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Instrumentation and handling effects on Antarctic fur seals (*Arctocephalus gazella*)

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Abstract

The use of biologging instruments has greatly improved our understanding of the behaviour, physiology and ecology of free-ranging marine mammals. However, handling wild animals and attaching instruments to streamlined bodies can cause stress and potentially influence behaviour and swimming/diving energetics. The goals of this study, undertaken on Bouvetøya, were (1) to determine if the first trip to sea after instrumentation is representative of subsequent trips in lactating Antarctic fur seals, to explore potential handling effects and assess possible biases in having multiple short-duration deployments (inflating N, using a limited number of tags) and (2) to evaluate potential effects of two different instrument combinations (SMRU satellite data relay loggers and very high frequency radio transmitters versus Wildlife Computers time–depth recorders and very high frequency radio transmitters) on trip durations, dive parameters, female body condition and pup growth. Handling did not appear to have any effects on the parameters studied; data from the first and second trips did not differ significantly. This implies that multiple short-term deployments are unlikely to result in biased data in this species. Instrument type did have measurable effects; time-at-sea was greater and pup growth was lower for pairs in which mothers carried bulkier instruments. This suggests that instrument streamlining is important to avoid negative impacts and that bulkier equipment should be deployed on lactating females with caution and only for short periods. The study highlights that instrument effects should be taken into account when comparing data from experiments collected using different equipment packages.

Data on foraging patterns are crucial for understanding the ecology of animals and how sensitive they might be to environmental changes (Wilson et al. 1986). However, for marine mammals direct observations are not often feasible in the wild since they feed at sea, often beneath the surface and are only on shore for short periods, if they come ashore at all (McMahon et al. 2008). Instrumentation of free-ranging marine mammals has therefore become a vital means of accruing information on their behaviour in their natural environments (e.g., Boyd et al. 2004; Trathan & Croxall 2004; Wilson & McMahon 2006; Hooker et al. 2007; Ropert-Coudert, Wilson et al. 2007). Animal-borne instruments have become increasingly sophisticated over the past few decades (Heaslip & Hooker 2008; McCafferty et al. 2007), enabling the collection of a wide diversity of behavioural and physiological data, as well as environmental data (e.g., Biuw et al. 2010). For example, heart beats, feeding events, diving parameters, water temperature, light levels and salinity are now possible to record with animal-borne instruments, which also permit the spatial tracking of animals (see Rutz & Hays 2009).

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Biologging/biotelemetry instruments can now store or relay vast data sets. But, acquiring samples from a large enough pool of individuals to be representative of a population remains a challenge, mainly due to the high economic cost of the instruments (Trathan & Croxall 2004). One way to achieve a larger sample size of individuals with a limited number of instruments is to reduce the deployment time per animal and redeploy the same tags on several animals in succession during a field season (Agnew 2004), thus recording only one or a few foraging trips per animal, but achieving a higher N (e.g., Beauplet et al. 2004). However, capturing, handling and restraining wild animals can cause significant stress that can potentially influence their post-release behaviour (Weimerskirch et al. 2002; Hawkins 2004; Wilson & McMahon 2006). The immediate, post-release period would be the most likely time in which the animal's behaviour might be abnormal as it becomes accustomed to the instrument and recovers from the capture experience. Studying only this period might introduce significant bias into behavioural/energetic analyses. In addition, fitting an instrument onto the streamlined body of a swimming/diving animal could potentially cause discomfort and create drag that could increase the energetic costs of locomotion, introducing bias to all collected data. It is therefore crucial to ensure that the results and conclusions inferred from biologging and telemetry data are valid by assessing the potential effects of instruments on animal behaviour, energetics and fitness whenever possible (Wilson et al. 1986; Croll et al. 1991; Walker & Boveng 1995; McMahon et al. 2008; Walker et al. 2012).

Previous studies have shown that instruments placed on marine mammals can cause changes in swim speed, dive frequency or attendance duration (see Boyd et al. 1991; Boyd et al. 1997; Walker & Boveng 1995; Francis et al. 1998; McCafferty et al. 1998; Littnan et al. 2004; McCafferty et al. 2007; Ropert-Coudert, Knott et al. 2007). However, considerable progress in technology and design has been made since the early days of biologging with regards to miniaturization and streamlining, which has helped reduce instrument effects on subject animals (McCafferty et al. 2007). Despite this, possible effects of instruments should not be ignored from an animal welfare or a scientific perspective (see Field et al. 2012). The latter is especially important when comparing data series that have been collected using a variety of different instruments (Trathan & Croxall 2004).

