1992; Mori et al. 2002
3. For relatively short travel durations, foraging time increases and then decreases with travel duration; over a wider range of travel durations, foraging time decreases with travel duration	Bottom duration	Travel duration	Houston and Carbone 1992
4. Proportion of time spent in the foraging area decreases with travel duration	Percent bottom duration (bottom duration/dive duration)	Travel duration	Houston and Carbone 1992
5. Swim speed should remain constant or decrease with dive depth, but should not increase with dive depth; therefore, descent duration should not stay the same or should increase with depth	Descent duration	Dive depth	Thompson et al. 1993
6. Dives are terminated earlier when prey are not encountered before some threshold time	Bottom duration	Prey presence or absence (controlled for descent duration)	Thompson and Fedak 2001
7. Dives are terminated earlier for all travel durations regardless of dive depth if no prey are encountered	Bottom duration	Prey presence or absence (controlled for travel duration and depth)	Thompson and Fedak 2001
8. Dives are terminated earlier when prey are not encountered in the early part of the dive	Bottom duration after first prey encounter	Time to first prey encounter (controlled for descent duration)	Thompson and Fedak 2001
9. Dives are terminated earlier when travel duration is short and prey density is low, but not when dives get deeper, no matter the prey density	Bottom duration	Prey encounter rate × percent travel duration + prey encounter rate × depth (controlled for time to first prey encounter)	Thompson and Fedak 2001

constant during diving. Therefore energy gain is proportional to the time spent at the bottom of a dive (prediction 1, Table 1; Kramer 1988), and depth and (or) travel duration increase with increasing dive duration (prediction 2, Table 1; Kramer 1988; Houston and Carbone 1992; Mori et al. 2002). Foraging time is predicted to first increase and then decrease as travel duration increases, and to decrease over a wider range of travel durations (prediction 3, Table 1; Houston and Carbone 1992). As travel duration increases, the proportion of time available for foraging decreases (prediction 4, Table 1; Houston and Carbone 1992). Depending on the costs of acceleration, swimming speed may also increase with depth (Houston 1986), but when energy intake and efficiency is considered, swimming speed may decrease with depth (prediction 5, Table 1; Thompson et al. 1993). In addition to terminating dives on the basis of oxygen stores, some models also predict that dives are terminated in relation to prey encounters and success rates.

Optimal diving models require us to choose the currency that is maximized during foraging, such as the proportion of time spent foraging, gross energy gain, and net rate of energetic gain and (or) energetic efficiency (Houston and Carbone 1992; Thompson and Fedak 2001). More complicated optimal diving models allow divers to make decisions related to encountered prey and prey-patch quality (e.g., Thompson and Fedak 2001). Models that consider prey include predictions such as seals will terminate dives earlier when prey are not encountered (predictions 6, 7, and 8, Table 1; Thompson and Fedak 2001), and that the benefit of terminating a dive when prey density is low varies with depth or travel duration (prediction 9, Table 1; Thompson and Fedak 2001).

Prey-patch quality (e.g., prey species and density) is difficult to measure in situ; however, we assume animals adjust their behaviour in response to patch quality. Diving behaviour (e.g., length of bouts) and animal movements (e.g., distance travelled and path tortuosity) have been shown to vary with prey type and foraging success and have been used to infer patch quality (e.g., Mori and Boyd 2004; Austin et al. 2006; Elliott et al. 2008). Patch quality has also been inferred indirectly from daily foraging success using calculations of changes in passive drift rates of seals related to relative lipid content in combination with movement data (Thums et al. 2013). More direct information on the timing of prey encounters can be collected with the use of stomach temperature sensors, jaw sensors that measure the angle of the mouth opening (intra-mandibular angle sensors (IMASEN) and Hall sensors), and accelerometers attached on the head and lower jaw to detect head, neck, and jaw movements (Kuhn and Costa 2006; Liebsch et al. 2007; Suzuki et al. 2009; Viviant et al. 2010). Stomach temperature sensors are unable to distinguish between multiple prey ingestions that are within quick succession of one another and therefore can often only provide data at the resolution of individual meals. Although jaw sensors and head- and jaw-mounted accelerometers show potential for identifying movements associated with individual prey ingestion, further validation is required to distinguish between successful and unsuccessful capture attempts, as well as to distinguish between foraging and nonforaging related movements. Foraging data collected using these methods are informative; however, data on the timing of individual prey encounters at the scale of individual dives are necessary to test predictions of ODT.

