



Tracking and data-logging devices attached to elephant seals do not affect individual mass gain or survival

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ABSTRACT

Understanding the cryptic lives of wide-ranging wild animals such as seals can be challenging, but with the advent of miniaturised telemetry and data-logging devices this is now possible and relatively straightforward. However, because marine animals have streamline bodies to reduce drag in their aquatic habitats, attaching external devices to their back or head may affect swimming performance, prey capture efficiency and ultimately, fitness. Given this, and allied welfare concerns, we assessed the short- and long-term consequences of external devices attached to southern elephant seal juveniles and adults under varying environmental conditions. We also assessed the effects of multiple deployments on individuals. There was no evidence for short-term differences in at-sea mass gain (measured as mass on arrival from a foraging trip) or long-term survival rate. The number of times that a seal carried a tracking device (ranging from 1 to 8 times) did not affect mass or estimated survival. Further, there were no tracking device effects in years of contrasting environmental conditions measured as ENSO anomalies. Consequently, we conclude that the current tracking devices available to researchers are valuable conservation tools that do not adversely affect the performance of a large marine mammal in terms of mass gain or survival probability over short (seasonal) or long (years) temporal scales.

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1. Introduction

Studies of how species respond to variation in their environment require a range of techniques to record pertinent data such as estimates of trends in population size, survival and recruitment, mark-recapture and telemetry of individual movements and other behaviours. Combining mechanistic behavioural approaches with population-level data is particularly powerful for predicting a species' response to future environmental change (Both et al., 2006; Parmesan and Yohe, 2003; Perry et al., 2005). For wide-ranging species, examining foraging dynamics is a particularly important component of these studies because such data summarise information on energy acquisition and expenditure at a variety of spatial and temporal scales. Studies designed to collect such information assume that natural behaviours are not compromised by the experimental procedures themselves. Furthermore, these types of field experiments may raise many ethical issues including the trade-off between individual welfare and information required to conserve threatened species (Minteer and Collins, 2005; Putman, 1995).

Documenting the life history of cryptic species can be especially difficult, particularly for marine species that are only rarely observed during brief feeding or breeding events close to or onshore (Bradshaw, 2007). Recent technological advances have provided detailed behavioural information that would be otherwise impossible to collect (Hooker et al., 2007 and references therein). Miniaturisation, long-life batteries and large data-storage capacity mean that data-logging devices can potentially be deployed for years (Hays et al., 2007b). However, it is still necessary that researchers weigh the benefits of these long-term deployments against their potential effects on reproduction, foraging success, energetics and survival of the sampled individuals. Some of the many considerations include the tracking device's (hereafter termed "device") ergonomics, location of attachment, mass relative to body size, additional energetic cost induced by drag, increased agonistic behaviour by conspecifics, and impairment of camouflage and foraging efficiency. Because many studies often require longitudinal information on particular individuals, repeated deployment of devices may also be required (Bradshaw et al., 2004a). It is possible that although a single or short-term deployment may not be harmful to an individual, the cumulative effects of multiple deployments may be ultimately detrimental (as is the case for flipper bands in penguins – Gauthier-Clerc et al., 2004). The need for information on the potential effects incurred

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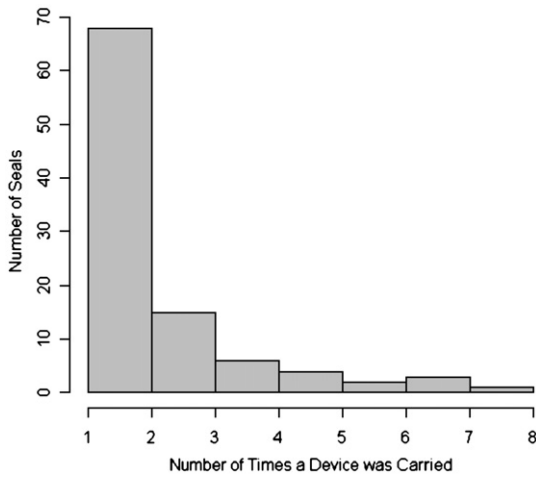


Fig. 1. The number of individual deployments of southern elephant seals that carried bio-logging devices from Macquarie Island from 1999 to 2005.

by multiple deployments of devices is especially important because detrimental impacts may only appear during periods of resource scarcity. For example, a device's effect may be exacerbated in years when prey are scarce (more dispersed or deeper in the water column), thus requiring that the foraging animal expends more energy to catch prey. Despite the importance of these potential detriments to animal performance, there has been little quantification of the effects of the devices especially over multiple deployments (see Wilson and McMahon, 2006 for a recent review).