Antarctic fur seals (*Arctocephalus gazella*; AFS) haul out on a number of isolated islands, including Bouvetøya. Adult females give birth annually during the austral summer (Bonner 1968). During lactation they undertake a regular cycle of four–five days foraging at sea alternating with two–three days attending their dependant pup ashore (Costa et al. 1989; Boyd 1999; Guinet et al. 2000), until their pups are weaned at a mean age of 114 days (Kovacs & Lavigne 1992). The at-sea behaviour of lactating adult females from various populations has been the subject of numerous studies employing a variety of attached devices (e.g., Staniland et al. 2007; Biuw et al. 2009; Casper et al. 2010; Goldsworthy et al. 2010; Gastebois et al. 2011). However, few studies have specifically considered the effects of disturbance due to handling or instrument deployment on the characteristics of the foraging behaviour that they are attempting to study. The goals of this study were (1) to determine if the first trip to sea after instrumentation is representative of subsequent trips in lactating AFS tagged at Bouvetøya and (2) to evaluate potential effects of different instrument types on trip durations, dive parameters, female body condition and pup growth.

Materials and methods

This study took place at Nyrøysa (54.41° S, 03.29° E) on the west coast of Bouvetøya, South Atlantic, during three austral summer seasons (2000/01, 2001/02, 2007/08). A total of 46 lactating AFS were instrumented with various combinations of biotelemetry gear during the study (Table 1). Females with newborn pups were selected, assuming that the presence of an umbilicus/placenta indicated that mothers were still in their perinatal period, that is, still ashore after giving birth, before departing for their first trip to sea. The mothers were manually restrained using a large cone-shaped hoop net (2.2 m long × 1 m in diameter) attached to an aluminium frame and handle (see David et al. 1990 for further details). Body mass was measured to the nearest

Table 1 Summary of instrument deployments on lactating Antarctic fur seals at Bouvetøya during three austral summers (2000/01, 2001/02, 2007/08): satellite relay data loggers (SRDLs), time–depth recorders (TDRs), platform transmitter terminals (PTTs) and very high frequency radio transmitters (VHFs).

Season	Animals captured (*n*)	SRDL (*n*)	TDR+VHF (*n*)	TDR+PTT +VHF (*n*)
2000/01	12	3	9	–
2001/02	10	3	7	–
2007/08	20	–	–	20

Table 2 Deployment and recovery statistics for Antarctic fur seals equipped with satellite relay data loggers (SRDLs), time–depth recorders (TDRs) and very high frequency radio transmitters (VHFs) at Bouvetøya in 2000/01 and 2001/02.

