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Development and application of telemetry techniques to investigate seal behaviour and survival.

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PhD

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Abstract

The work described in this thesis covers the development and application of telemetry techniques to investigate seal behaviour and survival. The accuracy of animal location fixes derived from the Argos satellite system was determined, and filtering methods were constructed which removed the more erroneous locations fixes. We developed Argos Satellite Relay Data Loggers (SRDLs) which collect and relay dive and behavioural information from marine mammals via the Argos satellite system. SRDLs were used to describe the foraging and dive behaviour of adult South Georgia southern elephant seals (*Mirounga leonina*) in relation to bathymetric and oceanographic features. SRDLs were also deployed on naïve southern elephant seal pups at Macquarie Island to determine the patterns of dispersal and to relate these patterns to oceanographic variability. Body condition measures and energy expenditure estimates suggested that the smaller weaned pups were almost at the stage of starvation before they encountered foraging areas. UK Grey seal (*Halichoerus grypus*) foraging was also studied using SRDLs. Most patterns of movement were within 40 km of haulout sites and foraging was inferred to take place in localised areas that were often the preferred habitat of sandeels (*Ammodytes* spp). Grey seals could also move many hundreds of kilometres from one region to another. Factors that influence the first year survivouship of grey seal pups were studied in a mark-recapture experiment at the Isle of May (UK). Survivourship was greater for females and for those weaned pups with a greater weaned body mass. Also higher post-weaning circulating levels of immunoglobulin decreased the probability of survival. A novel telemetry mark-recapture technique based on mobile phone technology was developed to collect 'resighting' data more efficiently and from which survivorship could be modelled with fewer assumptions.

Declaration

(i) I, Bernie McConnell, hereby certify that none of the work contained in the books or papers in this portfolio has been submitted by me for a higher degree in any other university.

date: 01 June 2004 signature of candidate

(ii) I was admitted as a research student in November 1997 and as a candidate for the degree of PhD in November 1998; the higher study for which this is a record was carried out in the University of St Andrews between 1997 and 2004.

date: 01 June 2004 signature of candidate

(iii) I hereby certify that the candidate has fulfilled the conditions of the Resolution and Regulations appropriate for the degree of PhD. in the University of St Andrews and that the candidate is qualified to submit this portfolio in application for that degree.

date: 01 June 2004 signature of supervisor .

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1. List of portfolio publications

Fedak, M., P. Lovell, B. McConnell, and C. Hunter. 2002. Overcoming the constraints of long range radio telemetry from animals: Getting more useful data from smaller packages. Integrative and Comparative Biology **42**:3-10.

Fedak, M. A., P. Lovell, and B. J. McConnell. 1996. MAMVIS: A marine mammal behaviour visualization system. Journal of Visualization and Computer Animation **7**:141-147.

Hall, A. J., B. J. McConnell, and R. J. Barker. 2001. Factors affecting first-year survival in grey seals and their implications for life history strategy. Journal of Animal Ecology **70**:138-149.

Hall, A. J., B. J. McConnell, and R. J. Barker. 2002. The effect of total immunoglobulin levels, mass and condition on the first-year survival of Grey Seal pups. Functional Ecology **16**:462-474.

McConnell, B., R. Beaton, E. Bryant, C. Hunter, P. Lovell, and A. J. Hall. 2004. Phoning home - a new GSM mobile phone telemetry system to collect mark-recapture data. Marine Mammal Science **20**:274-283.

McConnell, B., M. Fedak, H. R. Burton, G. H. Engelhard, and P. J. H. Reijnders. 2002. Movements and foraging areas of naive, recently weaned southern elephant seal pups. Journal of Animal Ecology **71**:65-78.

McConnell, B. J., C. Chambers, and M. A. Fedak. 1992a. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern-Ocean. Antarctic Science **4**:393-398.

McConnell, B. J., C. Chambers, K. S. Nicholas, and M. A. Fedak. 1992b. Satellite tracking of grey seals (*Halichoerus grypus*). Journal of Zoology **226**:271-282.

McConnell, B. J., and M. A. Fedak. 1996. Movements of southern elephant seals. Canadian Journal of Zoology-Revue Canadienne De Zoologie **74**:1485-1496.

McConnell, B. J., M. A. Fedak, P. Lovell, and P. S. Hammond. 1999. Movements and foraging areas of grey seals in the North Sea. Journal of Applied Ecology **36**:1-19.

Vincent, C., B. J. McConnell, V. Ridoux, and M. A. Fedak. 2002. Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. Marine Mammal Science **18**:156-166.

2. Introduction

This discussion critically reviews the portfolio of papers submitted for a PhD by the candidate, and which are attached to the end of this document. Section 3 introduces the biological objectives and then describes the development of telemetry methods to deliver the necessary data, and the visualisation methods required to explore them. Section 4 describes the use of these techniques to study the movement and foraging behaviour of grey seals (*Halichoerus grypus*) in the North Sea and southern elephant seals (*Mirounga leonina*) in the Southern Ocean. Section 5 describes a study of factors that determine first-year survival in grey seals and then describes the development of a novel telemetry system that can provide greatly improved mark-recapture data with which to populate survivorship models. Section 6 provides a summary and a statement of the candidate's contribution to the submitted portfolio of papers.

3. Telemetry System Development

Fedak, M., P. Lovell, B. **McConnell**, and C. Hunter. 2002. Overcoming the constraints of long-range radio telemetry from animals: Getting more useful data from smaller packages. Integrative and Comparative Biology **42**:3-10.