An important Southern Ocean predator that has been the subject of much research in this area is the southern elephant seal (*Mirounga leonina*). This species is particularly tractable to research because: (a) they are an important Antarctic apex predator that has shown protracted and substantial declines in some regions (McMahon et al., 2005b), (b) there are established demographic links in this species to environmental change (de Little et al., 2007; McMahon and Burton, 2005), (c) they are wide-ranging and incorporate information over broad spatial and temporal scales (Bradshaw et al., 2004a; Bradshaw et al., 2004b; Field et al., 2004; Hindell et al., 2003), (d) they are easily accessible during defined haul-out periods onshore (Hindell,

1991), and (e) their large size means that small devices are less likely to modify behaviour (Ropert-Coudert and Wilson, 2005). Although the effects of marking (McMahon et al., 2006) and handling (Engelhard et al., 2002, 2001; McMahon et al., 2005a) have been examined for this species, the potential effects of data-logger deployment on elephant seal performance in terms of energy (mass) gain and survival probability have never before been assessed empirically. Because the potential effects are likely to differ between small and large, and between young and old seals, we calculated age-specific survival estimates for seals from a wide range of ages (1–13 years) equipped with devices and those without, as well as assessing the consequences of multiple deployments on individuals. It might be expected that the growth of small and young seals could be compromised by the additional cost of carrying a device, with flow-on effects such as delayed age of primiparity, reduced population growth rate and elevated extinction risk in small populations.

The aims of this study were four-fold: (1) To determine if there was any evidence of an energetic cost to seals carrying data-loggers by comparing variation in arrival masses between instrumented and non-instrumented elephant seals at Macquarie Island (Pacific sector of the Southern Ocean). We predicted that the attachment of devices may increase the cost of transport (via increase in drag), thus potentially reducing individual fitness. This increased fitness cost, if it compromises survival via poorer foraging performance, may be measurable by either increased time at sea or decreased overall mass gain when compared to animals not carrying devices (Boyd et al., 1997; Ropert-Coudert et al., 2007a,b); (2) We hypothesised that the evidence for any short-term effects of data-logger deployment might be masked by subtler long-term effects on average demographic rates. We therefore estimated apparent survival rates of instrumented versus non-instrumented seals relative to the environmental conditions encountered while foraging; (3) To assess the additional influence of multiple deployments on individuals; (4) To assess the influence of inter-annual variability in environmental conditions on mass gain and survival when carrying a device.

2. Materials and methods

2.1. Deployment

A large sample ($n=12251$) of recently weaned southern elephant pups was hot-branded between 1993 to 1999 on Macquarie Island