| Date deployed | Seal ID no. | Duration (d) | Female weight (kg) | | | Pup sex | Pup weight (kg) | |
			At deployment	At recapture	Weight diff.		At deployment	At recapture
SRDL n =6								
2000 Dec 17	bv1-1553-00	24	35	32	−3	F	6.55	8.5
2000 Dec 17	bv1-22497-00	NA[a]	36	NA[a]	NA[a]	F	5.1	7.1
2000 Dec 17	bv1-2848-00	64	39	35	−4	F	5.25	7.4
2001 Dec 14	bv2-28489-01	45	42	33	−9	M	4.8	8.7
2001 Dec 14	bv2-28490-01	37	43	37	−6	M	5.65	9.6
2001 Dec 14	bv2-28491-01	48	53	39	−14	F	4.6	9.9
Means ±SD		43.6±14.7	41.3±6.5	35.2±2.8	−7.2±4.4		5.3±0.7	8.5±1.3
TDR n =16								
2000 Dec 18	bv1-003-00	50	41	42	+1	M	5.5	9.8
2000 Dec 18	bv1-024-00	43	27	29.5	2.5	M	4.75	9.5
2000 Dec 19	bv1-033-00	45	32	33	+1	M	5.2	11
2000 Dec 20	bv1-052-00	43	29	28	−1	F	5.1	7.9
2000 Dec 20	bv1-073-00	41	34	34	0	F	4.3	6.8
2000 Dec 21	bv1-092-00	40	37	34	−3	F	5.1	11
2000 Dec 21	bv1-105-00	42	36	30	−6	F	4.3	9
2001 Dec 15	bv2-468-01	39	47	45	−2	M	6.1	13.2
2001 Dec 15	bv2-479-01	39	38	31	−7	F	4.7	9
2001 Dec 15	bv2-457-01	39	48	38	−10	F	5.3	10.2
2001 Dec 15	bv2-587-01	40	34	32	−2	M	5.3	11.4
2001 Dec 15	bv2-966-01	39	36	38	+2	F	4.8	8.7
2001 Dec 16	bv2-438-01	38	43	32.5	−10.5	F	4	8.2
2001 Dec 16	bv2-550-01	43	42	35	−7	F	4.8	8.8
2001 Dec 17	bv2-758-01	38	43	42	−1	F	6	10
2001 Dec 17	bv2-999-01	41	44	34	−10	F	4.8	8.7
Means ±SD		41.2±3.1	38.2±6.1	34.8±4.3	−3.3±4.5		5.0±0.6	9.6±1.5
VHF n =11								
2001 Dec 18	b-162	38	37	33	−4	F	4.6	8
2001 Dec 18	b-176	38	43	37	−6	F	3.8	8
2001 Dec 19	b-178	38	38	32	−6	M	5.1	9.7
2001 Dec 19	b-182	38	41	NA[a]	NA[a]	M	5.6	8.6
2001 Dec 19	b-184	38	27	28	1	F	3.9	6.9
2001 Dec 19	b-186	38	30	29	−1	F	4.1	5.8
2001 Dec 19	b-188	37	33	29	−4	F	5.1	8.2
2001 Dec 21	b-192	36	30	31	1	F	5.3	7.6
2001 Dec 21	b-196	35	35	28	−7	F	4.5	7.1
2001 Dec 21	b-211	40	34	36	2	M	5.3	6.5
2001 Dec 21	NO-241	36	49	44	−5	F	5.1	7.9
Means ±SD		37.4±3.4	35.6±6.5	32.7±53.1	−2.9±3.4		4.8±0.6	7.7±1.1

[a]Data not available.

0.1 kg using a 100 kg Salter scale prior to instrument attachment and upon recovery (Table 2). All instruments were glued to the fur of the adult females in the mid-dorsal region with two-component industrial-grade epoxy (Huntsman AW2101/HW2951, Intertronics, Kidlington, Oxfordshire, UK, or 5-Cure, Industrial Formulators Inc., Port Coquitlam, BC, Canada). During their mothers' instrument deployment period the pups were also weighed several times by suspending them briefly in a canvas bag attached to a mechanical spring; the first weight was taken when the mothers' instrument(s) were deployed.

Different combinations of instruments were used in the different seasons (Table 1); all had at least one instrument with a protruding antenna. During 2000/01 and 2001/02, a total of six satellite relay data loggers (SRDLs; Sea Mammal Research Unit, St. Andrews, UK) and 20 Mk6 time–depth recorders (TDRs; Wildlife Computers, Redmond, WA, USA) in combination with very high frequency transmitters (VHFs; Model 5955, Advanced Telemetry Systems, Isanti, MN, USA) were deployed. The TDRs were removed after five–six weeks of deployment, prior to the expedition's departure from the island, while the SRDLs were left on the animals to

fall off naturally during the annual moult. The SRDL data used in the present study covered only the first five–six weeks of lactation, during which both SRDL and TDR data were collected. Instrument dimensions and weights are summarized in Table 3. The SRDLs sampled depth every 4 s while diving and the on-board processor was set to define the start of a dive to occur when the tag was wet and below 5 m for 8 s. A dive ended when the tag either returned to within 5 m of the surface or became dry. The Mk6 TDRs sampled depth every 10 s while the tag was wet and had a depth resolution of 2 m. Raw data files obtained from the Mk6 TDRs were extracted using purpose-built software provided by the manufacturer (Dive Analysis, Zero Offset Correction, Minimum-Maximum-Mean, Wildlife Computers). Any excursion from the surface to a depth ≥ 5 m for at least 8 s was considered a dive, matching the settings of the SRDLs.