Tests of ODT that include direct observations of individual prey encounter events have mostly been limited to captive experiments (Carbone and Houston 1994; Cornick and Horning 2003; Gallon et al. 2007; Sparling et al. 2007) or to free-ranging animals that are easily observed (Lea et al. 1996). For studies where animals are observed only from the surface (Lea et al. 1996; Walton et al. 1998), tests of ODT have been limited to testing predictions of the relationships between dive duration and surface duration. The development of bio-logging devices such as time–depth recorders (TDRs) and the use of underwater video cameras has permitted further testing of ODT for free-ranging animals (Boyd et al. 1995; Mori et al. 2002; Heath et al. 2007); however, inferred foraging behaviours from bio-logging devices often are not validated and a researcher must be present to record video footage in a particular location. More recently, the use of animal-borne cameras has opened up the possibility to validate behaviours inferred from TDRs and to examine foraging tactics with respect to encountered prey species (Bowen et al. 2002).

The development of underwater animal-borne video cameras (Marshall 1998, Marshall et al. 2007) provides the opportunity to directly collect information on the components of foraging (e.g., encounter rate, capture success, and handling time) concurrently with measures of the diving predator's behaviour (e.g., time, depth, temperature, speed, orientation, and location). Such data have been used to identify foraging habitat, prey species, and feeding success (e.g., Parrish et al. 2000, 2002, 2005; Hooker et al. 2002; Heaslip et al. 2012); prey-specific foraging tactics and prey profitability (Bowen et al. 2002); locomotor behaviour and energetic costs of foraging (Williams et al. 2000, 2004); diving physiology (Hooker et al. 2005); and three-dimensional foraging behaviour (Davis et al. 1999, 2001, 2003; Fuiman et al. 2007). When combined with data from TDRs, video-recorded behaviours of predator and prey (e.g., Bowen et al. 2002) can be used to test predictions of optimal diving models (e.g., Cornick and Horning 2003; Heath et al. 2007; Sparling et al. 2007). We used animal-borne cameras to study the foraging behaviour of adult male harbour seals (*Phoca vitulina concolor* De Kay, 1842) foraging off Sable Island, Nova Scotia, Canada.

Harbour seals are generalist predators that feed on a variety of both benthic and pelagic prey in Atlantic Canadian waters, including sand lance (*Ammodytes dubius* Reinhardt, 1837), Atlantic herring (*Clupea harengus* L., 1758), Atlantic cod (*Gadus morhua* L., 1758), pollock (*Pollachius virens* (L., 1758)), and northern shortfin squid (*Illex illecebrosus* (Lesueur, 1821)) (Bowen and Harrison 1996). During the breeding season, males are central-place foragers reliably returning to and hauling out on Sable Island after short foraging trips to sea (Walker and Bowen 1993*a*; Coltman et al. 1997). This behaviour provided an opportunity to fit individual seals with data-logging instruments and to reliably recover these instruments to download data. The objective of this study was to test whether dive and prey encounter data support predictions from foraging models of optimal diving (Table 1) by analyzing data on the characteristics of individual dives and the number of prey encounters during those dives.

Materials and methods

Fieldwork was conducted on Sable Island, Nova Scotia, Canada (43°55′N, 60°0′W), a partially vegetated sandbar that is approximately 1.5 km wide and 42 km long. Adult male harbour seals were captured and recaptured after brief foraging trips during the 1995–1997 May–June breeding seasons. Seals were captured with hand-held nets using standard methods (Bowen et al. 1992), weighed (±0.5 kg, 200 kg, Spring Scale; Salter Industrial Measurement Ltd., West Bromwich, West Midlands, UK), and sedated with approximately 0.2 mg/kg diazepam (Hoffmann-La Roche, Mississauga, Ontario, Canada) to facilitate attachment of the CRITTERCAM and to measure standard dorsal length (McLaren 1993).

The CRITTERCAM (National Geographic, Washington, D.C., USA; Marshall 1998) weighed approximately 2 kg in air with the epoxy mount and averaged about 1.8% of the body mass of the study animals. The aluminium housing was a cylindrical, 25 cm long waterproof tube with a conical floatation section at one end, an outer diameter of approximately 10 cm, and cross-sectional area that was approximately 4.5% of that of the seals in our study. In addition to video, the camera unit contained a TDR that sampled depth and temperature every 7 s for the entire deployment and a saltwater switch that turned the camera off when the animal was hauled out of the water. The camera was placed on the midline of the back behind the shoulders of the seal and was attached to the pelage using 5 min epoxy, nylon mesh, and stainless steel hose clamps (Bowen et al. 2002). The time elapsed from capture to release took approximately 30 min.

Cameras were programmed to sample video for 10 min every 45 min starting at 0530 or 0600 and ending between 1400 and 1500 local time. This sampling design took into account the limited length of videotape (3 h) and the behaviour patterns of male harbour seals (i.e., hauling out during the afternoon; Walker and Bowen 1993*a*). Seals wore the camera for about 3 days and a VHF radio transmitter (Advanced Telemetry Systems, Isanti, Minnesota, USA) glued to the fur on the seal's head was used to locate seals when they returned to land. The camera and hose clamps were removed upon recapture by cutting the mesh at the base of the camera, leaving only a small amount of mesh that was shed during the annual moult several weeks later. Seals were again weighed and were then released. Because of an ongoing study of male reproductive behaviour, the head-mounted VHF radio transmitter was not removed at this time.