Fedak, M. A., P. Lovell, and B. J. **McConnell**. 1996. MAMVIS: A marine mammal behaviour visualization system. Journal of Visualization and Computer Animation **7**:141-147.

McConnell, B. J., C. Chambers, and M. A. Fedak. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern-Ocean. Antarctic Science **4**:393-398.

Vincent, C., B. J. **McConnell**, V. Ridoux, and M. A. Fedak. 2002. Assessment of Argos location accuracy from satellite tags deployed on captive gray seals. Marine Mammal Science **18**:156-166.

All species of seal come onto land or ice for the energetically expensive processes of birth and lactation. During the remainder of the year they forage at sea, regaining sufficient condition to meet the material and energetic requirements of the next breeding season. This non-breeding period of energy gain may be interrupted, to varying degrees depending upon the species, by periods spent hauled out ashore or on ice. The proportion of time spent hauled out usually increases dung the period of moult.

In order to understand where, when and how foraging takes place, and to interpret the periods when seals may be observed and counted ashore or on ice, we need to be able to track and monitor their behaviour. Since there was a paucity of *a priori* information, the initial biological objectives were of an exploratory nature, rather than specific hypothesis testing. However, acquiring such data is a technically challenging task. Many species are capable of travelling far from land for prolonged periods. While at sea they may spend up to 90 percent of their time underwater, making them invisible to direct observation.

The design considerations and system realisation of an appropriate telemetry system capable of providing such at-sea foraging data are described by Fedak *et al.* (2002). The resultant telemetry device is termed a Satellite Relay Data Logger (SRDL). Its hardware design is outside the scope of this document (although BM did play a significant role in the development team). In this Section we concentrate on the data collection, storage and transmission strategies.

Data Requirements

Our primary aim is to track animal movements and to describe usage patterns. From these data we may infer foraging areas and transit routes, and then go on to relate these patterns to those of con-specifics and to geographic features. The second data requirement is dive behaviour. What dive strategies do seals use to travel and to explore and exploit foraging areas? Is foraging pelagic or epi-benthic? We now address how, technically, the two principal requirements of movement and dive behaviour can be met.

Movement

The Argos satellite system (Argos 1989) can provide location fixes and relay data from telemetry tags with an appropriate Argos RF (radio frequency) module. The system is based on a set of polar orbiting satellites that provide global coverage. However limitations imposed by Argos protocols, the discontinuous visibility of the satellites and the frequent submergence of seals (which prohibits radio communication) combine to reduce the quality of location fixes and the rate at which data may be relayed. However, track data can be improved with post-filtering techniques (see below).

Conventional GPS, whilst providing global location fixes, is unsuitable for tracking the majority of marine mammals. Their restricted surfacing periods, which may be interrupted by wave wash over the tag, radically reduces the probability of reception of the ephemeris data stream which are required for on-board location determination. Thus, there is a high probability of periods without a position being acquired.

Behavioural data

We consider three primary tag sensors from which a variety of behavioural information may be inferred. A wet–dry sensor is used both to inhibit transmission attempts under water and to determine periods when the animal is hauled out. The wet-dry sensor (like all the other sensors) is polled once every 4 s. A Haulout event starts when the sensor continuously returns dry for a period of 10 min. It ends when the sensor continuously returns dry for a period of 2 min.

A pressure sensor determines the depth. A Dive event starts when the depth is greater than 6 m for a period of at least 8 s. It ends when the sensor returns dry. During a dive a flow sensor is regularly polled to measure distance travelled through the water.

Data processing and relay

There are two general strategies to get data ashore. Data may be stored in memory and the device physically retrieved. Although used to great effect in many studies, such a system has three inherent weaknesses. First, many species of marine mammal may not be readily recaptured for device retrieval. Second, even if individuals can be retrieved, the data are biased to those that survive. We learn nothing about behaviour that may influence the mortality of, say, juvenile seals. Third, without the Argos location determination system, alternative location determination systems are required. The most frequently used system, termed geo-location, uses light levels to determine the time of local sunrise and sunset. From these data daily locations may be estimated, but with far less accuracy than by using the Argos system (Hill and Braun 2001).

The second strategy, and the one employed here, is to relay data in near real time using the Argos satellite system. However the low effective data bandwidth of an Argos SRDL on a seal means that only about one per cent of data that are collected can be relayed without error. Therefore, intelligent context-driven data compression and pseudo-random transmission scheduling are employed to ensure that the data relayed ashore are an unbiased representation of the actual behaviour of the seal.

Onboard processing

As described above, the tag can be in one of three states: 'Haulout', in a 'Dive', or 'Surface' (neither in a Haulout nor in a Dive). Data are collected and indexed based upon the tag's current state. When a dive is completed, a dive-end event is triggered and an algorithm detects, and only stores, the four most significant inflections in the time-depth profile buffer. This allows the most efficient transmission of data and later reconstruction of dive shape. Swim speed data during a dive are also summarised within the periods bounded by the inflections. Haulout events are stored simply as the start and end times of the haulout.

In addition to such-event driven records (dive and haulout) the tag also summarises information at regular time intervals. The usual configuration is that percentage of time spent hauled out, diving, and at the surface is computed and stored every six hours. Such time-driven records are termed summary records.

Transmission Scheduling

Even though raw data are compressed onboard as either event- or time-based records the rate at which these records accrue still exceeds the available Argos bandwidth. Therefore, a representative *sample* of the data is transmitted. A pseudo-random sampling of stored records ensures that the data received ashore, while not necessarily complete or contiguous, are not biased to one particular type of behaviour.