During 2007/08, three instruments were simultaneously deployed on each of 20 adult female AFS: (1) a 0.5 W Sirtrack Kiwisat 101 platform terminal transmitter (PTT; Sirtrack Inc., Havelock North, New Zealand); (2) a TDR (Mk9 Wildlife Computers); and (3) a Sirtrack VHF to facilitate recapture. All three instruments were glued to the fur along the main axis of the animal in the mid-dorsal region (behind the scapulae), with the TDR and the VHF in front of the PTT (see Table 3 for details on the instruments' characteristics). The TDRs were programmed to record depth at a resolution of 0.5 m, and light level every second, both when wet and dry in order to record attendance patterns precisely. Any excursion from the surface to a depth ≥ 5 m for at least 8 s was defined as a dive to match the definition of the instruments from the two preceding study periods.

Start and end times of trips were defined based on dive and conductivity switch records from the TDRs, or based upon distance from the island for animals with SRDLs and PTTs. To obtain the best possible representation of the real path followed by the animals, a speed–distance–angle filter (see Freitas et al. 2008) was applied to the tracks recorded by the SRDLs and PTTs. All statistical analyses were conducted using R, version 2.12.1 (R Development Core Team 2009). All distances from the island refer to great circle distances and the maximum corresponds to the most distant point reached within a trip. When statistical models were used, model fitting was based on the examination of the residuals and Kolmogorov–Smirnov tests were used to assess whether or not data were normally distributed.

Handling effect/instrumentation effect

First and second trips were compared from a total of 84 trips, performed by 42 animals, across three summer seasons (Table 4). Four instruments malfunctioned and were not included in the analysis. Only the first two trips were compared in order to minimize possible confounding effects of date\lactation stage. Each trip parameter (trip duration, maximum distance reached from the island, total distance swam, mean dive duration, mean dive depth) was compared between trip 1 and trip 2 using linear mixed effect models (LMEs). These models were fitted with the trip number, departure date and year as fixed effects and animal identification number (ID) as a random effect. The mixed-effect structure accounts for correlations in the data arising from individual animal effects; in this case trips 1 and 2 are performed by the same animal and hence not independent.

Instrument effect

Only records from 2000/01 and 2001/02 were useful for exploring potential impacts of different instrument types on trip parameters because in 2007/08 all animals bore the same gear combination resulting in a confounding effect between "year" and "instrument type." In this latter season, deployment periods were also much reduced compared to the first field seasons. For the two years with comparable data, attendance patterns (trip duration and haul-out duration), mean dive duration

Table 3 Summary of the characteristics of instruments deployed on Bouvetøya during three austral summers: satellite relay data loggers (SRDLs), time–depth recorders (TDRs), platform transmitter terminals (PTTs) and very high frequency radio transmitters (VHFs).

Instrument	Length	Width	Height	Weight (air)	Weight (water)	% body mass[a]	% frontal area[b]
VHFs[c]	82	20	20	36	20	0.06	1.0
VHFs[d]	45	30	24	70	15	0.12	1.2
TDRs (Mk6)	65	35	15	53	18	0.13	1
TDRs (Mk9)	67	17	17	30	12	0.07	0.6
SRDLs	105	70	35	400	135	1	4.5
PTTs	156	62	19	275	100	0.7	1.9

[a]Assuming an average body mass for an adult female Antarctic fur seal of 40 kg.
[b]Assuming an average frontal area for an adult female Antarctic fur seal of 490 cm^2.
[c]VHFs deployed during the 2000/01 and 2001/02 seasons.
[d]VHFs deployed during the 2007/08 season.

Table 4 Summary statistics for trip 1 and trip 2 for Antarctic fur seal females at Bouvetøya equipped with satellite relay data loggers (SRDLs) and very high frequency radio transmitters (VHFs; 2000–02), time–depth recorders (TDRs) and VHFs (2000–02), and platform transmitter terminals (PTTs) and TDRs and VHFs (2007/08). Maximum distance and total distance swam could only be calculated for animals carrying SRDLs or PTTs.

		Trip 1		Trip 2	
	n^a	Mean	SD	Mean	SD
Duration (h)	42	60.8	23.9	58.6	32.3
Max. distance (km)	24	56.8	31.2	59.1	37.9
Total distance (km)	24	175.3	87.9	186.1	129.1
Mean dive duration (s)	42	59.1	13.5	57.42	13.6
Mean dive depth (m)	42	20.4	7.7	20.5	8.3

[a]Number of animals used in the analysis.