This research was conducted in accordance with guidelines of the Canadian Council on Animal Care. Study protocols were approved by the University Committee on Laboratory Animals (Dalhousie University's animal ethics committee) and by the Animal Care Committee of Fisheries and Oceans Canada.

Video analysis

As in Bowen et al. (2002), the Observer version 2.0 (Noldus 1991) software package was used to calculate the duration and frequency of diving, and to describe foraging behaviour (e.g., seals pursuing individual fish, schools of fish, or rooting in the bottom substrate). In contrast with Bowen et al. (2002), this study analysed foraging behaviour at the level of individual dives rather than the 10 min video-sampling units. Only video samples where seals were thought to be foraging (having detected prey at some point during a video sample) were used in this analysis. Video samples with seals exhibiting social and mating behaviours were presented elsewhere (Boness et al. 2006). We measured descent and ascent durations (travel duration), time spent at depth (termed bottom duration, a proxy for time spent foraging), time of the first prey encounter (operationally defined as head orientation towards a prey identified within the camera's field of view), number of prey encounters (i.e., individual fish or schools), number of capture attempts, and prey encounter rate (number of prey encounters/ bottom duration) for each prey species from the video. Number of capture attempts was greater than the number of encounters because multiple capture attempts could be made on individuals pursued either singly or from schools. Bottom duration was defined by a change in orientation of the seal associated with an inflexion in dive angle. Surface durations were not included in our analysis since few were complete as a result of the short duration

Table 2. Number of complete dives, prey encounters recorded from video, and proportion of dives with prey encounters per harbour seals (*Phoca vitulina concolor*).

		No. of dives per seal		No. of prey encounters per seal		Proportion of dives per seal with prey encounters	
Year	Seals (*n*)	Mean ± SE	Range	Mean ± SE	Range	Mean ± SE	Range
1995	7	18.1±3.5	4–31	18.3±4.6	4–34	0.53±0.069	0.33–0.75
1996	10	30.0±3.9	15–46	48.8±24.1	2–255	0.37±0.084	0.07–0.94
1997	15	14.6±1.2	7–23	57.2±12.2	16–197	0.79±0.045	0.48–1.00
All years	32	20.2±1.9	4–46	46.1±9.6	2–255	0.60±0.049	0.07–1.00

Note: Instruments were deployed on 32 seals over the 3 years of sampling. Two seals had deployments in both 1995 and 1997, and these deployments were treated as independent samples. Six seals sampled during the 1996 season had two deployments each, and these two deployments per seal were treated as one sample.

of video-sampling units. Maximum dive depth in metres was determined for each dive from concurrently collected TDR data. Prey were identified to the level of species by freezing playback of the video and (or) with the use of digital stills extracted from the video.

Statistical analysis

Generalized additive mixed models (GAMMs) and generalized linear mixed models (GLMMs) were used to model the relationships among the variables: prey encounters, prey encounter rate (no. of prey encounters/bottom duration), time to first prey encounter (time from reaching bottom to first prey encounter), bottom duration and percent bottom duration (bottom duration/dive duration), bottom duration after first prey encounter, travel duration (ascent + descent durations), dive duration, and depth. We also examined the factor variables: prey presence or absence, percent travel duration (travel duration/dive duration, which was split into three categories (<20%, 20%–35%, and ≥35%) following Thompson and Fedak 2001); the interaction terms included prey encounter rate × depth and prey encounter rate × percent travel duration. Models using these variables were fitted for each of the ODT predictions (Table 1). For predictions 6–9, the variables descent duration, travel duration, depth, and time to first prey encountered were related to the response variables and were included as control variables (Table 1). For models that included prey encounters or prey presence, we included a prey species term to explore whether foraging behaviour varied with prey species. The intercept of these models was permitted to vary randomly across animals, nested within year, and within-seal residual autocorrelation was modelled using a first-order autoregressive correlation structure to account for repeated measurements on the same animal for sequential dives. Analyses were performed using the "gamm" function of the "mgcv" package (Wood 2006) in R version 2.14.1 (R Core Team 2011). We used the Gaussian distribution (identity link) for continuous data (i.e., dive duration, bottom duration, descent duration, and bottom duration after first prey encounter), Poisson distribution (log link) for count data (i.e., prey encounters), and quasibinomial distribution (logit link) for proportion data (i.e., percent bottom duration). The significance of terms included in the models was examined using P values and approximate P values from the "mgcv" output. Significance levels were set at $\alpha = 0.05$. Model selection was not conducted for the models fitted for each of the ODT predictions (Table 1), as we were interested only in the extent to which the data supported specific theoretical predictions concerning the specified variables. Model fits were assessed using adjusted R^2, residual plots, and partial residual plots. Values are reported as means ± SE.