Location Accuracy and Post Processing

The infrequent and irregular transmissions (uplinks) to the Argos satellites from a SRDL on a seal results in a high proportion of low quality location fixes. Argos assigns a Location Quality (LQ) index to locations but the system does not provide confidence intervals for the three purportedly worst and most frequent LQs (0, A and B). Vincent *et al.* (2002) used SRDLs on captive grey seals to estimate the errors associated with a range of LQ fixes. The data were pre-filtered with the technique of McConnell *et al.* (1992a) (see below). They demonstrated that, for each LQ, the errors were normally distributed and they calculated confidence intervals. Two important findings come from this work. First, longitudinal error was consistently and significantly greater than latitudinal error. Second, the quantification of error from 'un-guaranteed' Argos locations permitted their use and interpretation by many researchers who had previously dismissed these low quality fixes from their results. Significantly, un-guaranteed LQ A fixes were as accurate as guaranteed LQ 1 fixes.

Even though confidence intervals were now available for all location quality of fixes, the preponderance of low-grade locations at sea could still obscure the actual movements of marine mammals. McConnell *et al.* (1992a) thus developed a forward-backwards filtering algorithm that rejects fixes that would require an unrealistic swimming speed to achieve.

A description of this method follows. *A priori,* we decide on a realistic maximum sustained swim speed (s_{max}). For each location *i* we calculate the speeds required to have swum from the previous location (*i*-1) and the location before that (*i*-2), and to the subsequent location (*i*+1) and the location after that (*i*+2). We than assign to location *i* the root mean squared of these four speeds (s_i). A location may have an unrealistically high s_i due to the influence of a neighbouring (up to two away) location with large error. We thus do not simply delete every location where $s_i > s_{max}$. Rather, we examine each sequence of locations where $s_i > s_{max}$ and just delete the location with the maximum s_i in each sequence. s_i values are then recalculated from the remaining locations and the process is repeated until there are no locations with $s_i > s_{max}$.

While this is essentially a destructive filter in that it ignores locations with a large error, it has proved effectual in many studies and is frequently used.

Data visualisation

The success of SRDLs, and their deployment by many workers, has highlighted the need to devise a computer visualisation system to display and interactively explore the vast and complex data sets of movement and dive behaviour that are relayed ashore. This need was met by the MAMVIS application (Fedak et al. 1996b, Fedak et al. 2002), which was developed to permit the animation of seal behaviour within a 3-D geography. The changing patterns of animal behaviour can thus be related to local bathymetry and temporally changing, remotely-sensed oceanographic data sets, such as sea surface temperature and ice cover. In addition, modelled oceanographic data, such as ocean circulation, may also be displayed

4. Seal Foraging Ecology

This section describes a series of SRDL studies on the foraging movements and behaviour of southern elephant seals (*Mirounga leonina*) in the Southern Ocean and grey seals (*Halichoerus grypus*) in the UK.

Southern elephant seals

Initial study at South Georgia

> **McConnell**, B. J., C. Chambers, and M. A. Fedak. 1992. Foraging ecology of southern elephant seals in relation to the bathymetry and productivity of the Southern-Ocean. Antarctic Science **4**:393-398.

Southern elephant seals are among the most proficient of mammalian divers and are a major component of the Antarctic food web. About half the population breeds at the sub-Antarctic Island of South Georgia. After breeding, they spend about 70 days at sea before embarking on their annual moult for a period of about a month. They then forage at sea until the next breeding season. A previous study by Hindell et al. (1991) at Macquarie Island using geo-location time-depth recorders (Geo-TDR's) had revealed that southern elephant seals were capable of travelling thousands of kilometres from their breeding sites. Yet little was known of their detailed movements of the South Georgia population, or their interaction with their oceanic environment until McConnell et al. (1992a) deployed SRDLs on three post-breeding female southern elephant seals there in 1990.

All tagged seals swum in a directed manner southwest away from South Georgia to the Antarctic Peninsula, up to 2650 km away. Subsequently movement was slower and less directed. Over the shallower continental shelf of the Antarctic Peninsula one animal consistently dived to the seabed in localised areas. These dives were square shaped with a high proportion of time at the seabed and suggested epi-benthic feeding. During this phase, dives were shorter and a smaller proportion of time was spent underwater. We suggested that this may be due to a decreased anaerobic dive limit (ADL) due the increased metabolic requirements of digesting and assimilating food (the specific dynamic effect). This effect, although demonstrated in captive animals, had never before been observed in free-ranging seals.

McConnell *et al.* (1992a) went on to suggest from these initial results that long distance travel to relocatable hydrographic or topographical features, such as shelf breaks, may allow large predators to locate prey more consistently than from mid-ocean searches. The main emphasis in this hypothesis is the predictability of prey concentrations – based on either transient or permanent oceanographic features. This theme was continued in the next study at South Georgia two years later.

Second study at South Georgia

McConnell, B. J., and M. A. Fedak. 1996. Movements of southern elephant seals. Canadian Journal of Zoology-Revue Canadienne De Zoologie **74**:1485-1496.

In 1992 McConnell *et al.* (1996) tagged a further nine southern elephant seals at South Georgia. Three of these were tracked over more than one foraging period (either post-moult or post-breeding). Their analysis included the three seals from the previous study.

