

A conceptual model of the variation in parental attendance in response to environmental fluctuation: foraging energetics of lactating sea lions and fur seals

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ABSTRACT

1. A conceptual model is described and tested using empirical data that predicts how air-breathing marine vertebrates that are tied to shore for reproduction, but feed at sea, should respond to changes in prey availability.

2. The model examines the trade-off between changes in trip duration and foraging intensity as measured by field metabolic rate. It predicts that parents should increase the intensity of effort, and hence metabolic rate, prior to increasing the duration of foraging trips to maintain nutrient delivery to the young.

3. The model was tested with data on the foraging energetics and trip duration of four species, northern and Antarctic fur seals and California and Australian sea lions, each studied over two contrasting seasons.

4. The response of these marine predators to changes in prey availability due to climate driven environmental perturbation was found to support the conceptual model.

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INTRODUCTION

Air-breathing marine vertebrates that breed on land and feed at sea are constrained by the separation of feeding from breeding (Bartholomew, 1970; Costa, 1991a; Boyd, 1998; Trillmich and Weissing, 2006). Adults make periodic trips to feed at sea to acquire resources followed by intermittent visits to the rookery/colony to feed their offspring. The timing of these trips is determined by the proximity of the foraging

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grounds, the fasting ability of the offspring and the reproductive physiology of the adults (Costa, 1993). In mammals, lactation confers the greatest flexibility in the timing and optimization of the provisioning pattern, thus requiring that the female be the sole provider of nutrition to the offspring (Costa, 1991a, b).

The fundamental provisioning pattern of a species has evolved to the long-term average characteristics of the timing and geographic distribution of prey resources in a specific habitat. However, climate driven processes cause changes in the distribution and abundance of prey, often requiring modification of the optimal parental provisioning pattern (Croxall *et al.*, 1988; Inchausti *et al.*, 2003). Variations in prey availability are associated with dynamic oceanographic features such as seasonal variation in sea ice extent, upwelling, and changes in the thermocline and/or mixed layer depth (Murphy *et al.*, 1998; Palacios, 2004). One of the most severe and best documented responses in provisioning pattern is the response of pinnipeds to changes in prey availability associated with El Niño or ENSO events (Trillmich *et al.*, 1991). While some pinnipeds (true seals) and seabirds (albatrosses) have evolved life history patterns that buffer them from interannual or seasonal variations in prey resources, others such as penguins, fur seals, and sea lions are sensitive to variations in the availability of food resources near their breeding rookeries (Costa, 1991a, 1993; Trillmich *et al.*, 1991; Williams and Croxall, 1991a, b; Croxall *et al.*, 1999). For adults provisioning offspring, the most common response to variations in food availability is to change the duration of foraging trips to sea (Costa *et al.*, 1989; Boyd *et al.*, 1991; Trillmich *et al.*, 1991; Merrick and Loughlin, 1997; Boyd, 1998; Mattlin *et al.*, 1998; Croxall *et al.*, 1999; Georges and Guinet, 2000; Beuplet *et al.*, 2004). However, other responses have been observed, including changes in diving behaviour, activity patterns (Feldkamp *et al.*, 1991; Boyd *et al.*, 1995; Boyd, 1996, 1999), and energy expenditure (Costa *et al.*, 1989, 1990; Costa and Gales, 2003).

The successful weaning and subsequent survival of offspring is directly related to the rate of nutrient and energy delivery (Prince and Ricketts, 1981; Trillmich and Limberger, 1985; Costa, 1991b; Trillmich *et al.*, 1991; Arnbohm *et al.*, 1993; Fedak *et al.*, 1994; Trillmich, 1996; Arnould and Hindell, 2002; Trillmich and Weissing, 2006). Parents should avoid increases in trip duration whenever possible (Boyd, 1998; Trillmich and Weissing, 2006), because the amount of energy delivered per shore visit to the offspring is relatively constant for many marine pinnipeds and seabirds (Costa, 1991a, b). Therefore, if a parent spends more time to deliver the same amount of energy, the offspring receives less overall energy. As a result, more of the offspring's energy is spent on maintenance and its growth will slow. In the worst case, sustained negative energy balance will result in offspring death.