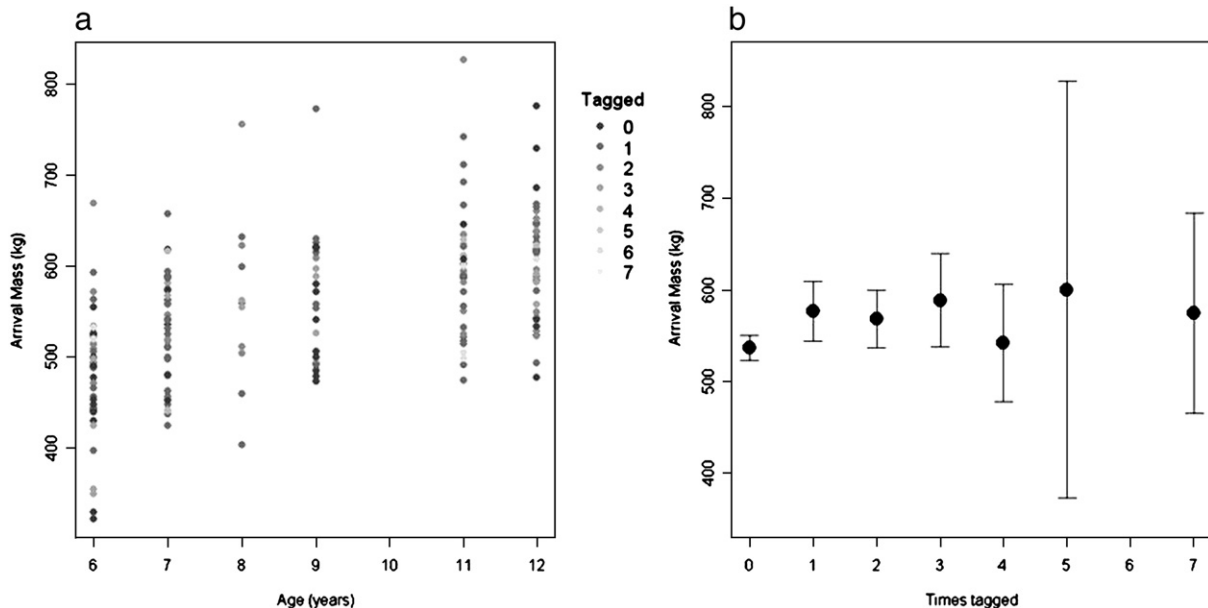


Fig. 2. Post-moult arrival weights of adult female elephant seals expressed as a function of (a) age and (b) the number of times the seal had carried a device.

Table 1

Ranking of the generalised linear mixed-effects models (GLMM) relating arrival mass (AM) during the post-moult period at sea to age (age), number of times that an individual carried a tag (num), and individual seal (ID)

Models	k	LL	AIC _c	ΔAIC _c	wAIC _c	%DE
AM-age+(1 ID)	2	-1030.7	2069.528	0.000	6.66E-01	6.76
AM-age+num+(1 ID)	3	-1030.6	2071.511	1.983	2.47E-01	6.77
AM-age+num+age*num+(1 ID)	4	-1030.6	2073.588	4.060	8.74E-02	6.77
AM-num+(1 ID)	2	-1095.0	2198.132	128.604	7.89E-29	0.95
AM-1+(1 ID)	1	-1105.5	2217.017	147.488	6.26E-33	0.00

The models are ranked in order of Akaike Information Criterion corrected for small sample size (AIC_c) weights (wAIC_c). LL: maximum log-likelihood of the model; k: number of estimated parameters; ΔAIC_c: difference between the model's AIC_c and the minimum AIC_c; %DE: per cent deviance explained by model.

(54° 30' S, 158° 50' E) (McMahon et al., 2006). Of these, 124 (aged between 1 to 9 years at deployment) were equipped with time–depth recorders (Mk6, Mk7 and Mk8 – Wildlife Computers, Redmond, USA), light-loggers (Platypus Engineering, Hobart, Australia) or platform transmitter terminals [PTT] (Sea Mammal Research Unit, St. Andrews, Scotland). Data-loggers and transmitters were attached to seals that were captured during one of their two annual haul-outs: (1) at the end of breeding and (2) at the end of the moult between 1999 and 2005 (see Baillieu et al., 2007; Bradshaw et al., 2004a; Field et al., 2004 for attachment procedures, and Field et al., 2002; McMahon et al., 2000 for capture details), and then recaptured upon their subsequent return to the island, representing an average of 70 and 280 days at sea, respectively for post-breeding and post-moult deployments. Time–depth recorders were combined with VHF transmitters and weighed <350 g, and platform transmitter terminals weighed 550 g. These represented <1.0% of the departure mass for the smallest seal in the study (78 kg). Because TDRs were combined with VHF transmitters to facilitate retrieval, PTTs and TDRs were of similar size and mass, and both had protruding antenna. We therefore did not distinguish between unit type in the analysis. Daily searches of the isthmus beaches and tussock areas (main study area) and monthly searches of the entire island were made to resight (and recapture) marked seals and to search for seals that were equipped with devices (1999–2005). Seals were caught within 3 days of coming ashore for attachment and retrieval.

Table 2

Ranking of the generalised linear mixed-effects models (GLMM) relating arrival mass (AM) during the post-breeding period at sea to age (age), number of times that an individual carried a tag (num), and individual seal (ID)

Models	k	LL	AIC _c	ΔAIC _c	wAIC _c	%DE
AM-age+num+(1 ID)	2	-690.3	1390.939	0.000	5.78E-01	6.82
AM-age+num+age*num+(1 ID)	3	-689.5	1391.579	0.640	4.19E-01	6.92
AM-age+(1 ID)	4	-696.6	1401.537	10.598	2.89E-03	5.96
AM-num+(1 ID)	1	-736.9	1482.098	91.159	9.26E-21	0.52
AM-1+(1 ID)	5	-740.7	1487.644	96.705	5.79E-22	0.00

The models are ranked in order of Akaike Information Criterion corrected for small sample size (AIC_c) weights (wAIC_c). LL: maximum log-likelihood of the model; k: number of estimated parameters; ΔAIC_c: difference between the model's AIC_c and the minimum AIC_c; %DE: per cent deviance explained by model.