Twelve adults were tracked for an average of 119 days as they left their breeding or moulting beaches. The tracks could be generalised into three phases. The initial phase was a rapid, directed movement from South Georgia at a rate of about 70 $km.day^{-1}$. The second phase consisted of slower, often meandering tracks interspersed with slow or stationary periods. For three of the four seals tracked for a sufficient period, the third phase was a rapid and directed return to South Georgia.

Within this general pattern, there were two geographical variants of female movement. Four travelled directly to continental shelf areas, either off the Antarctic Peninsula or off the Falkland Islands. Both of the two seals which were tracked for a sufficient period showed stationary periods in very localised areas during phase 2, diving either to the continental shelf seabed or in mid-water just seawards of the shelf break. The other females travelled up to 3000 km away in the distant Southern Ocean. While phase 1 and 3 still exhibited rapid directed movement, their phase 2 consisted of meandering movements, interspersed with periods of slower movement.

This contrasts with the distinct stop-start phase 2 movements of the continental shelf feeders. There was no obvious correlation between the location of open-ocean phase 2 behaviour and remotely sensed oceanographic frontal systems or ocean ridges – both of which are associated with increased productivity.

The three males in the study did not show the 3-phase movement pattern. Rather they stayed close to South Georgia and foraged either in the nearby deep waters, or on the narrow continental shelf near South Georgia.

This study demonstrated that southern elephant seals can adopt a variety of foraging strategies, both in geographical location and in affinity for the continental shelf. The sample size was, however, insufficient to determine whether foraging patterns were sex-related. The magnitude of these movements suggested that the foraging ranges of elephant seals from all the major breeding sites in the Southern Ocean sites may, potentially overlap. Indeed our results suggest that most of the Southern Ocean is potentially available to elephant seals. Yet there are marked differences in the population dynamics of southern elephant seals from different breeding colonies.

Initial foraging strategies of pups at Macquarie Island

McConnell, B., M. Fedak, H. R. Burton, G. H. Engelhard, and P. J. H. Reijnders. 2002. Movements and foraging areas of naive, recently weaned southern elephant seal pups. Journal of Animal Ecology **71**:65-78.

Whilst the breeding stock at South Georgia has remained stable over the past 45 years (Boyd et al. 1996), the Macquarie Island stock has declined significantly and this has been ascribed to a reduction in first-years survivorship (Hindell 1991).

Female southern elephant seals expend variable, often large, amounts of their stored body resources on their pups during lactation. There is some evidence that pups with higher weaning masses have a better chance of surviving their first year (McMahon et al. 2000). Pregnant females come ashore on a few sub-Antarctic islands, give birth and nurse their pups for an average of 24 days. After weaning they mate and then abandon their pups, which remain ashore for a further six weeks fasting. Mothers may vary in mass by a factor of three at parturition, but across the entire size range, they expend material roughly proportional (35%) to their mass at that time (Fedak et al. 1996a). The pups may treble their birth mass during suckling, but weaning mass is strongly dependent on the mother's parturition mass, with the pups of larger mothers weighing up to three times those of smaller ones. The value of such a variable maternal investment can only be understood in terms of the pup's subsequent behaviour.

By the time the pups finally depart the breeding site, they will have lost, on average, 32% of their weaning mass (Arnbom et al. 1993). During the post-weaning fast behavioural and physiological developments take place in preparation for life at sea. However the fast has a likely cost in that the body reserves remaining at departure, to provide for the pup until it finds food, will be diminished. The value of the resources passed to a pup by its mother and the cost of its post weaning fast will depend critically on the time it takes for pups to locate prey. This in turn is influenced by the predictability of prey distribution, and the information and strategy the pups use to help them locate prey.

Therefore, to understand the costs and benefits of maternal investment in phocid seals, we need to know the proximity (in time and space) of foraging areas from natal areas and have an idea of the problems that naïve pups face in locating these areas and how they might solve them. This was the primary aim of McConnell et al.'s study (2002)

They used SRDLs to track 30 newly-weaned pups on their first trip to sea from their natal site at Macquarie Island in 1995 and 1996. Track duration varied from 2 to 196 (mean, 84) days. Seven seals were tracked for the entire duration of their first trip.

As in the tracks of adults, the movements were grouped into three phases (Figs 1 and 3 in McConnell et al. 2002). Phase 1 (mean duration 30 days) was characterised by rapid and directed dispersal from Macquarie Island at daily travel rates of up to 140 km.day^{-1}. Phase 2 (mean duration 67 days) consisted of slower travel rates (generally < 20 km.day^{-1}) where activity was often centred on localised patches up to 1900 km from Macquarie Island. This phase was sometimes interrupted by bouts of increased travel rate as the seal moved to another patch. Phase 3 (mean duration 42 days) consisted of prolonged increased travel rates as the seals returned to Macquarie or, in one case, Chatham Island.

MAGNETIC CUES

While the tracks to the west and south were diverse and meandering, the tracks to the southeast were very similar. There may have been a number of interacting factors that produced such a clustering of paths. Potential candidates include communication between animals, or the following of common clues such a sea surface temperature or the chemistry of the water. Another candidate, and one which we attempted to test, was the use of a specific geo-magnetism model in navigation. Based upon a visual inspection of the southeasterly track group, the most parsimonious hypothesis was that they all maintained a constant course of magnetic east. However, even if this were the case, their actual tracks would be modified by the prevailing eastwards currents. We therefore constructed a GIS-based model that simulated tracks based on a constant heading of magnetic east, at variable swimming speed, but modified by ocean current vectors at 100 m depth. The resulting simulated tracks, shown in Fig 3d of McConnell et al (2002), produced a pattern similar to, but not identical to, the actual tracks. The result was inconclusive; but we certainly do not reject the notion that southern elephant seal pups may use some form of geomagnetic navigation.