Results

Video footage of foraging behaviour was recovered from 38 separate deployments of the CRITTERCAM on 32 adult male harbour seals over 3 years (Table 2). All instruments were recovered. Two seals had deployments in both 1995 and 1997, and these deployments were treated as independent samples. Six seals sampled during the 1996 season had two deployments, and these two deployments per seal were combined and treated as one sample. Video samples with foraging behaviour contained 20 ± 1.9 complete dives and 46 ± 9.6 prey encounters per seal, and prey were encountered in 60% ± 4.9% of these dives (Table 2). Dive durations from video samples with foraging behaviour averaged 3.4 ± 0.04 s (range = 0.8–7.2 s, median = 3.3 s) and maximum dive depth averaged 25 ± 2.0 m (range = 2–65 m, median = 23 m). A total of 2275 capture attempts for 1474 prey encounter events was recorded. The prey species encountered varied among seals: 22 seals encountered cryptic sand lance (i.e., hidden in the sandy bottom), 5 seals encountered flounders (American plaice, *Hippoglossoides platessoides* (Fabricius, 1780), or yellowtail flounder, *Limanda ferruginea* (Storer, 1839)), 28 seals encountered unknown cryptic fish species (probably sand lance), 19 seals encountered schooling sand lance, and 6 seals encountered other fish species. Individual seals each encountered from one to five prey species (3.4 ± 0.16, median = 3). For some prey encounters, fish were too far from the camera, light level was too low resulting in poor image quality, or prey were seen too briefly to allow identification (Bowen et al. 2002). For further description and quantitative analysis of foraging behaviour see Bowen et al. (2002).

Tests of model predictions

As predicted, the number of prey encounters increased linearly with bottom duration; however, relatively little of the observed variation was explained by the data (prediction 1, Table 3; Supplementary Fig. S1[1]). As predicted, dive duration was longer when travel duration was longer (prediction 2, Table 3; Fig. 1*a*) and when dives were deeper (prediction 2, Table 3; Fig. 1*b*). Over a wide range of travel durations, bottom duration decreased as predicted; however, for short travel durations (i.e., <50 s), bottom duration did not first increase and then decrease as predicted by theory (prediction 3, Table 3; Fig. 2*a*). Although bottom duration appeared to decrease at longer travel durations, we had few observations beyond 100 s with which to test this prediction. When expressed as a proportion, time spent foraging decreased with increasing travel duration (prediction 4, Table 3; Fig. 2*b*). Descent duration increased with increasing dive depth, suggesting that swim speed did not increase with dive depth as predicted (prediction 5, Table 3; Fig. 3). However, it is possible that the angle of descent could have also changed to contribute to the observed relationship.

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[1] Supplementary figures are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2013-0137.

Table 3. Parameter estimates, significance of linear terms, approximate significance of smooth terms, and goodness of fit (adjusted R^2) for the fitted mixed models used to test optimal diving theory predictions for harbour seals (*Phoca vitulina concolor*).

				Parametric coefficients				Approximate significance of smooth terms			
Prediction	Follows prediction	Response variable	Covariate	Estimate	SE	*t*	*P*	Estimated df	*F*	*P*	Adjusted R^2
1	Somewhat	Prey encounters	Intercept	–0.6046	0.3708	–1.631	0.103				0.05
			Bottom duration	0.0065	0.0009	6.982	<0.0001				
2	Yes	Dive duration	Intercept	146.2665	6.4881	22.544	<0.0001				0.37
			Travel duration	0.3141	0.0850	3.694	0.0002				
			Dive depth	1.9600	0.2084	9.403	<0.0001				
3	Somewhat	Bottom duration	Intercept	151.5870	4.8610	31.180	<0.0001				0.05
			Travel duration					3.638	10.88	<0.0001	
4	Yes	Percent bottom duration (bottom duration/dive duration)	Intercept	2.2027	0.0552	39.94	<0.0001				0.72
			Travel duration	–0.0191	0.0006	–30.78	<0.0001				
5	Yes	Descent duration	Intercept	28.5520	1.6870	16.920	<0.0001				0.44
			Dive depth					2.928	72.95	<0.0001	
6	Yes	Bottom duration	Intercept	150.4717	7.3856	20.374	<0.0001				0.04
			Descent duration	–0.3986	0.1158	–3.443	0.0006				
			Prey present	23.2387	4.5692	5.086	<0.0001				
7	Yes	Bottom duration	Intercept	142.6396	6.7753	21.053	<0.0001				0.13
			Travel duration	–0.6676	0.0848	–7.876	<0.0001				
			Dive depth	1.7628	0.2195	8.033	<0.0001				
			Prey present	12.0741	4.6639	2.589	0.0099				
8	Yes	Bottom duration after first prey encounter	Intercept	148.4491	9.5353	15.568	<0.0001				0.31
			Time to first prey encounter	–0.6197	0.0514	–12.070	<0.0001				
			Descent duration	–0.2742	0.1537	–1.784	0.0754				
9	No	Bottom duration	Intercept	143.7014	8.9461	16.063	<0.0001				0.50
			Time to first prey encounter	0.2636	0.04515	5.837	<0.0001				
			Prey encounter rate	–575.3411	349.2931	–1.647	0.1006				
			Percent travel duration ≥0.2	–49.0775	7.7214	–6.356	<0.0001				
			Percent travel duration ≥0.35	–82.3735	9.1650	–8.988	<0.0001				
			Dive depth	1.5856	0.2641	6.005	<0.0001				
			Prey encounter rate × percent travel duration ≥0.2	5.6572	192.1192	0.029	0.9765				
			Prey encounter rate × percent travel duration ≥0.35	–833.5062	412.3912	–2.021	0.0442				
			Prey encounter rate × depth	24.2846	12.3479	1.967	0.0502				

