1 Title

2 Biologging of emperor penguins – attachment techniques and associated deployment performance

3 Author list

4 Aymeric Houstin^{1,2}, Daniel P. Zitterbart^{3,4,5}, Alexander Winterl^{3,4}, Sebastian Richter^{3,4}, Víctor Planas-
5 Bielsa¹, Damien Chevallier², André Ancel², Jérôme Fournier^{6,7}, Ben Fabry³, Céline Le Bohec^{1,2}

6 Author Affiliations

7 ¹ *Centre Scientifique de Monaco, Département de Biologie Polaire, Principality of Monaco*

8 ² *Université de Strasbourg, CNRS, IPHC UMR 7178, F-Strasbourg, France*

9 ³ *Department of Physics, Friedrich-Alexander-University Erlangen-Nürnberg, Erlangen, Germany*

10 ⁴ *Applied Ocean Physics and Engineering, Woods Hole Oceanographic Institution, Woods Hole, USA*

11 ⁵ *International Research Organization for Advanced Science and Technology (IROAST), Kumamoto
12 University, 2-39-1 Kurokami, Kumamoto 860–8555, Japan*

13 ⁶ *CNRS, UMR 7204 CESCO - Station marine MNHN, Place de la Croix, Concarneau, France*

14 ⁷ *MNHN, Centre de Recherches sur la Biologie des Populations d'Oiseaux, Paris, France*

15

16 Corresponding Author information

17 Correspondence is to be addressed to Aymeric Houstin houstina@gmail.com and Céline Le Bohec
18 celine.lebohec@iphc.cnrs.fr

19

20

1 Abstract

2 An increasing number of marine animals are equipped with biologgers, to study their physiology,
3 behaviour and ecology, often for conservation purposes. To minimise the impacts of biologgers on
4 the animals' welfare, the *Refinement* principle from the Three Rs framework (*Replacement*,
5 *Reduction*, *Refinement*) urges to continuously test and evaluate new and updated biologging
6 protocols.

7 Here, we propose alternative and promising techniques for emperor penguin (*Aptenodytes forsteri*)
8 capture and on-site logger deployment that aim to mitigate the potential negative impacts of logger
9 deployment on these birds. We equipped adult emperor penguins for short-term (GPS, Time-Depth
10 Recorder (TDR)) and long-term (*i.e.* planned for one year) deployments (ARGOS platforms, TDR), as
11 well as juvenile emperor penguins for long-term deployments (ARGOS platforms) in the Weddell Sea
12 area where they had not yet been studied.

13 We describe and qualitatively evaluate our protocols for the attachment of biologgers on-site at the
14 colony, the capture of the animals and the recovery of the devices after deployment. We report
15 unprecedented recaptures of long-term equipped adult emperor penguins (50% of equipped
16 individuals recaptured after 290 days). Our data demonstrate that the traditional technique of long-
17 term attachment by gluing the biologgers directly to the back feathers is detrimental to the birds. It
18 causes excessive feather breakage and the loss of the devices at an early stage. We therefore
19 propose an alternative method of attachment for back-mounted devices. This technique led to
20 successful year-round deployments on 37.5% of the equipped juveniles. Finally, we also disclose the
21 first deployments of leg-bracelet mounted TDRs on emperor penguins.

22 Our findings highlight the importance of monitoring potential impacts of bilogger deployments on
23 the animals and the need to remain critical towards established and new protocols.

24

25

1 Introduction

2 Over the last decades, biologging technology - the “use of miniaturised animal-equipped tags for
3 logging and/or relaying data about an animal’s movements, behaviour, physiology and/or
4 environment”¹ - has rapidly progressed and led to fundamental advances in ecology of *e.g.*
5 terrestrial²⁻⁴ and marine predators⁵⁻⁷ including seabirds⁸⁻¹⁷. This technical evolution that included
6 miniaturisation, design optimisation, storage capacity and power consumption, was supported by the
7 development of new analytical techniques and processing software^{18,19}.