EFFECT OF SEX YEAR AND WEANING MASS

A statistical comparison of tracks is confounded by the fact that that each has a high degree of serial and spatial auto-correlation. Therefore we restricted our between-track comparisons to the phase1-2 transition and phase 2-3 transition locations. A bespoke nearest neighbour analysis was designed. However, neither sex, year nor weaning mass influenced these transition points. The lack of apparent sexual segregation in pups tracks contrasted with the apparent segregation in adult foraging areas (Hindell 1991, Campagna et al. 1995, McConnell and Fedak 1996, Campagna et al. 1999). However, our failure to observe sexual segregation in pups does not necessarily reject Stewart's hypothesis (1997) that sexual segregation is driven by differing energy requirements, since Bell *et al.* (1997) showed that there was no difference in male and female growth rates of pups returning to Macquarie Island after their first trip to sea. Thus, under Stewart's hypothesis, any sexual segregation would not be expected until later in the pups' development.

OCEANOGRAPHIC FEATURES

Phase 2 tracks (where we infer most of the foraging took place) were associated in the south-eastern group with the Pacific Antarctic Ridge and in the south west group, to a lesser extent, with the Indian Antarctic Ridge. The southern limits of Phase 2 tracks in the south-eastern group were closely aligned with, but significantly to the north of, the southern Antarctic Circumpolar Circulation front (ACC) as mapped by Orsi (1995). However Orsi's frontal map was based on historical records, and the position of the fronts associated with the ACC can vary significantly through time (Moore et al. 1999, Pakhomov et al. 2000, Trathan et al. 2000). Thus there is a degree of uncertainty in the actual position of the ACC fronts and boundaries during our study years. However, Nicol *et al.* (2000) have recently shown the importance of the area to the south of the Southern Boundary of the ACC (SB-ACC) on local productivity at all trophic levels. Tynan (1998) also documented concentrations of krill (*Euphausia superba* Dana) and sperm whale (*Physeter macrocephalus* L.) near the SB-ACC (as mapped by Orsi) and concluded that the SB-ACC "provides predictably productive foraging for many species, and is of critical importance to the function of the Southern Ocean ecosystem". Our study suggested that the area around the southern extent of the ACC is also important as foraging grounds for a significant proportion of southern elephant seal pups.

MATERNAL INVESTMENT AND SURVIVAL

Using calculated estimates of body composition at weaning and estimates of the rate of utilisation of body reserves for the period before animals reach the second, foraging phase of their trip, we estimated that large pups had reserves remaining to supply their needs whereas pups in the small group were approaching critical limits. However these estimates are based on several assumptions and extrapolations.

First, we did not measure body composition in our study animals, but assumed that their body composition at weaning and the composition of the mass they lost were similar to that reported for southern elephant seals elsewhere by Carlini *et al.* (2001).

Second, we made the conservative assumption that pups at sea will use materials at the same rate as they do while ashore. While we expect that energy requirements are likely to be higher at sea, it is possible that opportunistic feeding balances this to some degree. Third, we assumed that 10% body fat reserve and 30% protein loss represent critical levels for survival.

It seems likely that year-to-year variability in oceanographic conditions (Sharhage 1988) will influence the time it takes pups to find food and the rate at which it can be consumed. Thus we would predict a significant variability in pup survival - body reserves that are adequate in one year may be inadequate or superfluous in others. Indeed, Hindell *et al.* (1991)have shown that first year survival at Macquarie has ranged from 42-46% to as little as 2% during a period of rapid population decline. In northern elephant seals, Le Boeuf *et al.* (1994) found that first year survivorship ranged annually between 20% and 49%. However, the response of pup survivorship to oceanographic conditions will depend upon the extra level of maternal expenditure that is provided to insure pups against the consequences of occasional, extreme years. If mothers routinely provide superfluous resources to their pups, a decrease in survivorship would only be apparent in years when the oceanographic conditions were *extremely* unfavourable. The pattern of pup survivorship would be further complicated if mothers' expenditure was modified by one, or a series of many, unfavourable years. Such a hypothesis is testable with long term parallel biological and oceanographic studies. Finally, we should be aware that the maternal *cost* would be reduced if the pup were capable of converting any superfluous resources into increased growth, or capacity for growth or subsequent fitness.

There could be a trade-off between the mother's material expenditure on her pup and the information the pup has, from either the mother herself or other sources, to help it find food. If food sources were local, reliable and/or the pups were directed to them by information from their parents, then fewer reserves may be required to give a reasonable expectation of survival until finding food. In such a scenario, mothers could give less, and the value of a large expenditure would be reduced. Thus, pups would not require as large a reserve to survive and an extended post weaning fast would be less costly. However, if food were distant, patchy and unpredictable the value of a given maternal material expenditure may be greater. The availability of good information and cues to direct pups to food could influence the time and effort needed to find food and thus reduce the level of maternal expenditure required.