Fig. 1. Observations and predicted effect of travel duration (*a*; controlled for dive depth) and dive depth (*b*; controlled for travel duration) on dive duration (prediction 2, Tables 1 and 3) of harbour seals (*Phoca vitulina concolor*). Solid lines represent mean predicted values and broken lines represent ±SE.

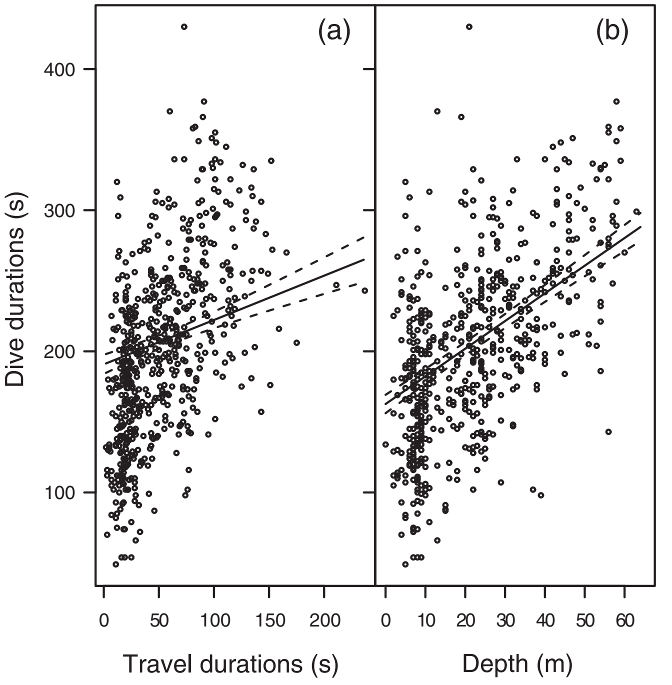


Fig. 2. Observations and predicted effect of travel duration on (*a*) bottom duration (prediction 3, Tables 1 and 3) and (*b*) on percent bottom duration of a dive, a proxy for the proportion of time spent foraging, (prediction 4, Tables 1 and 3) of harbour seals (*Phoca vitulina concolor*). Solid lines represent mean predicted values and broken lines represent ±SE.

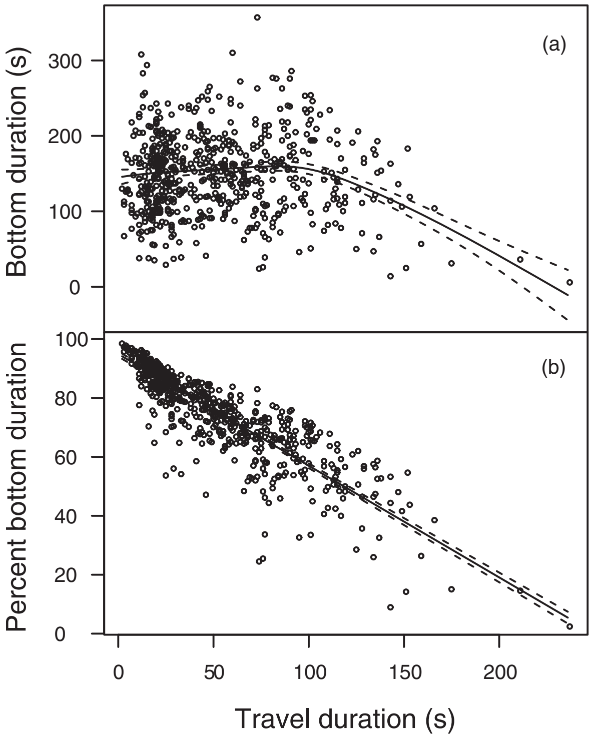
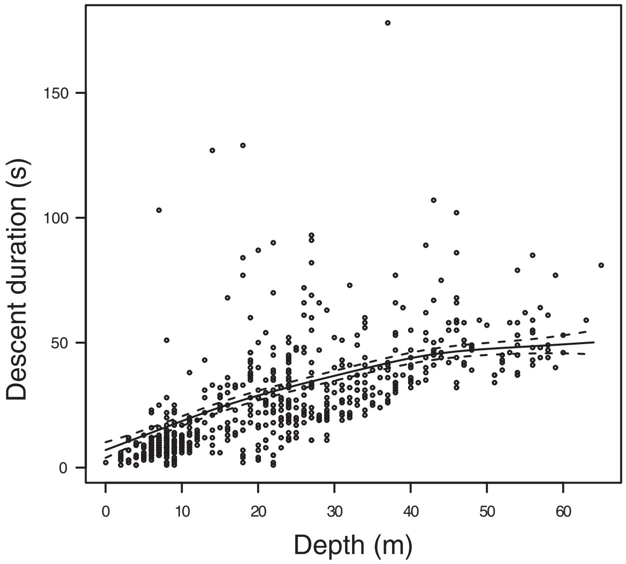