8 Biologgers can cause discomfort to the tagged animal and may even impede their movements,
9 especially in the case of diving seabirds like penguins where the increased water drag can increase
10 the energy expenditure²⁰⁻²⁴. However, the miniaturisation of devices²⁵, the establishment of
11 guidelines^{26,27} and the activities of study review boards that oversee the ethical treatment of animals
12 in scientific studies²⁸⁻³¹ help to mitigate negative impacts and to comply with the Three Rs
13 framework (*Replacement, Reduction, Refinement*)³².

14 Yet, especially in the case of penguin tracking studies, the inability to observe the animals carrying
15 the devices at sea bears the risk that deleterious effects may not be obvious²³ or may even remain
16 unnoticed if birds are not resighted. For instance, after decades of flipper banding thousands of
17 penguins³³ (and see references in Jackson et al.³⁴), it was only in the 2000’s that studies³⁵⁻³⁸
18 assessed its long-term effect, and showed that flipper bands dramatically decreased the survival and
19 breeding success of their carrier. This finding raised important questions about ethics and bias in
20 scientific studies; an issue already highlighted by Wilson et al.³⁹ in 1986. Flipper banding of penguins
21 is a prime example of why it is necessary to study potential impacts of device deployments on
22 animals. It has to be noted that of the five studies⁴⁰⁻⁴⁴ where emperor penguins (*Aptenodytes*
23 *forsteri*) have been tagged with external biologgers for a year-round deployment duration, none has
24 reported the recovery of the device or a sighting of an equipped bird after deployment. The causes of
25 signal loss remained unclear^{42,45} and the fate of the device-carrying birds uncertain.

1 Nonetheless, data obtained from biologgers are often of such importance for conservation biology
2 that the benefits may outweigh the risk for the animals ^{46,47}, if the risks to animals are kept minimal.
3 For example, tracking studies that determine the home range and movement corridors of species are
4 often a prerequisite for conservation management policies ^{48–51} as demonstrated by the
5 establishment of the Ross Sea Marine Protected Area (MPA) in 2017. This first MPA adjacent to
6 Antarctica was partly justified by the range of Adélie penguins (*Pygoscelis adeliae*) during their
7 energy-intensive premoult period ^{52,53}.

8 Emperor penguins have not yet been tracked in the Weddell Sea and in the Atlantic sector of the
9 Southern Ocean, thus not much is known about their distribution in these areas. To improve the
10 scientific knowledge about this species and to provide data in support of the development of a MPA
11 in the Weddell Sea area, we have equipped adult and juvenile emperor penguins. Biologger types
12 were chosen according to our research questions and subject to seasonal constraints. We document
13 for the first time the resighting and recapture of long-term equipped emperor penguins as well as
14 device retrieval. Indeed, while back-mounted loggers have already been successfully used for long-
15 term deployments on emperor penguins ^{43,44}, their physical impact has never been assessed
16 presumably due to the logistical difficulties in resighting the birds before the annual moult.

17 Furthermore, we present the first leg-band biologger attachment and deployment on emperor
18 penguins. Several leg-band devices had been successfully tested and deployed on other penguin
19 species (Adélie and macaroni (*Eudyptes chrysolophus*) penguins, see ^{11,30,54,55}) and it was shown that
20 the leg-band devices minimised drag, induced little behavioural disturbance and did not jeopardize
21 birds' survival. To date, no such deployment had been reported on emperor penguins. Additionally,
22 we describe and discuss methods for catching, handling or retrieving (resight and recapture) emperor
23 penguins. These necessary procedures lack standardisation across studies. Some use a rugby-like
24 catch method ^{56,57}, others would use a crook ^{42,58} or a fixed enclosure ^{59,60}, and the impacts of these
25 procedures on the targeted bird are rarely reported.

- 1 Summarising, in this manuscript, we describe and review protocols for on-site capture, handling and
- 2 release of emperor penguins, biollogger attachment and recovery techniques that aims to minimise
- 3 the impacts on the birds' welfare.