To assess the short-term effects of devices on seals, we weighed all of the animals to the nearest kilogram in a net sling suspended from an aluminium tripod using an electronic balance precise to 1.0 kg. To ensure that mass measurements were accurate, the scales were tared each day prior to operation with a known-mass gymnasium weight. Measuring and comparing mass changes to quantify the effects of devices in endotherms, like seals, is both a convenient and appropriate way to evaluate fitness because mass changes reflect foraging success during the previous trip to sea (Bradshaw et al., 2004a) and are greater in endotherms than they are in ectotherms (e.g., marine turtles) where the rates of mass change are generally small (Hays, 2008).

2.2. Arrival mass

To test the hypothesis that mass gain varied between seals carrying or not carrying a device, we were obliged to use arrival mass as the response. Although mass gain during the time at sea would likely represent a better index, we only rarely had access to non-instrumented seals when returning to Macquarie Island. Therefore, to examine the evidence for an effect of carrying a device on a seal's subsequent arrival weight, we fitted a series generalized linear mixed-effect models (GLMM) to the data using the `lmer` function implemented in the R Package (R Development Core Team, 2004). The mixed-effects structure of the GLMM allows us to partition the variance within and among individuals from that associated with the

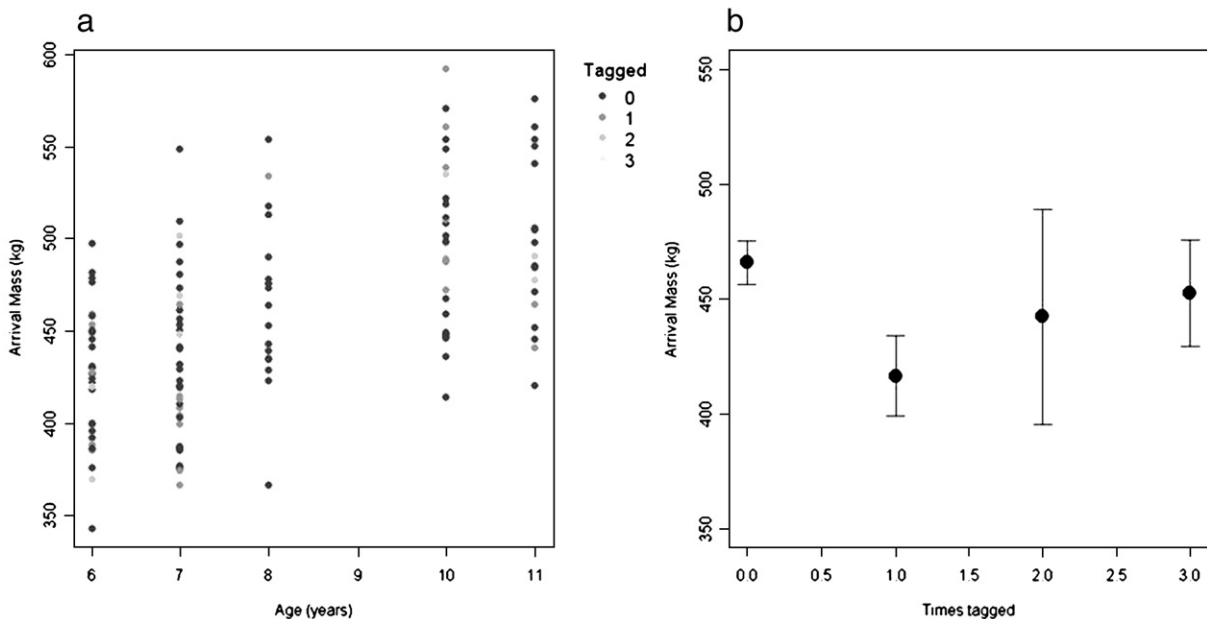


Fig. 3. Post-breeding arrival weights of adult female elephant seals expressed as a function of (a) age and (b) the number of times the seal had carried a device. We also collected less data from this time only getting 4 years as opposed to 6 years for post-moult.