Fig. 3. Observations and predicted effect of dive depth on descent duration (prediction 5, Tables 1 and 3) of harbour seals (*Phoca vitulina concolor*). Solid lines represent mean predicted values and broken lines represent ±SE.



We found evidence for a relationship between prey presence and bottom duration, indicating that seals shortened dives if prey were not encountered (prediction 6, Table 3) regardless of travel duration and dive depth (prediction 7, Table 3; Supplementary Fig. S2[1]). However, little of the variation in bottom duration was explained by these models. Seals spent less time at the bottom of dives when prey were not encountered in the early part of the dive as predicted (prediction 8, Table 3; Supplementary Fig. S3[1]).

Contrary to prediction, we did not find evidence for a relationship between prey encounter rate, our proxy for prey density, and bottom duration. Dives were not terminated earlier when travel duration was short and prey encounter rate was low, and prey encounter rate did not influence the relationship between depth and bottom duration (prediction 9, Table 3).

We also examined the relationships between diving behaviour and encounters with sand lance. Cryptic sand lance was observed in 112 dives from 22 seals and schooling sand lance was observed in 111 dives from 19 seals. Seals had fewer separate prey encounters per dive when feeding on schooling sand lance compared with cryptic sand lance (prediction 1, Table 4) and spent relatively more time at the bottom of a dive when foraging on cryptic sand lance compared with schooling sand lance (predictions 6 and 7, Table 4). There was no significant difference in bottom duration between dives with cryptic and schooling sand lance for predictions 8 and 9.

Discussion

Although diving behaviour is ultimately constrained by physiological limits, within those limits, air-breathing predators can choose the duration and depth of dives, the speed and angle of travel to and from the bottom of the dive, and foraging tactics while at depth (Thompson et al. 1993). Controlled laboratory experiments provide some support for the predictions of diving models, but few studies have simultaneously measured diving behaviour and direct observations of individual prey encounters to test model predictions in free-ranging marine predators. Video observations of foraging in free-ranging harbour seals, combined with simultaneous measures of the components of diving behaviour, enabled us to test a number of predictions of both dive-cycle and prey-encounter models of optimal diving. We found qualitative support for most model predictions. However, there was little

Table 4. Parameter estimates, significance of linear terms, and goodness of fit (adjusted R^2) for the fitted mixed models used to explore the influence of prey species on foraging behaviour of harbour seals (*Phoca vitulina concolor*).

Prediction	Response variable	Covariate	Estimate	SE	t	P	Adjusted R^2
1	Prey encounters	Intercept	0.8946	0.2489	3.595	0.0004	0.17
		Bottom duration	0.0044	0.0012	3.678	0.0003	
		Sand lance (schooling)	–0.7380	0.1213	–6.082	<0.0001	
6	Bottom duration	Intercept	151.9133	7.7493	19.604	<0.0001	0.07
		Descent duration	–0.4320	0.1325	–3.261	0.0012	
		Sand lance (cryptic)	26.2111	6.8683	3.816	0.0002	
		Sand lance (schooling)	20.4513	6.2378	3.279	0.0011	
7	Bottom duration	Intercept	144.1043	6.8863	20.926	<0.0001	0.16
		Travel duration	–0.6661	0.0988	–6.743	<0.0001	
		Dive depth	1.6570	0.2829	5.858	<0.0001	
		Sand lance (cryptic)	19.5990	7.0570	2.777	0.0057	
		Sand lance (schooling)	6.9633	6.6387	1.049	0.2948	

Note: Covariate prey species is the sand lance (*Ammodytes dubius*).

support for two of the nine predictions that we tested (predictions 3 and 9, Table 1). We found that bottom duration did not first increase and then decrease for shorter travel durations (predictions 3 and 9, Table 1; Fig. 2*a*) and that bottom duration was not shorter for dives with short travel durations and low prey encounter rates (prediction 9, Table 1). Nonetheless, we note that we may not have had entirely appropriate data with which to test these predictions, as we assumed that the rate of prey encounters was a good measure of prey density and this may not be true.