1 **Methods**

2 **Study site, species, and deployments**

3 This study was conducted at the Atka Bay emperor penguin colony (70°37'S, 08°09'W) in close
4 vicinity (~ 10 km) of the German research base Neumayer Station III (70°39'S, 08°15'W) during two
5 consecutive summer campaigns (November to January 2017-2019). During these campaigns, we
6 deployed biologgers for short- and long-term deployments. Monitoring periods of weeks to months
7 in summer ^{61–64} are referred to as “short-term”, while year-round planned monitoring that include
8 austral winter are referred to as “long-term” ^{62,65,66}.

9 The deployment protocols possible to implement on emperor penguins largely depend on the
10 species’ phenology (and logistic constraints). The Emperor penguin is the only bird species breeding
11 during the austral winter ⁶⁷, almost exclusively on sea ice ⁶⁸ all around Antarctica ⁶⁹. After a courtship
12 period in March and April, depending on the colony’s latitude, and an incubation period of around 64
13 days, the chicks hatch in the middle of the austral winter. As central place foragers ⁷⁰, male and
14 female do alternate trips at sea to find food for their sole offspring. By October, the chick is thermally
15 independent and is left on its own while both parents go foraging at sea and return to feed their
16 chick independently ^{67,71}. These recurring returns of each adult to feed its chick, approximately once
17 per week, allow deployment and retrieval of short-term data loggers. In December or January, chicks
18 moult and fledge. By the end of the austral summer, the adult emperor penguins moult. For both,
19 moulted chicks (*i.e.* juveniles) and adults, a reliable attachment of long-term logging devices on their
20 back is only possible after moulting is largely completed. The majority of juvenile birds will not return
21 to the colony for at least two years ⁷² and previous studies suggest that most of the adults moult on
22 the pack ice ^{62,73–75}. There is also no certainty that adults moulting at the colony are actual breeders
23 from that particular colony and that they will return in the next season. Therefore, successfully
24 retrieving the devices is unlikely and the use of transmitting devices is by far the most prevalent
25 technique to ensure data collection.

1 In this study, we used two capture methods (corral or crook, see the capture protocols section for
2 details) to catch three categories of birds (a pair of an adult with its chick in November/December,
3 juveniles and moulted adults in January) in order to deploy and/or recover six different types of
4 loggers (see Additional file 1). Depending on the duration (short- or long-term) of planned
5 equipment, biologgers were attached by one of four techniques (back-attachment-tape/-
6 cyanoacrylate-glue/-tape-epoxy and leg-band). The four deployment protocols are briefly presented
7 below and summarised in Table 1. Additionally, all birds, *i.e.* adults and chicks, were marked with
8 subcutaneous passive integrated transponder (PIT of 3.85×32 mm and 0.8 g, Texas Instruments
9 Remote Identification System, TIRIS, Texas, USA) implanted between the tail and left leg (Additional
10 file 2) allowing remote identification of individuals with automatic reading systems. All protocols
11 adhered to current best-practise standards to reduce the risk of physical harm and stress to
12 individuals and the colony.

13

14 a) Short-term deployment: back-taped loggers

15 We equipped 16 adults in 2017/2018 and 20 adults in 2018/2019 with a GPS-Acc-VHF logger (a
16 combination of a Global Positioning System (GPS), a 3-axis Accelerometer (Acc) and a Very High
17 Frequency (VHF) locator beacon) and a separate Time-Depth Recorder (TDR) (see Additional file 1 for
18 technical details on the loggers). Both are archival devices and, therefore, need to be retrieved to
19 download the data. The VHF locator beacon sends a device-specific signal that allows to locate the
20 equipped birds in the colony and facilitate device recovery. To minimise deleterious effects such as
21 extra drag on diving animals ^{20,76}, we followed the recommendations of previous studies. The
22 hydrodynamically-shaped devices represented less than 1% of the penguin's cross-sectional area,
23 weighed less than 3% of the bird's mass (Table 1) ²⁷ and were attached on the lower back of the birds
24 with adhesive tape.