Given that an increase in trip duration is the least preferred response to environmental perturbation, it is important to consider what other options a pinniped or seabird has (Merrick and Loughlin, 1997; Mattlin *et al.*, 1998; Beuplet *et al.*, 2004). In response to reductions in prey availability a marine predator could change its foraging behaviour in the following ways: (1) change the type of prey consumed and/or forage in a different location; (2) work harder while at sea. Modifications in foraging behaviour might require changes in prey type, such as switching from easier to acquire, shallow abundant, low energy prey (small, lipid-poor prey), to prey that is harder to obtain but that has higher energy content. For example, they might pursue more energy dense prey that requires deeper longer dives to the benthos (Costa and Gales, 2003). Changes in the type of prey consumed may also be associated with changes in where the prey is obtained. For example, feeding on mesopelagic prey would require foraging further offshore beyond the continental shelf (longer trips), whereas benthic or epipelagic foraging could be carried out closer to the rookery (shorter trips). Finally, an adult could work harder at sea, that is, increase the amount of time spent foraging, or the intensity of foraging effort (increased time spent swimming, more active and/or difficult diving pattern). Any change in foraging intensity or time spent foraging should be associated with a higher field metabolic rate (FMR).

THE MODEL

A graphical representation of this conceptual model is shown in Figure 1. This model proposes that as prey availability declines, the parent first responds by increasing foraging effort (dashed line: changing swim speed, diving intensity, time foraging or swimming), as indicated by an increased field metabolic rate but without an increase in trip duration (this is what occurs in the shaded region). There is a limit to how much an animal can increase its foraging intensity or effort and as the animal approaches its maximum metabolic effort (metabolic ceiling), it has no alternative but to increase foraging trip duration (solid line). At some point the amount of energy delivered per foraging trip is insufficient to sustain the pup over the intervening foraging trips and the pup goes into a negative energy balance and eventually dies.

Such a model provides a series of predictions or outcomes that can be used to assess whether the model can be used to describe what occurs in nature. The first prediction is that one would expect to see a change in FMR that is associated with a different diet, or more intense foraging effort and this change would not be associated with any change in the foraging trip duration or energy delivery to the offspring. Further, the amount of energy returned to the rookery should remain constant irrespective of adult foraging effort. The second prediction is that during extremely severe events, no increase in FMR will be sufficient to obtain enough prey, and the parent will have no alternative but to increase both FMR and trip duration. A final prediction is that in some environments parents may normally operate at or near their maximum metabolic ceiling, and thus in these habitats they would have a limited ability to further increase their foraging effort. In this situation, one would expect a relatively high FMR under any condition and when prey availability declines there will be an increase in foraging trip duration with no change in FMR.

RESULTS

Using the available literature the responses of four species of otariids were examined to see if they lend support to this model. Species examined include northern fur seals, *Callorhinus ursinus*, California sea lions, *Zalophus californianus*, Antarctic fur seals, *Arctocephalus gazella*, and Australian sea lions, *Neophoca cinerea*. The northern fur seals and Australian sea lions were studied over what appeared to be two 'normal'

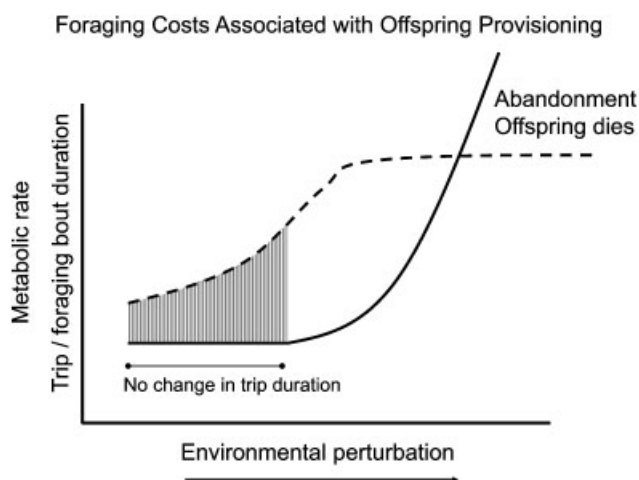


Figure 1. A conceptual model of how parents should respond to environmental perturbation that causes a reduction in prey availability. The dashed line represents FMR and the solid line is trip duration.

seasons, while the California sea lions and the Antarctic fur seals were studied during and after a profound ENSO event and the following 'normal' year.