Table 3

The five most parsimonious models showing the effects on model parsimony of applying the over-dispersion metric \hat{c} in program MARK

	ΔQAIC_c	Model Likelihood	k	Deviance
Model – $\hat{c}=1.0000$				
$[\varphi(a5+t+\text{sex}+\text{device})$ $p(a9+t+\text{sex}+\text{device})]$	0.00	1.000	38	76974
$[\varphi(a5+t+\text{sex}) p(a9+t+\text{sex})]$	28.18	0.000	36	77006
$[\varphi(a5+t+\text{sex}) p(a8+t+\text{sex})]$	31.71	0.000	35	77012
$[\varphi(a5+t+\text{sex}) p(a7+t+\text{sex})]$	33.66	0.000	34	77016
$[\varphi(a7+t+\text{sex}) p(a7+t+\text{sex})]$	36.87	0.000	36	77015
Model – $\hat{c}=2.1219$				
$[\varphi(a5+t+\text{sex}+\text{device})$ $p(a9+t+\text{sex}+\text{device})]$	0.00	0.980	38	36275
$[\varphi(a5+t+\text{sex}) p(a9+t+\text{sex})]$	11.16	0.004	36	36290
$[\varphi(a5+t+\text{sex}) p(a7+t+\text{sex})]$	11.62	0.003	34	36295
$[\varphi(a5+t+\text{sex}) p(a8+t+\text{sex})]$	11.77	0.003	35	36293
$[\varphi(\text{Age}11^{\wedge}3+t+\text{sex}) p(a9+t+\text{sex})]$	15.18	<0.001	34	36298
Model – $\hat{c}=2.7009$				
$[\varphi(a5+t+\text{sex}+\text{device})$ $p(a9+t+\text{sex}+\text{device})]$	0.00	0.930	38	28500
$[\varphi(a5+t+\text{sex}) p(a7+t+\text{sex})]$	7.41	0.025	34	28515
$[\varphi(a5+t+\text{sex}) p(a9+t+\text{sex})]$	7.91	0.019	36	28512
$[\varphi(a5+t+\text{sex}) p(a8+t+\text{sex})]$	7.96	0.019	35	28514
$[\varphi(\text{Age}11^{\wedge}3+t+\text{sex}) p(a9+t+\text{sex})]$	10.20	<0.001	34	28518

While \hat{c} adjustments did affect model weightings, the top-ranked model remained the most parsimonious in all adjusted cases ($\hat{c}=2.1219$ and $\hat{c}=2.7009$) and there was little support for any of the nearest competing models [$\Delta\text{QAIC}_c \geq 7$ – highlighted (Burnham and Anderson, 2001)]. k is the number of parameters included in each of the models.

fixed effects of main interest. The five models defined and compared were: (1) $AM\text{-}num+(1|ID)$, (2) $AM\text{-}age+num+(1|ID)$, (3) $AM\text{-}age+num+age \times num+(1|ID)$, (4) $AM\text{-}age+(1|ID)$ and (5) $AM\text{-}1+(1|ID)$, where: AM =arrival mass (kg), num =the number of times a seal had been equipped with a device, age =age in years, ID =seal identity. Note that model 4, containing age alone, was the control model because all seals necessarily aged during the course of the study. All weights were corrected to an estimated arrival weight based on the number of days ashore prior to capture and an estimated constant rate of mass loss calculated from the difference between subsequent weighings during the moulting period ($4.03 \text{ kg}\cdot\text{day}^{-1}$). We analysed only adult female data because the arrival masses for sub-adults were confounded by their tendency to make multiple visits to Macquarie Island during winter, making it difficult to compare individuals. We analysed the post-moult and post-breeding datasets separately because the two periods at sea are fundamentally different with respect to duration, function and destination.

Arrival mass (log-transformed) was set as the response variable, and models included various combinations of seal age and the number of times that a device was carried as fixed effects. Individual seals were coded as a random effect to account for repeated measures. Each model was constructed using a Gaussian error distribution and an identity link function. Model goodness-of-fit was assessed as the percent deviance explained (%DE). We used an index of Kullback-Leibler (K-L) information loss to assign relative strengths of evidence to the different competing models (Burnham and Anderson, 2002), Akaike's Information Criterion corrected for small sample sizes (AIC_c). These indices of model parsimony identify those model(s) from a set of candidate models that minimize K-L information loss (Burnham and Anderson, 2004). The relative likelihoods of candidate models were calculated using AIC_c weights (Burnham and Anderson, 2002), with the weight ($w\text{AIC}_c$) of any particular model varying from 0 (no support) to 1 (complete support) relative to the entire model set.