25

1 b) Long-term deployment: back-glued loggers

2 In January 2018 we equipped 8 adult emperor penguins that had completed their moult with an
3 Advanced Research and Global Observation Satellite (ARGOS) platform and a separate
4 accelerometer. ARGOS platforms sent the birds' location via the Collecte Localisation Satellites (CLS)
5 ARGOS service (Toulouse, France). The streamlined devices were attached by direct contact between
6 cyanoacrylate glue and the feathers in the middle of the lower back of birds^{29,77}.

7

8 c) Long-term deployment: back-taped-epoxied loggers

9 In January 2019, we equipped 8 juveniles with ARGOS platforms. The devices were attached to the
10 lower back of birds with adhesive tape that was secured with epoxy glue. Importantly, the epoxy glue
11 did not come in contact with the back feathers.

12

13 d) Long-term deployment: leg-banded loggers

14 In January 2018, the same 8 birds equipped with ARGOS loggers (see section b above) were also
15 equipped with an additional TDR sensor that was attached with a leg-bracelet. Similar leg-bracelets
16 had been successfully deployed on other penguin species^{11,30,54,55,78}.

1 Table 1 General information on deployments and captures

Category of attachment	Back-taped	Leg-banded	Back-glued	Back-taped-epoxied
Deployment duration	Short-term	Long-term		Long-term
Age class	ADULT	ADULT		JUVENILE
Logger type	GPS - VHF - TDR	TDR - ARGOS		ARGOS
Monitored period	summer	winter		winter
Number of individuals equipped	36	8		8
Average mass of birds (mean $\pm$ sd in kg)	27.3 $\pm$ 2.7	20.83 $\pm$ 2.6		14.00 $\pm$ 1.32
Capture setup	with its chick at the colony edge	alone at the edge of groups		groups on their way to the sea
Capture technique	corral + crook	crook or corral		corral
Minimum of persons required	3	2 to 3		3
Recapture technique	crook	crook		not possible, not returning
Minimum of persons required	2	2		to breeding site

2

3 Capture protocols

4 A very limited number of scientists have ever handled a non-anaesthetized adult emperor penguin.
5 Handling such an animal can be difficult as they are strong but fragile birds (especially the flippers)
6 with a body mass ranging from 15 (this study) to *ca.* 40 kg depending on age, sex, season and
7 location^{67,79}. While it is always better to transfer such skills directly in the field, this may not always
8 be possible due to the limited number of qualified and experienced persons able to train others.
9 Therefore, our study and the associated protocols aim to fill part of this gap.
10 The techniques developed in this study to approach, capture and handle an adult emperor penguin
11 require, as a minimum, two qualified field staff (referred to hereafter as specialists).

1 1) Adult-Chick capture protocol

2 Here, we present a technique to capture an adult emperor penguin with its thermally independent
3 chick during the late chick-rearing period. To avoid larger disturbances, it is ideal to capture birds at
4 the outer rim. Therefore, the first step is to observe the outermost 3-4 rows of animals from a
5 distance, to locate adults that are feeding the same chick several times and that are either stationary
6 or moving towards the outer edge of the colony. Note that allofeeding behaviour is quite common in
7 emperor penguins⁸⁰ but allofeeders usually do not stay with the same chick at this time of the
8 season (Houstin and Le Bohec, unpublished observations).

9 *Capture equipment*

10 Three main tools are required:

- 11 - One 2 to 3 m long stick (*e.g.* lightweight bamboo sticks) used to direct targeted birds out of
12 the colony (Fig. 1a).
- 13 - One 2.5 m long light crook made of stainless steel or aluminium, bent at 50 cm from one end
14 by an angle of approximately 135° (Fig. 1a), used to direct birds and catch them if necessary.
15 Note that a crook is more efficient than a hook from which penguins manage to escape by
16 twisting their neck.
- 17 - A corral made of three separate panels (Fig. 1a). Each panel consists of plastic pipes joined
18 together to form a 3 m by 0.8 m frame. For every meter in length, a vertical plastic tube is
19 added for stability. A polypropylene net (aviary net with a mesh size of 2 cm) is connected to
20 the frame using cable ties. This construction results in lightweight (*e.g.* 4.5 kg), sturdy and
21 field serviceable panels. When the panels are connected (Fig. 1b), the triangle formed can be
22 closed with two large reusable cable ties at each of the three joints. We suggest covering one
23 of the panels with a plain fabric, even if this makes the panel more difficult to handle when
24 there is wind. The fabric reinforces the corral, provides shade to the birds and prevents them

1 from attempting to go through the net. It also protects the fieldworkers from wind and
2 allows them to hide behind the panel to calm the birds before release.