Northern fur seal

Data from northern fur seals foraging during the same time of season in 1981 and 1982 from St. George Island, Alaska (Costa and Gentry, 1986) supports prediction one, that animals can modify their foraging intensity without leading to changes in trip duration by switching prey or other changes in foraging behaviour. This study found that while FMR was significantly higher one year, the rate of mass gain and trip duration remained the same between years (Figure 2). Further, they used a comparison of FMR to water influx rate as an index of differences in prey biomass consumed

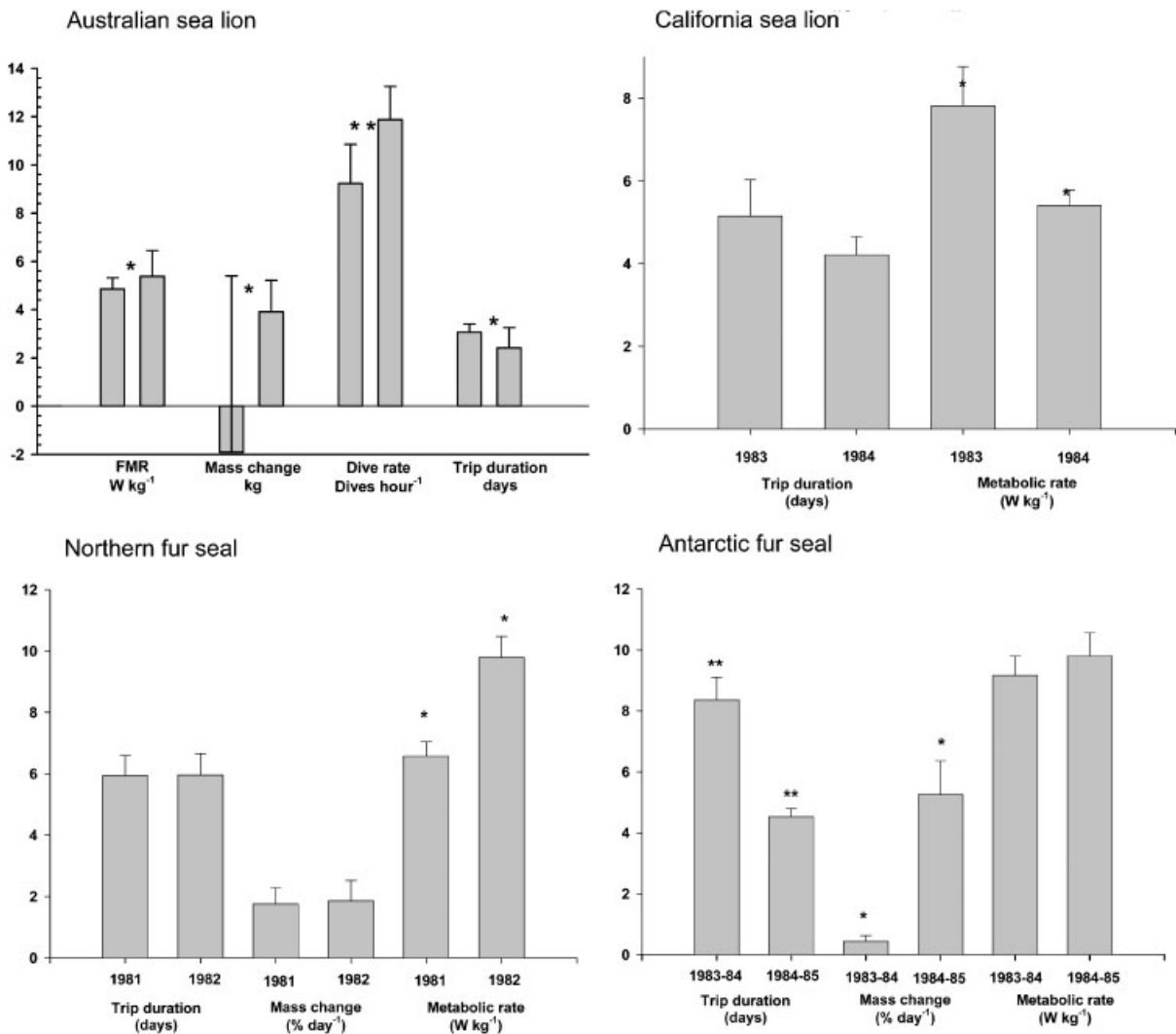


Figure 2. Changes in trip duration, mass change and metabolic rate are given for two different years for female Northern and Antarctic fur seals, California and Australian sea lions. Data are also provided on dive rate for Australian sea lions. Data are from Costa and Gentry (1986), Costa *et al.* (1989, 1990), Costa and Gales (2003).