and average depth per trip were compared using LMEs. These models were fitted with tag type, trip departure dates and year as fixed effects and animal ID as a random effect, to take into account individual variability and the different number of trips performed by each individual. Due to transmission bandwidth constraints in the Argos system, the dive records collected by the SRDLs were compressed and not every recorded dive was transmitted (see Fedak et al. 2001). Transmitted dives are randomly selected from a buffer containing 600 dives, and about 30% of the total number of dives was transmitted during these deployments (see Biuw et al. 2009 for details). In order to assess potential biases due to the different sampling regimes between the SRDLs and the TDRs, both the entire TDR records and a random sampling of 30% of the same records were used in the analysis. The effect of the tags on the female's body condition was assessed by comparing the mass change per day between deployment and recovery of the instruments using an ANOVA. The pup growth rates were compared using LME. Pups of instrumented mothers were included in the analysis if there were at least two weight measurements taken during the tagging period of their mothers. The models were fitted with pup age, year and instrument type borne by the mother as fixed effects and animal ID as a random effect, to take into account the lack of independence of repeated measurement of individual pups. Mass measurements from mothers (and their pups) carrying SRDLs or TDRs were used in this part of the analyses.

Results

Summary statistics for trip parameters for trips 1 and 2 are presented in Table 4. None of the parameters were significantly different for the two trips (Table 5). Date was not a significant variable in any of the models, but year influenced the mean dive duration and the mean dive depth. Both variables were significantly greater in 2007/08 compared to the two first seasons.

A total of 189 trips and 168 haulout periods were used to compare the attendance patterns and the trip parameters between the two instrument groups (Table 6). A summary of the LMEs used to explore these data is presented in Table 7. The mean trip duration was significantly greater for SRDL animals (mean$_{SRDL}$ = 103.9 ± 33.7 h) compared to TDR instrumented females (mean$_{TDR}$ = 65.4 ± 21.5 h). Instrument type and date were significant variables in the LME model, while year was not significant. The mean haulout duration was not significantly different between the two instrument groups (SRDL animals 45.3 ± 10.9 h; TDR animals 37.7 ± 17.0 h), nor were any of the other variables tested in the model. Dive duration and dive depth were only influenced by date and year but not by the instrument type carried by the female. The data sub-sampling

Table 5 Summary of the linear models used to compare the trip parameters between trip 1 and trip 2. Maximum distance refers to the maximum distance from the island reached within a trip and total distance refers to the total distance swam during a trip. For maximum distance and total distance only, animals fitted with satellite relay data loggers (SRDLs) or platform transmitter terminals (PTTs) were used in the analysis.

Trip parameter	Model term	F value	df	p^a
Trip duration	Trip number	0.17	40	0.68
	Date	0.01	40	0.90
	Year	1.33	39	0.27
Maximum distance[b]	Trip number	0.20	22	0.65
	Date	0.21	22	0.64
	Year	0.61	21	0.55
Total distance	Trip number	0.18	22	0.67
	Date	0.01	22	0.95
	Year	0.45	21	0.65
Dive duration[b]	Trip number	0.46	39	0.50
	Date	0.37	39	0.37
	Year	5.70	38	**<0.01**
Dive depth[b]	Trip number	0.02	39	0.90
	Date	0.02	39	0.87
	Year	4.77	38	**<0.05**

[a]High significance levels in boldface.
[b]Parameters log-transformed.

Table 6 Summary statistics for haulout periods and trip durations for seals equipped with satellite relay data loggers (SRDLs) or Mk6 time–depth recorders (TDRs) at Bouvetøya in 2000/01 and 2001/02.