3 *Corral capture procedure*

4 When the target adult-chick pair is located, the two specialists (one with the bamboo stick, and the
5 other one with the crook) move towards the birds from two sides, starting approximately 40 m away
6 from the colony. The first step for the specialists is to position themselves “behind” the pair, so that
7 the birds are between them and the outer edge of the colony. The second step is to guide the pair
8 slowly out of the colony by walking one-step at a time behind them. The specialists move very slowly
9 to minimise the disturbance of the colony. The resulting disturbance is minimal (Additional file 3)
10 especially if compared to a natural event like the intrusion of a Weddell seal (*Leptonychotes*
11 *weddellii*) into the colony (Additional file 4). Meanwhile, the two assistants are positioned at a
12 distance of approximately 100 m from the colony edge with the three corral panels and await
13 instructions by radio communication at a minimal volume. Situational awareness is crucial to
14 anticipate the location where the pair will exit the colony and to ensure a fast least-disturbing
15 capture.

16 Once the pair is ~30-40 m outside the colony, one assistant hands one of the panels to the specialist
17 with the bamboo stick, and returns to his/her own position. Once the panels have been placed
18 equidistantly (~30 m) around the penguin pair, everybody moves closer to the pair and close the
19 corral around it. It is to be noted that the last few meters (< 5 m) before the corral is fully closed, the
20 team has to move in a smooth, swift and highly coordinated manner, so that no escape route is
21 presented. If correctly executed, the penguins will remain stationary, looking for the best escape
22 route, and find themselves in the closed corral before an escape is attempted. The specialist with the
23 crook helps to close and secure the corral with reusable cable ties. If the adult attempts to escape,
24 use the crook to catch the bird and prevent the escape (see section 2 - single adult capture protocol).
25 Four persons are the optimal number to carry out this capture protocol. If everybody is experienced,

1 it can be executed comfortably, for the animals as well as for the scientists, with three people. The
2 whole procedure is presented in detail in additional file 3. After capture and manipulation, we
3 recommend to let parent and chick rest and calm down for a few minutes in the corral to increase
4 the chance that they stay together upon release. To release the birds in a particular direction, the
5 cable ties of the edge facing the desired exit direction are unzipped and the corral sufficiently opened
6 to allow the birds to go through (Additional file 5).

7 We used this method to capture a pair of adult with its not-yet-moulted chick to increase our
8 chances of recapture. Indeed, breeders with moulted chicks ready to fledge or with chicks having
9 sufficient reserves to perform their moult and fledge on their own are more prone to end their
10 breeding cycle, defined by the “abandon” of their chick⁵⁶. Devices were recovered after one to three
11 foraging trips.

12

13 2) Single adult capture protocol

14 Two techniques can be used to capture a single adult emperor penguin; the choice depends on the
15 behaviour of the bird while approaching, the availability of assistants, and the weather conditions.

16 As described above for the pair of an adult and its chick, the corral can be used to trap a single adult
17 in a very similar way. Nonetheless, due to the fact that solitary birds are more mobile and usually
18 more vigilant to their environment the corral method may be difficult, which is especially true during
19 heavy winds or a blizzard.