2.3. Survival probability

Individual capture–history matrices were constructed from the resight histories (McMahon and Burton, 2005; McMahon et al., 2003) and used as

input files for program MARK (White and Burnham, 1999). Multiple sightings of a seal within a seal year (15 October t – 14 October $t+1$) were treated as a single sighting in the capture–history matrix. Age-specific estimates of apparent survival (φ) and recapture or resighting probability (p) were estimated using the Cormack-Jolly-Seber (CJS) model in program

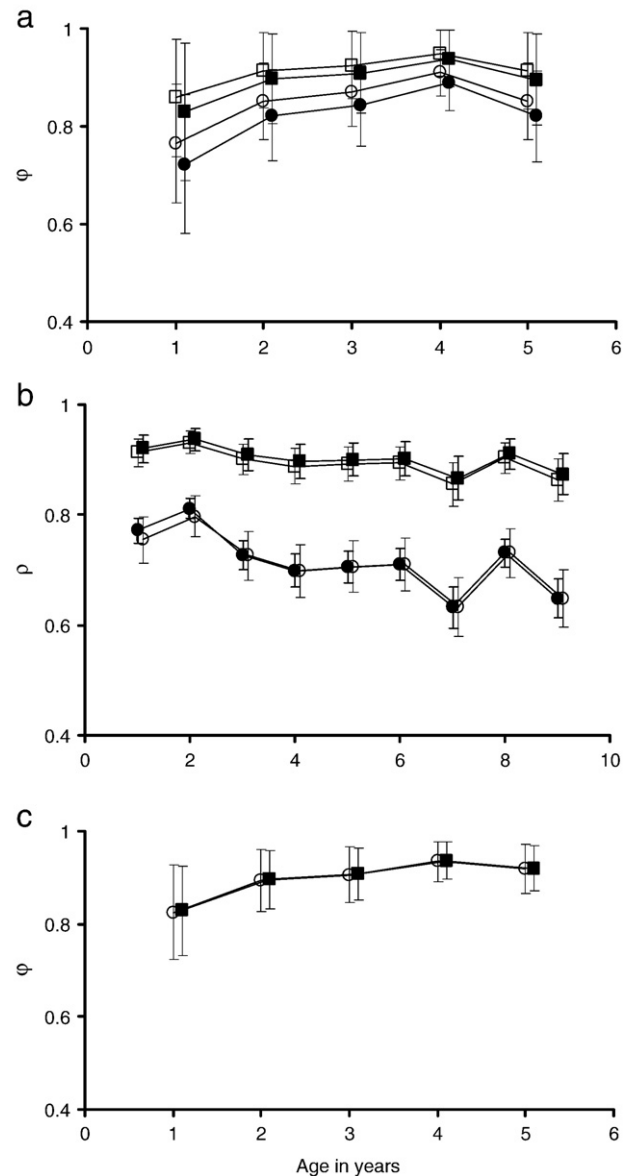


Fig. 4. (a) Survival estimates (φ) for male seals carrying time depth recorder devices (open squares), and male not carrying devices (open circles), and survival estimates for female seals carrying devices (closed squares) and those without devices (closed circles). Data are only presented to age five because survival for all seals is constant after age five. While no differences between survival estimates were apparent, seals carrying devices (squares) had higher survival estimates than seals that were not equipped with devices. Because this may have been the result of differences in capture probabilities we calculated the recapture probabilities (b). The recapture probability estimates (p) for male seals carrying time depth recorder–devices (open squares), and males not carrying devices (open circles), and recapture estimates for female seals carrying devices (closed squares) and those without devices (closed circles). Data are only presented to age nine because survival for all seals is constant after age nine. Recapture probability estimates for seals carrying devices (squares) were higher than for seals that were not equipped with devices. (c) Survival estimates (φ) for elephant seals carrying devices (closed squares), and those not carrying devices (open circles) were identical even when including the effects of environmental stochasticity in the form of the Southern Oscillation Index. Again data are only presented to age five because survival for all seals is constant after age five. In all cases the vertical lines represent the 95% confidence intervals for each estimate.

MARK (White and Burnham, 1999). Southern elephant seals in general, but particularly breeding females, show strong site fidelity to their natal areas (Bradshaw et al., 2004a; McMahon et al., 1999; Nicholls, 1970) and consequently, we do not expect much permanent emigration from Macquarie Island.