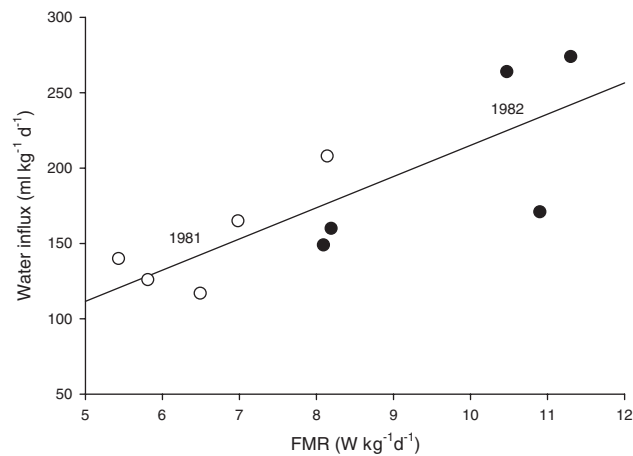


Figure 3. Plot of FMR as a function of water influx of Northern fur seal females foraging between two seasons (Costa and Gentry, 1986). Fur seals in 1981 (open circles) were feeding primarily on adult pollock and during 1982 (solid circles) they were feeding on 0 age pollock (Sinclair *et al.*, 1994).

between years. This is based on the assumption, validated by feeding studies, that animals do not drink while at sea; thus all of their water is derived from their prey (Costa, 1987). Therefore animals in 1982 had a higher prey intake, but they also had a higher FMR, indicating that they worked harder to obtain that prey (Figure 3). Conversely animals in 1981 had a lower FMR and consumed a lower amount of prey, but still gained the same mass over the foraging trip. This suggests that animals in 1981 were foraging on higher quality prey compared to 1982. An independent study carried out simultaneously on the feeding habitats of northern fur seals supports this suggestion, as female fur seals were feeding primarily on adult 5–6 year old pollock in 1981, while in 1982 they fed primarily on 0 age pollock (Sinclair *et al.*, 1994). Zero age pollock are smaller, have higher water content and lower energy density than adult pollock, and they are dispersed throughout the water column, requiring more effort to capture. Adult pollock are larger, are located near the benthos, and have lower water contents, and with higher energy density, fewer individuals need be consumed, requiring less foraging effort and a lower FMR. Changes in pollock availability between the two years of this study appear to be related to climate driven processes that alternate between warm and cold regimes in the Bering Sea (Hunt *et al.*, 2002).

California sea lions

Support for the second prediction, that during severe reductions in prey availability parents will have to increase both their FMR and trip duration, comes from California sea lion females foraging during the 1982–1983 El Niño. The 1982–1983 El Niño event was one of the most severe on record and the response of California sea lion females reflects the severity of that event. California sea lions foraging from San Miguel Island increased their foraging effort as indicated by both a higher FMR and longer trip durations (Figure 2). Females also showed significant alterations in diving behaviour as well as diet shifts (Feldkamp *et al.*, 1991). Female California sea lions had some scope to increase their FMR, but this was apparently insufficient to accommodate the severe reduction in prey availability so they also increased trip duration (Ono *et al.*, 1987; Costa *et al.*, 2000). These longer trips had an adverse effect on pup growth and survival—mothers were unable to supply sufficient milk to sustain their pups, and many were abandoned and starved (Ono *et al.*, 1987). As the model predicts, during severe reductions in prey availability, the parent has no alternative but to increase both FMR and trip duration.

Antarctic fur seals

Support for the last prediction, that in some habitats parents normally operate at their metabolic ceiling and can only increase their trip duration in response to perturbations, can be found from Antarctic fur seals breeding on Bird Island South Georgia during 1983–1984 and 1984–1985. Like California sea lions, Antarctic fur seal females faced reductions in prey availability resulting from one of the most severe ENSO events recorded in the Southern Ocean (Costa *et al.*, 1989; Boyd and Roberts, 1993). The FMR and body mass gained by Antarctic fur seal females was equivalent between the two years. The fact that the FMR of Antarctic fur seal females was as high as the highest rate measured for similar sized northern fur seals suggests that they were foraging at or near their metabolic ceiling. This would leave them with little room to respond to environmental change. Consistent with the model was that trip durations increased and in fact were twice as long during the low prey year (1983–1984) compared to the ‘normal year’ (1984–1985). These data are consistent with the idea that females were normally foraging at their metabolic ceiling and had no choice but to increase their trip durations. However, subsequent FMR measurements on Antarctic fur seals both at Bird Island South Georgia (Arnould *et al.*, 1996) and at Cape Shirreff, Livingston Island (Costa *et al.*, 2000) indicates that foraging intensity can vary between colonies and over time.