20 An alternative and efficient technique is to use a crook to catch the bird (Additional file 6) as
21 explained in Cockrem et al.⁵⁸. The crook capture requires two people and in contrast to the corral
22 protocol and the deployment of loggers can also be conducted in bad weather. Once the bird is
23 isolated, one specialist places the crook around the neck of the bird preventing the penguin to
24 escape by tobogganing, *i.e.* moving on its belly. Meanwhile, the other specialist grabs the tibiotarsi of
25 the bird and holds them firm. The crook is gently removed and placed away from the capture site,

1 and the penguin secured by the two specialists, one in front of the bird and one at the back. The
2 crook-carrying specialist should be carrying the necessary supplies for manipulation in his/her
3 backpack, because, after the capture, he/she will have his/her hands free, while the other specialist
4 is still holding the bird.

5 We used this technique to recapture adults for device recovery or to capture non-breeding (*e.g.*
6 moulting or post-moulting) adults.

7

8 3) Fledging juvenile capture protocol

9 For their first departure at sea, juvenile emperor penguins usually leave the colony in small groups. A
10 group capture with the corral is, therefore, more efficient and potentially less stressful for the birds.
11 The protocol is similar to the adult-chick-pair capture, but here an entire group of juveniles is slowly
12 encircled by three corral bearers. As emperor penguins are social animals, it is likely that keeping the
13 group together reduces the stress of manipulated individuals and facilitates the remainder of their
14 travel towards the sea after release. Juveniles of interest are removed individually from the corral for
15 the manipulation and returned afterwards. All juveniles are released together after all target animals
16 have been handled.

17

18 **Adult emperor penguin handling protocol**

19 Similarly to Cockrem et al.⁵⁸, and as shown in the Additional file 7, the bird is caught and maintain
20 upright by one specialist (S1). Once the bird is secured in this position, the second specialist (S2)
21 approaches and bends the penguin's head towards the ground while S1 grabs the legs above the
22 ankles to lay the bird on its belly. When the bird is lying on the ground, S2 kneels over the bird with
23 its head between (below) the legs of S2. In this position, the bird is immobilised. It is crucial that the
24 flippers, the most fragile part of the bird, are unrestrained and untouched, throughout the whole
25 process. If an assistant is available, he/she can hold the legs of the birds and stretch them (foot soles

1 pointing towards the sky). Working with three people allows S1 to deploy the loggers seated next to
2 the penguin and reduces manipulation time. Most penguins stay quiet in this position with some few
3 second long bursts of intense activity: a gentle but firm pressure on the back and pulling the foot
4 soles upper and further from the ground helps to calm the bird.

5

6 **Equipment protocols**

7 During manipulation, the bird's eyes were always covered with a hood to reduce stress level ²⁹ and
8 birds were handled at distance from the edge of the colony to avoid conspecifics' disturbance
9 (usually > 40 m, thus well above the 5 m limit recommended in the General guidelines produced by
10 the Antarctic Treaty Consultative Meeting ⁸¹).

11

12 a) Short-term deployment: back-taped loggers

13 Before starting with the attachment, we used a cardboard stencil and waterproof tape that is a bit
14 larger than the logger to demarcate the precise location of the equipment and the placement of the
15 strips of adhesive tape on the penguin (see this in detail in Additional file 8). Following studies from
16 Wilson et al. ^{77,82} and numerous subsequent short-term studies on other penguin species ⁸³⁻⁸⁷, we
17 used a rounded knife to lift a few feathers from the back of the penguin and insert pre-cut strips of
18 waterproof adhesive tape (*e.g.* Tesa® tape 4651, Beiersdorf AG, Hamburg, Germany). To further
19 reinforce the attachment, we added glue (*e.g.* cyanoacrylate glue, Loctite 401, Loctite, Henkel AG.,
20 Düsseldorf, Germany) between the adhesive part of the tape strips and the logger. Cable ties (*e.g.*
21 Panduit, Panduit Corp, Illinois, USA) should be tightened with a cable tie gun. For a deployment
22 period of more than one month, we recommend to add glue on top of the tapes. After manipulation
23 was completed, we marked the bird before release with a hair-dye painted number that will last until
24 the following moult (*e.g.* Schwarzkopf, Palette dark-blue N°909, Henkel AG., Düsseldorf, Germany,
25 see Additional file 9 to behold a marked bird).