In summary, maternal expenditure strategy in southern elephant seals would appear to be a complex response to many factors. However, a necessary key to understanding the importance of these factors is an appreciation of the difficulties faced by naïve pups on their road to nutritional independence in a new and variable environment. The elephant seal population on Macquarie Island has declined markedly since the 1950s (Hindell et al. 1991), and is now less than half what it was. In recent years, there has been a steady decline of about 1.6% per year (Hindell et al. 1994) A number of theories have been put forward to explain why the Macquarie and other southern Indian Ocean populations are declining while those of the South Atlantic are stable or increasing (Hindell et al. 1994). We suggest that, whatever the cause for the decline, the complex relationship between maternal expenditure, pup condition at weaning and long term trends in oceanic conditions needs to be understood before any convincing conclusions can be drawn.

Grey seal foraging

McConnell, B. J., C. Chambers, K. S. Nicholas, and M. A. Fedak. 1992. Satellite tracking of grey seals (*Halichoerus grypus*). Journal of Zoology **226**:271-282.

McConnell, B. J., M. A. Fedak, P. Lovell, and P. S. Hammond. 1999. Movements and foraging areas of grey seals in the North Sea. Journal of Applied Ecology **36**:1-19.

Grey seals are large, numerous marine top predators. The British population estimate for 1994 was approximately 108,000, increasing at about 5% per year (Hiby 1994) The high population size and high growth rate prompted calls for the UK grey seal population to be controlled under the Conservation of Seals Act 1970. However, management decisions should be based on an understanding of complex seal-fishery interactions (Yodzis 1998). An essential component of modelling these interactions is the temporal and spatial distribution of seal activity (Harwood and Croxall 1988).

The first Argos satellite tag ever to be deployed on a seal was deployed on a grey seal in 1985 by McConnell (1986). Over the next four years improved versions of this tag were deployed on a further two grey seals captured off the east coast of England (McConnell et al. 1992b). These deployments demonstrated the huge potential for the Argos satellite system to track seals at sea. They also demonstrated that grey seals may travel repeatedly between distant (265km) haulout sites. Building upon this pioneering work, McConnell et al. (1999) deployed SRDLs on 12 grey seals at the Farnes (Northumberland, NE England) and 2 at Abertay (Fife, E Scotland) during 1991 and 1992.

A total of 1461 seal days of data (mean 104.3 days per seal) was collected, and this covered all months of the year except February and March. The seal movements were on two geographical scales: long and distant travel (up to 2100 km away); and local, repeated trips from the Farnes, Abertay and other haulout sites to discrete offshore areas.

Long distance travel included visits to Orkney, Shetland, the Faeroes, and far offshore into the Eastern Atlantic and the North Sea. During travel bouts the seals moved at speeds of between 75 and 100 km.day^{-1}. Most of the time, long distance travel was directed to known haulout sites. Such long distance travel implies that grey seals that haul out at, say, the Farnes are not ecologically isolated from those that haulout in other regions. Such geographical mixing has important consequences in modelling epidemiology, fishery interactions and population management. For example, local control measures will have a reduced effect if there is frequent exchange with a large reservoir of animals from other regions.

In 88% of trips to sea, individual seals returned to the same haulout site from which they departed. The mean duration of these trips was 2.33 d although there was considerable variation both among sites and among individuals. Trip destinations at sea were often localised areas and these were frequently revisited. These areas were frequently characterised by a gravel/sand seabed sediment type. This is the preferred burrowing habitat of sandeels (Wheeler 1978), an important part of grey seal diet (Hammond and Prime 1990, Hammond et al. 1994). This, and the fact that dives in these areas were primarily to the seabed, suggests that these were foraging areas.

However we do not exclude additional feeding, either when close to haulouts sites or during bouts of travel. The limited extents of return-trips from a haulout site (mean 39.8 km) suggest that the direct impact of seal predation may be greater on fisheries within this coastal zone, especially those near seal haulout sites, rather than on fisheries further offshore.

On average, of 43% of all the seals' time was spent within 10 km of a haulout site, although localised foraging areas were identified considerably further offshore. This poses the question of why grey seals interrupt foraging at sea with haulout bouts shore. There may be more than one reason. First, proximity to a haulout may provide safety from predation from, for example, killer whales (*Orcinas orca*). Second, these periods near or on a haulout may be used for rest or social interaction. Brasseur (1996), demonstrated that captive harbour seals (*Phoca vitulina*) deprived of a suitable haulout area, later compensated by hauling out for longer periods. This result suggests that there may be some physiological need to haul out. Third, we may be underestimating foraging activity near haulout sites.

5. First-year survival in grey seals

Factors affecting first year survival

Hall, A. J., B. J. **McConnell**, and R. J. Barker. 2001. Factors affecting first-year survival in grey seals and their implications for life history strategy. Journal of Animal Ecology **70**:138-149.

Hall, A. J., B. J. **McConnell**, and R. J. Barker. 2002. The effect of total immunoglobulin levels, mass and condition on the first-year survival of Grey Seal pups. Functional Ecology **16**:462-474.

As in southern elephant seals, grey seal females may expend large amounts of their stored body resources on their pups during lactation. They can lose 40-50% of their body mass during lactation (Fedak and Anderson 1982, Pomeroy et al. 1999). However this expenditure is variable and the resulting weaning mass of grey seal pups can vary by a factor of two. While modelling studies (Thompson et al. submitted) have concluded that relatively small changes in phocid weaning mass could have a large effect on survival during the first 50 days of life, the existing empirical information is equivocal. Le Boeuf et al. (1994) found that first year survival of Northern elephant seal (*Mirounga angustirostris*) pups was not related to mass or condition at weaning, even though animals in the highest weight category were twice as heavy as those in the lowest. However McMahon et al. (2000) found that southern elephant seal pups which returned to Macquarie Island at age 1 had been significantly heavier at weaning than those which did not return. Also, Northern fur seals (*Callorhinus ursinus*) at age 2 were found to have been of above average mass at weaning (Baker and Fowler 1992).