Season deployed	Instrument	Seal ID no.	Haulout duration (h)			Trip duration (h)		
			Mean	SD	n	Mean	SD	n
2000/01	SRDLs	bv1-1553-00	53.5	10.8	5	151.2	61.5	6
2000/01		bv1-22497-00	34.4	10.5	9	75.2	46.5	10
2000/01		bv1-2848-00	59.2	26.1	5	118.1	55.9	6
2001/02		bv2-28489-01	38.7	15.9	8	79.7	25.7	9
2001/02		bv2-28490-01	52.3	16	6	126.6	29.7	7
2001/02		bv2-28491-01	33.8	10.2	10	72.3	17.3	11
		Mean	45.3	10.9		103.9	32.7	
2000/01	TDRs	bv1-003-00	32.7	9.6	8	72.9	70.2	9
2000/01		bv1-024-00	44.5	11.4	5	110.3	37.9	6
2000/01		bv1-033-00	30.8	7.7	9	64.4	17.3	10
2000/01		bv1-043-00	42.8	36.7	8	44.7	61.4	9
2000/01		bv1-052-00	29.6	19.8	10	44.6	28.3	11
2000/01		bv1-073-00	36.6	13.4	7	61.3	53.6	8
2000/01		bv1-092-00	35.4	13.2	6	85	27.4	7
2000/01		bv1-094-00	21.6	7.8	8	60.5	37.8	9
2000/01		bv1-113-00	96.7	37.8	2	17.9	11	3
2001/02		bv2-468-01	22.8	9.5	10	50.1	20.3	11
2001/02		bv2-479-01	33.8	28.8	6	77.1	34.4	7
2001/02		bv2-587-01	32.5	14.1	6	87	41.5	7
2001/02		bv2-777-01	31.3	0.2	2	72.9	15.3	3
2001/02		bv2-438-01	28.3	9	8	53.6	39.1	9
2001/02		bv2-758-01	33.4	8.1	8	61.9	17.5	9
2001/02		bv2-999-01	40.3	13.9	6	82.1	24.5	7
		Mean	37.7	17		65.4	21.5	

performed by the SRDLs did not affect the results, as the estimates and the p-values were similar between the model using the complete TDR data set or a matching random 30% sample of the TDRs data records, simulating sampling similar to the SRDL (Table 7).

The females instrumented with SRDLs had similar masses to those instrumented with TDRs when capture and instrument deployments took place (mean$_{SRDL}$ = 42.2 ± 6.6 kg; mean$_{TDR}$ = 37.8 ± 6.4 kg; ANOVA $F_{1,23}$ = 2.02; p = 0.17). The percentage mass loss per day (mean$_{SRDL}$ = −0.39 ± 0.15%; mean$_{TDR}$ = −0.18 ± 0.28%; ANOVA $F_{1,23}$ = 2.59; p = 0.12) and the total mass loss over the period of instrumentation (mean$_{SRDL}$ = −7.2 ± 4.4 kg; mean$_{TDR}$ = −2.8 ± 4.4 kg; ANOVA $F_{1,23}$; p = 0.055) were not statistically different for the two groups, although the mean values for the SRDL group were more than twice that of the TDR group for both parameters.

Pup start masses were not significantly different between the two instrument groups (mean$_{SRDL}$ = 5.3 ± 0.7 kg; mean$_{TDR}$ = 5.0 ± 0.5 kg; ANOVA $F_{1,20}$ = 1.19; p = 0.28). Over the study period, pup growth was close to linear in each treatment group (Fig. 1). The simplest LME model fitted to explore pup growth rate used pup age, instrument type borne by the mother and the interaction between age and instrument. Pup sex and the interaction

between age and pup sex were tested but there was no significant differences (Table 7). However, pups with SRDL-instrumented mothers grew significantly slower than those with TDR-instrumented mothers (growth rate$_{SRDL}$ = 0.078 ± 0.011 kg day^{-1}; growth rate$_{TDR}$ = 0.104 ± 0.025 kg day^{-1}).

Discussion

There were no detectable differences in the recorded trip parameters (trip duration, maximum distance, total distance, mean dive duration and mean depth duration) between the first trip performed following capture and handling and the subsequent trip. Nor were there any obvious behavioural changes observed upon the release of instrumented mothers and their pups in the treatment groups; all pairs showed apparently normal behaviour when reunited, as has been reported in previous studies (Doidge et al. 1986, but also see Geertsen et al. 2004; Hooker et al. 2007; Walker et al. 2012). Despite having undergone what is likely a moderately stressful experience (the capture and instrument deployment) immediately prior to the first trip, behaviour during this first trip to sea did not differ from the subsequent trip in any manner that was measured. Consequently, using data

Table 7 Summary of linear mixed models fitted to explain the variability in attendance patterns, dives parameters and pup growth rates between the two instrument groups: satellite data relay loggers (SDRLs) in combination with very high frequency radio transmitters (VHFs); and time–depth recorders (TDRs) combined with VHFs. For dive depth and dive duration, the values in parenthesis correspond to the entire data set while the others correspond to a random sample of 30% of the recorded dives. The *p*-values in boldface are significantly different between the two instrument groups. The reference level for the instrument factor is "SDRL" and "2000/01" for the year.