1 We used this technique to deploy GPS-Acc-VHF (Axy-Trek from TechnoSmArt) and TDR (g5+ from
2 Cefas) devices (see Additional file 1 for technical details and Fig. 2a to view an equipped bird) on
3 adult emperor penguins at the end of their breeding cycle (see respective movies of deployments in
4 Additional files 8 and 10).

5

6 b) Long-term deployment: back-glued loggers

7 According to protocols from previous studies ^{40–42}, that conducted long-term deployment of
8 biologgers on the back of penguins, we fixated the lower side of the loggers directly to the feathers
9 using cyanoacrylate glue (Loctite 401). The attachment was secured with polyamide cable ties as
10 described above (Fig. 2b).

11 We used this technique to deploy Spot-367 ARGOS loggers from Wildlife Computers and WACU
12 accelerometer from MIBE-IPHC-CNRS on adults close to finishing their moult (see Additional file 11 to
13 identify an emperor penguin in that stage).

14

15 c) Long-term deployment: back-taped-epoxied loggers

16 Similar to the short-term deployment protocol, the logger is attached to the feathers using pre-cut
17 lengths of Tesa® tape on the entire logger length (sparing exposed sensors if any). The overlap
18 between tape strips is reinforced with cyanoacrylate glue (Loctite 401). We used two polyamide
19 cable ties around the head and one at the bottom of the logger to secure the attachment. The
20 supernumerary cable tie on the head is added for extra safety. Once all the adhesive strips and cable
21 ties were fixated, we applied epoxy adhesive (Loctite EA 3430) on the mounting (sparing exposed
22 sensors if any) to reinforce the waterproofness and robustness, adapting methods from other studies
23 ^{88,89}. The attachment procedure is shown in the Additional file 12.

24 We performed this deployment on fledging chicks. We selected the individuals most advanced in
25 their moult, *i.e.* presenting no more down on their back (Fig. 2c). The lower survival rate of the
26 juveniles during the first year at sea compared to adults ⁹⁰, their non-return to breeding colonies

1 before several years⁷² and their unfinished growth, prevent the use of other types of externally
2 attached devices.

3

4 d) Long-term deployment: leg-banded loggers

5 To reduce drag and behaviour disturbance induced by devices on the back of penguins, we
6 developed a leg-band (bracelet) for mounting TDR-loggers on emperor penguins.

7 We designed two similar types of bracelet, a first version that we deployed (Fig. 2b), and a second
8 version incorporating slight changes and improvements. A detailed manual of the mounts is provided
9 in Additional file 13. We designed the bracelet to mount a Lotek Lat 1800 TDR (see Additional file 1
10 for specifications) but the bracelet can be easily adapted to other types of TDR.

11 The TDR is fixed to a rubber cable tie (Panduit, ERTM-C20) covered with heat-shrinkable sheath and
12 attached around the bird tibiotarsus by closing the cable tie just above the ankle, like a bracelet. A
13 built-in lock prevents the cable tie to tighten itself after deployment. The bracelet fits loosely with
14 ~1 cm space between the bracelet and the leg. The shape of emperor penguin's legs prevents the
15 bracelet from spinning around the leg. When properly set up and attached (Additional file 13), the
16 attachment does not interfere with egg or chick placement on the bird feet during the breeding
17 season. Deployment time lasts less than 3 minutes. On retrieval, the bracelet is easy and quick to
18 remove (within a few seconds) by cutting the rubber cable tie with pliers.