Capture–resight matrices were constructed as follows. For each seal, two individual time–variant factors identified when seals were equipped with a device (coded 1) and when they were not (coded 0). An example history of a typical individual was:

101111111111, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 1, 1, 0;

where the first 12 numeric codes define the capture history of the seal (101111111111, 0, 1, 0, 0, 0, 0, 0, 0, 0, 1, 1, 0), then its sex (male = 1, 0; female = 0, 1) in the next two columns (101111111111, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 1, 1, 0), and the last 12 columns, we define whether the animal was equipped with a device or not (101111111111, 0, 1, 0, 0, 0, 0, 0, 0, 0, 0, 1, 1, 0). Seals in this study could only carry a device for a maximum of one year because they undergo an obligatory annual moult. Individuals are exposed to a variety of environmental conditions over time, so we included the mean Southern Oscillation Index (SOI, available from www.bom.gov.au) from March to September as an extra covariate in the models constructed (de Little et al., 2007; McMahon and Burton, 2005) to reflect environmental variation.

Parametric goodness–of–fit (GOF) tests within MARK were used to test whether the CJS model assumptions were met. To accommodate lack of fit, the amount of over–dispersion (\hat{c}) was quantified. Program RELEASE (Burnham et al., 1987) run in MARK was used to explain the causes for any the lack of fit (using the saturated model $[\varphi(\text{sex}^*t) p(\text{sex}^*t)]$, where sex = seal gender and t = time). Consequently, when there was sufficient evidence for over–dispersion, we corrected for the extra–binomial variation in the data by the variance inflation factor \hat{c} , (Lebreton et al., 1992) to adjust the deviance in the calculation of the AIC_c (quasi–likelihood AIC_c = QAIC_c) and parameter standard errors (Lebreton et al., 1992).

3. Results

3.1. Arrival mass

We deployed devices on 124 adult seals that were also weighed after their time at sea. Many seals were equipped with a device more than once over the period of investigation (Fig. 1), although most individuals only ever carried a device once, and some carried a device up to eight times. Post–winter arrival weights averaged 550 ± 82 kg, although this varied considerably among individuals (Fig. 2a). The control model (age only, with seal coded as a random factor) was the top–ranked model ($w\text{AIC}_c = 0.66$), although it only accounted for 6.8% of the deviance (Table 1). The model including the number of times that a seal carried a device made a negligible addition to the per cent device explained (0.01%), suggesting little evidence for a measureable effect on arrival mass (Fig. 2b). Seals weighed substantially less after their post–breeding trip to sea (mean arrival mass = 458 ± 51.5 kg), due partly to the much shorter duration of the post–breeding trip (70 days for the post–breeding trip versus 280 days for the post–moult trip).

Post–breeding arrival mass results were similar to the post–moult results (Fig. 3); however, the control model received little support ($w\text{AIC}_c = 0.002$). The top–ranked model ($w\text{AIC}_c = 0.58$) included age and the number of times an animal carried a device (Table 2). Most importantly, adding the number of times that a seal carried a device added less than 1% to the %DE, again indicating little evidence of an important or measureable effect on arrival mass.

3.2. Survival

Our first model set ignored individual time–variant covariates. The most highly ranked of these basic models included sex and time (t) effects:

$\varphi(\text{sex}^*t) p(\text{sex}^*t)$. To this model we added various age , time and sex effects as well as the individual time–variant factor device (i.e., whether or not a seal carried a device over an interval) (Table 3). The top–ranked model was $\varphi(\text{age}5+t+\text{sex}+\text{device}) p(\text{age}9+t+\text{sex}+\text{device})$ where $\text{age}5$ = survival probability to 5 years of age, $\text{age}9$ = survival to 9 years, and device = times when a device was attached. The goodness–of–fit simulations indicated some over–dispersion ($\hat{c}_{\text{bootstrap}} = 2.701$, $\hat{c}_{\text{median}} = 2.122$), thus demonstrating moderate violation of the assumption that all individuals were equally catchable or have similar apparent survival probabilities. We accounted for this by applying the \hat{c} correction factor, but this did not affect model ranking (Table 3).