Trip parameter	Model term	Value	SE	df	p
Trip duration	Intercept	63.85	16.73	166	**<0.001**
	Instrument (TDR)	−2.13	0.68	19	**<0.01**
	Date	0.00	0.00	166	**<0.01**
	Year (2001/02)	0.37	0.62	19	0.56
Haulout duration	Intercept	−188.13	141.42	144	0.18
	Instrument (TDR)	−9.51	5.02	20	0.07
	Date	0.00	0.00	144	0.09
	Year (2001/02)	−6.21	4.60	20	0.18
Dive depth[a]	Intercept	7.79 (6.79)	0.50	26 318	**<0.001**
	Instrument (TDR)	−0.09 (−0.1)	0.08	19	0.25 (0.24)
	Date	0.00	0.00	26 318	**<0.001**
	Year (2001/02)	0.28	0.07	19	**<0.001**
Dive duration[a]	Intercept	5.45 (5.58)	0.46	26 318	**<0.001**
	Instrument (TDR)	0.08 (0.07)	0.07	19	0.27 (0.33)
	Date	0.00	0.00	26 318	**<0.001**
	Year (2001/02)	0.17	0.58	19	**<0.05**
Pup mass	Intercept	5.14	0.40	88	**<0.001**
	Age	0.08	0.01	83	**<0.001**
	Instrument (TDR)	−0.22	0.50	29	0.66
	Instrument (VHF)	−0.37	0.53	29	0.48
	Sex (M)	0.47	0.40	29	0.25
	Age ×instrument (TDR)	0.03	0.01	88	**<0.05**
	Age ×instrument (VHF)	0.00	0.01	88	0.89
	Age ×sex (M)	0.01	0.01	88	0.14

[a]Parameters log-transformed.

from the first trip after instrumentation or deploying instruments on a large number of animals for only one or two trips in order to increase the sample size (and minimize the risk of longer-term deployments) seems to be a reasonable protocol for AFS studies.
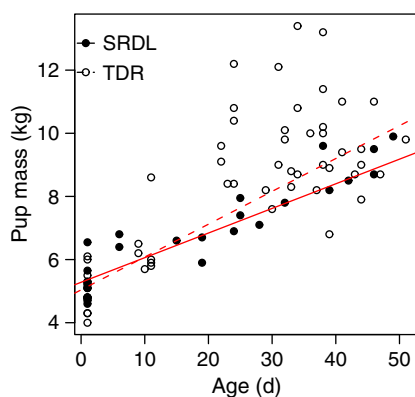

Fig. 1 Mass versus age for pups of females instrumented with satellite relay data loggers (SDRLs), time–depth recorders (TDRs) and very high frequency radio transmitters (VHFs) during the 2000/01 and 2001/02 austral summers at Bouvetøya. The fitted lines represent predictions from a linear mixed-effects model describing pup mass as a function of the age and the instrument type carried by the mother.

AFS females instrumented with larger instruments (SDRLs+VHFs) in this study performed substantially longer trips than those carrying smaller instruments (TDRs+VHFs). Similar findings have been shown for various other marine mammal species (Baker & Johanos 2002; Walker et al. 2012) and penguins (Croll et al. 1991; Ropert-Coudert, Wilson et al. 2007). In previous studies, AFSs carrying VHFs +TDRs showed extended attendance patterns compared to those carrying only VHFs (Walker & Boveng 1995). Boyd et al. (1997) purposely studied the consequences of adding drag and increasing the cost of transport on lactating females of this species by attaching a wooden block on the animals' backs, mimicking the shape and position of an instrument similar to the SRDLs used in this study. These authors also found that animals carrying the largest and heaviest load performed longer trips. In other species, such as the Juan Fernández fur seal (*Arctocephalus philipii*), the first trip of females carrying a TDR was up to four times longer than trips performed by females carrying no instrument (Francis et al. 1998). But, in contrast Boyd et al. (1991) did not find any difference in attendance patterns between AFS with and without TDRs.