The effects of instrument attachment on the behaviour of pinnipeds has been reported for a number of species (e.g., Kooyman et al. 1986; Walker and Boveng 1995; Boyd et al. 1997), including effects related to the attachment of animal-borne cameras (Bowen et al. 2002; Littnan et al. 2004; Heaslip and Hooker 2008). For this study, Bowen et al. (2002) found that dive durations for male seals carrying cameras (4.0 ± 0.12 min, n = 37) were similar to males fitted with smaller TDR and VHF transmitters only (3.8 ± 0.13, n = 31; Coltman et al. 1997), and that the rate of mass loss for the camera animals was significantly less (–0.4 ± 0.16 kg/day, $t_{[34]} = 3.1$, P = 0.004) than for males without cameras during the breeding season (–0.9 kg/day; Walker and Bowen 1993*b*, their Fig. 2). However, comparable trip duration data over short periods of time for seals without cameras were not available to assess whether seals with cameras spent more time at sea. Although the attachment of a relatively large animal-borne instrument (1.8% mean body mass) may have affected the behaviour of seals, we expect that any such effects were minor over the short duration of deployments.

The most common assumption of optimal diving models is that resource acquisition increases linearly with time spent foraging (Kramer 1988). Although we found some support for this assumption (prediction 1, Table 3; Supplementary Fig. S1[1]), relatively little of the variation in bottom duration (i.e., time spent foraging) was explained by the number of prey encounters, indicating that other factors also influenced prey encounter rate. Variability in prey encounter rate could be the result of differences in prey behaviour (e.g., schooling vs. individual fish), variation in prey density, or a reduction in patch quality during a dive or sequence of dives as prey are disturbed and consumed. For dives where seals were foraging on sand lance, we did find that prey encounters varied with prey behaviour, with fewer prey encounters for schooling vs. cryptic sand lance (prediction 1, Table 4).

Thompson and Fedak (2001) predicted that seals should adjust their dive duration in response to perceived changes in prey density. Sparling et al. (2007) tested this prediction for grey seals (*Halichoerus grypus* (Fabricius, 1791)) by experimentally varying prey density and distance to surface in a large experimental pool and seals responded by leaving low-quality patches earlier. Similarly, captive Steller sea lions (*Eumetopias jubatus* (Schreber, 1776)) also increased dive duration and foraging time with prey encounter rate (Cornick and Horning 2003). We did not find a relationship between prey encounter rate, our assumed proxy for prey density, and bottom duration; we also did not find any suggestion that there was a benefit to terminating dives when prey encounters and travel times were relatively low. However, we had a narrow range of prey encounter rates with which to test these predictions and the number of prey encountered per dive may not be a reasonable proxy for prey density. Unfortunately, the relatively narrow field of view of the video camera precluded the estimation of prey density from the video.

The timing of when prey are encountered occur during a dive may also influence the amount of time spent foraging. We did find that the decision to terminate a dive was influenced by prey presence regardless of travel durations, dive depth, and the time to first prey encounter. The early termination of dives when prey were encountered relatively later in a dive supports a giving-up rule whereby seals terminate dives irrespective of the numbers or rate of encountered prey, for example, when prey are encountered later in a dive (Thompson and Fedak 2001). Additional variation in the relationship between bottom duration and prey encounters could also be introduced by variation in swimming speed among dives associated with pursuing fast or slow moving prey (e.g., Bowen et al. 2002).

Swimming speed was not measured for individual dives, but the positive relationship between descent duration and dive depth suggests that swim speed did not change with dive depth to depths of about 40 m (prediction 5, Table 3; Fig. 3). However, for dives >40 m, there was an indication that decent duration levelled off with increasing dive depth, suggesting that seals either increased their swim speed and (or) descended at a steeper dive angle. Without information on swim speed and dive angle, we are not able to test this prediction thoroughly. Captive grey seals reduced their swim speed significantly as travel duration increased (Gallon et al. 2007), supporting the prediction that swim speed should decrease for deeper dives or that seals should swim at the minimum cost of transport (Thompson et al. 1993). Contrary to prediction, free-swimming species including Antarctic fur seals (*Arctocephalus gazella* (Peters, 1875)), New Zealand sea lions (*Phocarctos hookeri* (Gray, 1844)), and northern (*Mirounga angustirostris* (Gill, 1866)) and southern (*Mirounga leonina* (L., 1758)) elephant seals have been shown to increase swim speed with dive depth (Boyd et al. 1995; Hindell and Lea 1998; Crocker et al. 2001; Hassrick et al. 2007). It is possible that such increases in speed may not in fact be costly if they are a result of negative buoyancy at greater depths and a change in swim method with longer passive glide phases.

The models of Thompson et al. (1993) also predict that both the net rate of energy gain at low prey density and foraging efficiency will be maximized if seals remain stationary when hunting active prey. Male harbour seals in our study did not behave this way; in fact, they swam continuously while hunting schooling sand lance and flatfish (Bowen et al. 2002). Harbour seals foraging in Froan, Norway, swam continuously at close to the maximum cost of transport as predicted in both the efficiency and the net-rate maximizing models (Thompson et al. 1993).