We thus set out to investigate the effect of weaning mass (and condition) and sex on the first year survival of grey seals pups from the Isle of May, Scotland using a mark-recapture technique.

In brief, a cohort of 204 weaned pups was marked with a new type of tag which allowed individuals to be identified when resighted alive (Hall et al. 2000) as well as when found dead. Sex, mass and morphometric condition measures (a proxy of lean to fat ratio) were recorded at weaning. Subsequently monthly boat surveys were carried out to resight (recapture) marked animals. Sightings by the public of both live and dead tagged animals were also recorded. The data, clumped into two-month blocks, were analysed using the joint live recapture / live resighting / dead recovery model of Barker (1997).

In general, the results demonstrated that post-weaning survival is greater for pups with higher weaning condition, and that the effect is greater for males than for females. Regardless of pup condition and time of year, the odds of survival for female pups over a 2-month interval was estimated to be 3.37 (SE = 1.30) times higher than for males. Regardless of sex, a one standard deviation increase in pup condition was estimated to increase the odds of survival by a factor of 1.422 (SE = 0.226). For a male pup in average condition the estimated annual survival after adjusting for tag-loss was 0.193 (SE = 0.084); for a female pup in average condition it was 0.617 (SE = 0.155).

The greater importance of condition for males implies that high quality females should invest more heavily in their male pups because the marginal return, in terms of increased reproductive value, from any additional expenditure is twice that for females. Male pups in our sample were significantly heavier at weaning and in better condition than female pups. However, this does not provide conclusive support for our predictions, because we could not control for the effects of maternal size on weaned mass.

This study was then extended (Hall et al. 2002) to investigate the effect of immunological factors on first year survival of grey seals. This extension also included new mark-recapture data from another grey seal breeding site – the Farnes off Northumbria, England. In addition to the usual data obtained from the study seals, the serum gammaglobulin (IgG) levels were also determined close to weaning.

The intriguing finding from this study was that, in addition to in the influence of mass (or condition) and sex, higher post-weaning circulating levels IgG also significantly decreased the probability of survival to age one in grey seal pups. These IgG levels were not correlated with mass or condition and were thus not surrogates for these other parameters.

There are two mechanisms to explain elevated IgG levels. First, an individual may be in the process of fighting an antigen challenge. However, all the pups in the study were apparently healthy, without overt infections other than minor bite wounds sustained during the breeding season. Second, elevated IgG levels may represent a genetic disposition to respond more forcefully to any given antigen challenge.

The mechanism by which IgG levels may influence first year survivorship is unclear. It is possible that those with higher levels were fighting an infection to which they later succumbed. In this case we would expect there to be a significantly higher mortality in the first few months. There was, however, only marginal evidence for a time-dependent mortality. Alternatively there may be an energetic trade-off between the costs of body growth and maintenance and the costs of maintaining a high level of immunocompetence (Gershwin et al. 2000). Weaned pups have a limited amount of energy reserves until they make the successful transition to independent foraging at sea. If this energy reserve is insufficient even to maintain growth and protein synthesis, the added disadvantage incurred from having a high antibody production rate is an added disability. In addition, the burden for males appears to be greater than for females. This is in accord with studies in other species that have suggested that there is a sexual dimorphism in immunity which disfavours males (Klein and Nelson 1998, Moller et al. 1998).

While these two studies have yielded significant insight into the factors which affect first year survivorship, there were methodological limitations. Principally, the monthly resighting surveys covered only a small part of the animals' potential range and the number of animals resighted was low - thus reducing inferential power. Effort was thus directed at developing more efficient methods to gather the required mark-recapture data, and in a way that would require less complicated models to analyse.

Novel telemetry technique to determine survivorship

McConnell, B., R. Beaton, E. Bryant, C. Hunter, P. Lovell, and A. J. Hall. 2004. Phoning home - a new GSM mobile phone telemetry system to collect mark-recapture data. Marine Mammal Science. **20**:274-283.

Survival probabilities from mark-recapture models have been estimated for seal populations using various marking methods. However, the success of such studies depends upon obtaining a sufficient quantity and quality of resighting events. Apart from animal survival, the number of resightings depends upon the number of marked animals, the probabilities of tag retention and sightability and resighting effort. Flipper tagging is inexpensive, allowing large releases of tagged seals. However live resighting and dead recovery rates are often low, requiring long time series for sufficient data to be accumulated (Hastings and Testa 1998, Craig and Ragen 1999). Moreover, tag retention can be low and age-specific (Stobo and Horne 1994). Live resighting of branded animals has also been used (McMahon et al. 1999, Schwarz and Stobo 2000). While the mark retention is high, this marking technique is often restricted to species and to sex- or age-classes that predictably return to a breeding or moult colony each year where the resighting effort can be concentrated.