There was little evidence for a survival difference between males and females (Fig. 4). Likewise, there was little evidence for an effect of device on survival at any age (Fig. 4). Survival estimates for seals with devices were consistently higher than those without, although there was considerable overlap in the parameter estimates. One possible explanation may be that the recapture probability for seals that carried devices was higher (Fig. 3). To test whether the presence of a device affected survival or recapture probabilities, we applied the information–theoretic evidence ratio (ER) which is the $w\text{AIC}_c$ of one model divided by that of a simpler comparison model. Indeed, adding the device factor to the recapture probability models improved model performance ($ER = 51.7$). There was also weak evidence for an effect of environmental stochasticity as measured by the Southern Oscillation Index on survival probability ($ER = 2.6$), but little evidence for an SOI effect on capture probability ($ER = 1.2$). Importantly, survival of seals that carried devices was unaffected by SOI (Fig. 4).

4. Discussion

Assessing the potential effects of research procedures on animal performance is an important component of data interpretation and ethical justification of research (Wilson and McMahon, 2006). However, acquiring such information is not always straightforward, especially for animals that spend much of their lives in remote areas and challenging environments. Few studies have assessed the potential long–term impact of telemetry or data–logging devices on animal performance and fitness. One of the key reasons for investigating the potential effects of externally borne devices is concern for the welfare of the animals, but in addition and closely aligned to this, is concern for the integrity of the data being collected. Consequently, establishing that the research procedure does not compromise the animal's performance in the short term (e.g., foraging success during foraging trips) or long term (e.g., survival over many years) is an important step to ensure that the information collected accurately represents the life history of the animal under study.

Moreover, quantifying the effects of devices on animal performance can help drive technological advancements in instruments and attachment procedures that reduce potentially negative effects on study animals. For leatherback turtles, satellite tags have traditionally been attached using harnesses (e.g., James et al., 2006); however, it has been shown recently that harness attachments, when compared to direct attachment of devices to the carapace, compromise diving ability and reduce speed of travel (Fossette et al., 2008). Hence, direct attachment is now being adopted as the standard attachment system for leatherback turtles (Doyle et al., 2008). This work also highlights how subtle changes in travel speed and other behaviours may be indicative of negative device impacts, just as longer–term indicators such as mass and survival may change when devices are attached.

We found no evidence that devices attached to southern elephant seals used to study behaviour and foraging have any short–term (arrival mass) or long–term (survival) effects on performance. This conclusion held true for all seals of all age classes, even for the smallest seals that may be the most sensitive to research manipulation. Importantly, this was true even during periods when ENSO conditions were below average (i.e., low SOI values) when juvenile seal survival is

more likely to drop below average (McMahon and Burton, 2005). Although the potential effects of data-logging devices will depend on the target species and technology employed, our study provides a benchmark that can be used for other species. From our long-term monitoring dataset we addressed each of the three main welfare concerns for ecological research: (1) the stress due to handling and capture, (2) eco-physiological limitations of device attachment and (3) long-term effect of handling and device attachment.

While our results are encouraging, using arrival mass as a proxy for changes in body condition may not necessarily reflect changes in body energy content (Coltman et al., 1998), although for elephant seals mass is thought to provide a reasonable index of condition (Biuw et al., 2003). It is such small discrepancies that can pose problems when assessing device impacts and consequently highlights the need for more study on this topic using other indices of performance and fitness. Another component that we did not address specifically was that the additional drag created by attaching an external instrument to an otherwise highly streamlined body form (Wilson et al., 2004) is that its potentially negative effects on performance may be mitigated by altering the instrument's buoyancy. Indeed, for deployments of short duration that inevitably incur high drag, negative effects can be minimised by ensuring neutral buoyancy in the attached device (e.g., Hays et al., 2007a; Williams et al., 2004).

Two key findings set this study apart from previous work investing the effects of devices on animals: (1) we could detect no amplification of effects in poor years (i.e., low SOI) when negative effects are hypothesised to be exacerbated due to food shortages either in the form of reduced quantity or quality; and (2) we could find no evidence that multiple deployments reduced fitness (quantified by survival estimates). Together these observations lend powerful support to our main conclusion that devices attached to elephant seals of any size do not compromise fitness by showing that even under some of the more extreme deployment regimes, seal performance is not compromised. This is an important result for elephant seals but more importantly, it has wider applicability for studies focussing on species of similar size and foraging dynamics such as other seals and marine turtles (Hooker and Boyd, 2003; McMahon et al., 2005c). With increasing emphasis on using wide-ranging marine predators as autonomous oceanographic samplers (Biuw et al., 2007), establishing that there are no negative effects due to the presence of recording devices is an essential first step.

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