Arnould *et al.* (1996) measured on average lower FMRs than those measured by Costa *et al.* (1989). Their lower FMR measurements suggest that while conditions appeared ‘normal’ in 1984–1985, as females had normal foraging trip durations, they were still working harder than females at South Georgia some years later. Metabolic measurements carried out on female fur seals at Cape Shirreff, the furthest south rookery; indicate that these animals forage at a level equivalent to that measured at Bird Island in 1983–1985. These differences in FMR appear to be associated with differences in the amount of time females spend diving while at sea. Arnould *et al.* (1996) found in FMR measurements covering multiple years that the FMR of Antarctic fur seal females was directly proportional to the time spent diving versus surface swimming. They found that higher FMRs were associated with more surface swimming indicating that these females spent more time and energy looking for prey. Similarly, fur seals foraging from Cape Shirreff spent more time surface swimming than females at South Georgia, a finding consistent with the higher FMR measured at Cape Shirreff (Costa *et al.*, 2000).

Australian sea lions

As data on prey availability were not available for Australian sea lions it may not be surprising that the model predictions were mixed. Due to the unusual 18 month breeding cycle of the Australian sea lion, the field measurements were carried out with pups of the same age, but during different seasons; the winter of 1988 and during the summer of 1990. While there were significant differences in FMR between seasons, the change in trip duration was opposite to the prediction (Figure 2). While an increase in FMR was also associated with a significant increase in dive rate, animals made shorter trips. However, the changes in FMR, while statistically significant, were relatively small compared to the changes in FMR observed in the fur seals. Furthermore, females had a net loss of mass during the season where they had lower FMRs and longer trip durations. This suggests that female sea lions compensated for reduced prey availability by going into a negative energy balance and by using stored body reserves to produce milk for their pups. The larger size of Australian sea lion females (85 kg) might make this more feasible than the smaller fur seals (36–38 kg). Also, Australian sea lions are benthic foragers and while at sea, dive continuously with almost no surface swimming, therefore, their ability to increase or modify their FMR is probably very limited (Costa and Gales, 2003).

CONCLUSIONS

The available data lend support for the model that otariid females modify their foraging behaviour (intensity, prey choice, time spent foraging) in order to maintain foraging trip durations as short as possible. Longer foraging trips result in lower overall energy delivery to the pup because the rate of energy delivery goes down. Increases in trip duration should thus be the option of last resort. However, the ability of female fur seals and sea lions to modify their foraging behaviour varies between rookeries. Although the available data are insufficient to evaluate, it is likely that different foraging patterns have greater or lesser amounts of plasticity. For example, Arnould *et al.* (1996) have shown considerable variation in the amount of time spent searching and surface swimming between years and between individuals for epipelagic foraging Antarctic fur seals. In contrast, benthic foraging fur seals and sea lions spend more of their time diving while at sea and normally operate closer to their maximum aerobic diving ability (Costa and Gales, 2003; Costa *et al.*, 2004). This suggests that benthic foraging species would be less capable of responding to changes in prey availability and would thus have to increase their foraging trip duration sooner than an epipelagic forager. The range of responses to environmental fluctuation can depend on body size, foraging patterns (epipelagic versus benthic) or foraging location.

These results show that female fur seals and sea lions have the ability to respond to fluctuations in prey availability without changing the duration of their foraging trips. This has important implications for the use of trip duration as an index of prey availability. The analysis here indicates that trip duration (attendance pattern) may not be a very sensitive index of prey availability as animals may respond by changing foraging locations and/or foraging intensity to keep trip duration constant. However, while this model cautions that prey availability may change without changes in trip duration, it does provide strong support for the argument that an increase in trip duration is associated with a reduction in prey availability. Furthermore, while this model was developed and tested with data derived from fur seals and sea lions, it should be applicable to other vertebrates that similarly forage at sea and feed their young on shore. For example, changes in the rate of energy delivery and chick growth rate have been reported in a large numbers of seabirds (Chastel *et al.*, 1993; Phillips *et al.*, 1996, 1997; Shea and Ricklefs, 1996; Golet *et al.*, 2000; Weimerskirch and Lys, 2000). It would be instructive to test whether the energetic model proposed here works for these species as well.

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