For short travel durations, Houston and Carbone's (1992) model predicts that divers benefit from making short dives and maintaining low oxygen stores with higher rates of oxygen intake at the surface; as travel durations increase, divers increase oxygen stores to allow for increased foraging time, which enables them to reduce the number of trips between the foraging patch and the surface; and that maximum dive duration is reached as travel durations increase, further forcing the diver to decrease foraging time to compensate for longer travel durations. Not unexpectedly, seals dove longer when travel durations were longer (prediction 2, Table 3; Fig. 1*a*) and when dives were deeper (prediction 2, Table 3; Fig. 1*b*). Sparling et al. (2007) also found that the dive durations of grey seals increased with dive distance, as well as with an increase in prey encounter rate. Over a wide range of travel durations, bottom duration decreased as predicted for the few dives that we had with travel durations >100 s; however, for short travel durations, bottom duration did not first increase and then decrease (prediction 3, Table 3; Fig. 2*a*). Comparable results have been found for diving Common Eiders (*Somateria mollissima sedentaria* Snyder, 1941) (Heath et al. 2007). We may not have had sufficient data for dives with short travel durations to detect an increase in bottom duration for shallow dives. Estimates of oxygen intake at the surface and oxygen consumption at depth would be needed to rigorously test this prediction. A greater amount of the variation in bottom duration was explained when bottom duration was expressed as a proportion of dive duration (percent bottom duration), and percent bottom duration also decreased with increasing travel duration in agreement with predictions from theory (prediction 4, Table 3; Fig. 2*b*).

Our data provided qualitative support for many of the model predictions, but in some cases, relatively little of the observed variation in behaviour was explained by these models (Table 3). There are undoubtedly several reasons for this. First, our results were obtained during the breeding season over relatively short sampling periods and therefore may not reflect the range of foraging behaviours used by this species. The short deployment durations restricted the number of consecutive dives for which we have data and may have also reduced variability in the numbers and types of prey encountered. Diving data from complete dive bouts may be needed to provide the contrast in behaviour required to provide stronger tests of some predictions. Sampling over a longer period would permit us to test predictions related to the number of dives per bout (Mori 1998*b*) and those that are an extension of basic dive models such as allowing for nonlinearity in intake rate and heterogeneity in patch quality, abundance, and profitability (e.g., Thompson and Fedak 2001; Mori et al. 2002; Heithaus and Frid 2003; Houston et al. 2003). Sampling over a longer period would also permit testing of predictions at additional temporal scales (over seasons and foraging trips) so that we could examine how foraging decisions and the currencies being optimized may vary with respect to the seasonal life-history events of an individual (e.g., breeding and moult). Second, as noted in other studies, current models are too simplistic to predict the behaviour of diving animals (e.g., Halsey and Butler 2006). These deterministic models aim to explain how foragers make decisions that optimize energy intake over time under the constraint of oxygen stores in a stochastic environment and without perfect knowledge. Not included in these models is how animals may make trade-offs between foraging and other behaviours. Other factors that could influence time allocation during foraging dives are competition (Halsey et al. 2006); behaviours related to mating, especially for pinnipeds that mate aquatically such as harbour seals (Boness et al. 2006); and risk of predation (e.g., Wirsing et al. 2008). Including body mass as a covariate in models testing predictions of ODT (Mori 1998*a*, 2002) might also improve the amount of explained variation, as mass can be a significant predictor of dive behaviour as a result of differences in oxygen stores and metabolic rate (Costa 1993; Boyd and Croxall 1996; Schreer et al. 2001). Modifications in dive behaviour in the presence of predators may also depend on foraging mode and (or) prey species (e.g., schooling prey vs. cryptic prey) when the foraging mode affects vigilance (Wirsing et al. 2011). Foraging decisions of male harbour seals may vary with the risk of predation, as sharks are a known predator of harbour seals (Lucas and Stobo 2000; Bowen et al. 2003).

Despite physiological limitations, air-breathing divers are able to vary their foraging behaviour in response to prey cues. Our study is one of the few studies to simultaneously measure diving behaviour and direct observations of individual prey encounters, allowing us to test predictions of optimal diving models for free-ranging pinnipeds. We found that prey encounters increased with bottom time, dive duration increased with travel duration, bottom duration decreased with travel duration, and that seals maximized bottom duration when prey were present and when prey were encountered relatively earlier in a dive, but we did not find any relationship between bottom duration and prey encounter rate. From our modelling results, it was clear that there are other factors which influence how male harbour seals made foraging decisions. An examination of complete dive bouts in addition to prey field data, rather than only the prey encountered, could give us better insight into the decisions that these animals make to maximize their energy intake and ultimately fitness.

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