Foraging trip and haulout durations are usually correlated in AFS activity records (Costa et al. 1989; Boyd et al. 1991). But, in the present study, no significant difference in haulout duration was observed between the two instrument groups, despite the significant difference in at-sea trip duration. It is possible that an existing difference went undetected because of our relatively small sample sizes (see Walker & Boveng 1995), but it seems more likely that additional foraging costs were met via spending more time at sea, but this fact did not impact how long it takes to provision the pup with available milk stores before needing to again access food to restart the cycle. The increased trip duration observed could be related to lower prey capture rates as a consequence of the added drag, but is more likely due to increased costs to the female of swimming and diving. Hydrodynamic shape, density and position of a tag are known to affect streamlining and therefore the efficiency with which the animals move in a fluid (Wilson et al. 1986; Agnew 2004; Hooker et al. 2007; Walker et al. 2012). Instrument mass is likely of relatively minor importance for most marine mammal deployments because the instruments are close to being neutrally buoyant and are usually <5% of the animal's body mass; in this study equipment mass was a maximum of 1% of body mass (see Hawkins 2004; Walker et al. 2012). Boyd et al. (1997) showed that animals with larger, heavier tags swam slower both during surface swimming and diving compared to animals with smaller tags, although the present study did not detect any difference in dive depth or dive duration between the two groups with SRDLs and TDRs. If the net energy gain per dive is decreased due to increased drag of larger instruments, the animals might have to stay longer at sea in order to meet their energetic requirements before returning to the colony to feed their pup if they do not increase the time spent in individual dives. Increased foraging costs do occur naturally in fur seals in periods of reduced prey abundance (Boyd et al. 1991; Boyd et al. 1994) with the consequence of increased time spent at sea under such circumstances, comparable to the situation observed in the present study with the largest tags.

Foraging in female fur seals is influenced by two contrasting mechanisms: the amount of energy the female can store, while meeting her own energy needs, and the amount of time she can spend at sea, which is dependent on the pup's fasting abilities (Costa et al. 1989; Boyd et al. 1991; Arnould et al. 1996). If the female's energy expenditure at sea increases, the time needed to replenish her energy stores and accumulate new reserves to produce milk will increase but she will still be constrained by the pup's fasting limits. If the females cannot spend the necessary time at sea to recoup their metabolic and milk production costs, they will be forced to use more body reserves or lower energy delivery to the pup (or a combination). In the present study, SRDL animals lost on average twice as much mass per day (and total mass) compared to TDR animals, although this difference was not statistically significant. Small sample size ($n_{SRDL} = 5$) and high individual variance typically observed in AFS foraging behaviour (Walker & Boveng 1995) limit the power to detect differences between groups in this study. Boyd et al. (1997) reported a mass loss of 2 kg more for treatment animals (large instrument $n = 6$) compared to control animals (small instrument $n = 8$), but similarly failed to detect a statistically significant difference. It is difficult to assess if larger instruments would have any negative long-term effects on the carriers. The present study and that of Boyd et al. (1997) lasted for only the first third of the lactation period, though this does cover the most energetically demanding period for the females. Milk production decreases approximately 80 days after birth (Arnould 1996; Arnould et al. 1996) and the females might then be able to allocate more energy to replenish their own energy reserves regardless of the added foraging cost.

Several factors are known to influence AFS pup growth rates, such as sex, prey availability (Vargas et al. 2009) and mass loss rates during the fasting periods while their mother is at sea (Guinet et al. 1999). In the present study, sample sizes were too small to assess potential effects of sex and year but a significant difference in growth rate was detected with pups of SRDLs mothers growing more slowly. However, it should be noted that both sets of pups remained within the range of pup growth rates described in the scientific literature for AFS from South Georgia and Macquarie Island (Lunn et al. 1993; Guinet et al. 1999; Vargas et al. 2009). Both sexes were represented within each treatment group but, due to the unbalanced number of SRDLs and TDRs, there were more females in the TDR group. However, this lack of balance is counter to the trend observed between the equipment treatment groups because females normally have slower growth rates than males (Guinet et al. 1999; Vargas et al. 2009).

In conclusion, this study showed that data from the first trip after instrumentation is representative of subsequent trips and that handling does not appear to have any measurable effect on the parameters explored. Therefore, deploying instruments on a large number of animals for only one or two trips in order to increase the sample size (and minimize the risk of longer-term deployment costs) seems to be a reasonable protocol for AFS studies. Secondly, larger instruments seem to have at least temporary negative effects on lactating AFSs and

their pups. At-sea time was significantly longer for animals with larger instruments and pup growth was significantly lower, suggesting that larger instruments should be used for only short periods, or that the shape of the instruments should be altered prior to being used again on this species. Lastly, instrument effects should be taken into account when comparing time series collected under different equipment deployment regimes in order to avoid false conclusions regarding interannual variation or other explanatory variables.

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