We thus developed a novel phone tag to gather the appropriate data. The resulting telemetry system is based on GSM (Global System for Mobile Communications) mobile phone technology and it has the potential to provide more detailed mark-recapture data over an extensive geographical range, thus improving estimates of first year survival (McConnell et al. 2004). In brief, each seal is fitted with a mobile phone tag that is programmed to attempt to send a text message back to the laboratory at regular intervals. The thousands of GSM radio cells around the coast of Europe that are continuously listening for text messages from these seals now replace the human monthly survey effort in Hall et al.'s study. In the mark-recapture parlance, the successful receipt of a text message now replaces the conventional resighting event. GSM coastal coverage is variable, but usually extends to approximately 20 km offshore. We do not expect that live seals will remain continuously within the GSM coastal corridor. However, we do assume that there is a finite probability that a live animal will, at some time, return to the coastal corridor and succeed in sending a text message ashore. In addition to being a 'resighting' event in its own right, each received text message contains approximate location when the message was sent (GSM radio cell ID), haulout and diagnostic information. While their operation is described in the context of a generalised Cormack-Jolly-Seber live-resighting mark-recapture framework (Seber 1982), a bespoke model will be developed which accounts for the particular properties of these resighting data.

Design and operation

The phone tag hardware design is centred on a Siemens TC35 GSM wireless module, controlled by a micro-controller, which is potted in epoxy resin. A specially designed miniature antenna (Winkle et al. 2003) is embedded in the epoxy. The system is powered, for up to one year, by a C-size Lithium Thionyl Chloride cell.

Every 4 h the tag wakes from sleep mode, waits until it is dry and then attempts to register with a GSM network for a maximum of 95 s. If registration is unsuccessful, only diagnostic data for that attempt are appended to a 160-character buffer. If registration is successful the delay from dry to registration (*reg_wait*) and the ID code of the radio cell with which it has registered are also appended to the buffer. The O2 service provider has provided the locations and identification codes of their GSM radio cells in Great Britain, enabling the location of the radio cell serving the tag to be determined. A wet dry sensor is polled every 4 s. Its output is used to inhibit attempts to register underwater and to construct haulout records. Completed haulout records are also appended to the buffer. When the buffer is full it is emptied into one of the 20 'unsent text message' memory banks in the SIM card. Upon successful registration, any unsent text messages are sent.

In the parlance of the previous survivorship studies described above, this strategy is equivalent to an instantaneous boat survey around the coast of Europe every 4 h.

Results and discussion

Fifty-nine newly weaned grey seal pups were fitted with phone tags at the Isle of May Firth of Forth, Scotland) breeding colony in December 2002. The results are presented for the first three months of operation. They are discussed here with respect to telemetry system performance rather than being used in the final survival analysis itself.

For each tag, a 3-day bin was assigned a value of one if one or more of the 4 h attempts to register were successful. For each 3-day bin the scores were summed over all tags and are referred to as the 3-day registration rate. Through January, February and March the mean rates were 15.5, 4.1 and 8.2 respectively. The first three months of data indicate that GSM mobile phone networks in general, and our design of phone tag in particular, promise to provide useful resighting data on free-ranging pinnipeds. However, the quantity of the 'resighting' data obtained is determined not just by the efficiency of the phone-tag telemetry system, but also by the behaviour, movements and survival of the study animals. Whilst we have no absolute measure to determine the efficiency of the telemetry system short of carrying out the final survival analysis (in prep), the data we have received indicates that the system is performing well enough to provide the required data.

Some text messages were successfully sent from as far away as Norway and Germany. This indicates that our resighting effort was not limited to UK waters but extended to the entire potential range of grey seal pups (all European coastal regions). Thus, although there were local blind areas of GSM network coverage, and the coverage (resighting effort) was not geographically heterogeneous, it is unlikely that any animal would permanently emigrate from this resighting region. Thus survival models may be simplified to ignore emigration parameters.

Diagnostic data included in the received text messages indicated that when a study animal was at sea (not hauled out) the average delay from cold start to registration with the GSM network was only 9.6 s. It is thus likely that this system could be used in other marine mammal species that have short surfacing durations.

Our demonstration of proof of concept opens up the potential to exploit other data capabilities of GSM networks. General Packet Radio Service (GPRS) and Circuit Switched Data (CSD) channels allow data to be uplinked at rate of between one and two Kbyte.s^{-1}, for unlimited duration. This removes the 160-byte constraint of sending information via SMS text messages and the data bottleneck imposed by the Argos satellite system. A potential application of this technology would be a time-depth recorder (TDR) which remotely uplinks data to the user whenever the animal comes within GSM network coverage. In addition, text messages could also be sent *to* the phone tags enabling changes in their operation to be executed remotely.

6. Summary

The work described in the papers included in this portfolio has not only significantly expanded our knowledge of at-sea behaviour of marine mammals, but has significantly extended our technical and analytical *ability* to expand such knowledge. The major outputs are:

- Determination of Argos location fix accuracy and development of track filtering tools.

- Development of an Argos-based Satellite Relay Data Logger system that permits the collection and relay of track data and detailed behaviour from marine mammals at sea.

- Description of the foraging of adult southern elephant seals and proposal of factors that may influence their strategies.

- Understanding the initial foraging patterns of southern elephant seal pups in relation to maternal investment and variability in the oceanographic environment.

- Description of grey seal foraging patterns in the UK.

- Understanding of factors at weaning which influence first year survivorship in grey seal pups.

- Development of a novel mobile phone telemetry system to collect data to populate mark recapture models to estimate survivorship.

Statement of candidate's contribution to the portfolio of papers

By its very nature, the development and deployment of technical and analytical techniques requires input from a large team. The portfolio of papers submitted here is a subset of my complete publication list. It includes only those in which I have played a significant role in conception, writing, *and* which pursue a single coherent theme.

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