1 Results

2 Table 2 Comparison between at-sea-ecological studies that equipped emperor penguins over the 3 last 30 years

Category of deployment	Season	Age class	Type of device	Device dimension	Device weight	Recovery	Mean duration	sd	Range	# deploy	% recup (#)	Publication	Study site and year
long-term	W-Jan/Feb	ad	Argos	140x55x16	195	no	66	52	15-133	7	0 (0)	Kooyman et al. 2004	Ross Sea 2000
long-term	W-Mar	ad	Argos	109x32x26	100	no	114	98	12-323	20	0 (0)	Goetz & Kooyman 2018, 2015	Ross Sea 2013
long-term	W-Jan	ad	Argos, acc & tdr	107x18x21 70x16x16 36x13x10	45 10 9	yes	150	30	118-201	8	50 (4)	This study	Atka Bay 2018
long-term	W-Dec	juv	Argos	NA	120	no	64	12	43-81	8*	0 (0)	Kooyman et al. 1996 and 2007	Cape Washington 1994, 1995, 1996
long-term	W-Dec	juv	Argos	NA	NA	no	113	49	41-160	7*	0 (0)	Wienecke et al. 2010	Taylor glacier 1996
long-term	W-Dec	juv	Argos	NA	NA	no	121	55	38-189	10	0 (0)	Wienecke et al. 2010	Auster 2007
long-term	W-Dec	juv	Argos	NA	62	no	112	77	38-255	5*	0 (0)	Thiebot et al. 2013	Pointe Géologie 2010
long-term	W-Dec	juv	Argos	NA	62	no	193	93	30-344	13*	0 (0)	Labrousse et al. 2019	Pointe Géologie 2014
long-term	W-Jan	juv	Argos	107x18x21	45	no	233	108	73-382	8	0 (0)	This study	Atka Bay 2019
short-term	S-Nov	ad	Argos & tdr	78x50x23 67x17x17	105 30	yes	7	1	2-19	15	67 (10)	Zimmer et al. 2010	Pointe Géologie 2005
short-term	S-Nov	ad	acc or 122x22	128x27 or 122x22	101 or 73	yes	14	4	8-20	12	92 (11)	Watanabe et al. 2012	Cape Washington 2005
short-term	S-Nov	ad	gps & tdr	105x38x18 35x12	60 7	yes	16	6	9-25	21	90 (18)	This study	Atka Bay 2017 & 2018
short-term	S-Dec	ad	tdr	NA	NA	yes	NA	NA	NA	19	11 (2)	Robertson, 1991	Auster & Taylor glacier 1988
short-term	S-Dec	ad	gps & tdr	105x38x18 35x12	60 7	yes	14	6	9-18	15	30 (4)	This study	Atka Bay 2018 & 2019

4 Comparison between at-sea-ecological studies that equipped emperor penguins over the last 30 years in terms of type of
5 equipment, age class of birds and deployment duration. Only post-moult long-term deployments, *i.e.* pre-nuptial/pre-
6 winter travels (beginning in January-March) and breeding short-term deployments, *i.e.* November-December, are
7 considered in this table. Other studies have deployed devices specifically between May and October, *i.e.* breeding period
8 only^{17,62,65,66,91,92} or at the end of austral summer (end of December-January) trying to locate moulting areas^{73,75}. W-Mon =

1 Winter-month of deployment, S = summer, ad = adult, juv = juvenile. Mean duration, sd and range are expressed in days.
 2 Device dimensions are expressed in mm and weight in g. NA = not available. * For studies on juveniles, duration below 30
 3 days have been removed since those short period of deployment are mostly thought to be due to predation while for
 4 Kooyman et al.⁹³, only not hand-fed chicks have been considered. In bold, the greatest values within a category of
 5 deployment. In italic, data from other studies.

6

7 a) Short-term deployment: back-taped loggers

8 In 2017-2018, 16 deployments were performed: 10 between November 27th and December 2nd, of
 9 which 6 devices were recovered and redeployed between December 10th and 12th. None of the
 10 devices of the second deployment session were recovered, resulting in 38% recovery.

11 In 2018-2019, 20 deployments were performed, 10 between November 05th and 07th, which all were
 12 recovered and redeployed between November 25th and December 6th. Six devices of the second
 13 deployment were recovered, resulting in 83% recovery. We conducted intense VHF and visual
 14 (binocular) surveys for equipped birds (approx. every 4 hours), thus we are confident that we
 15 retrieved all the loggers from returning birds. All VHF units of recaptured birds were working and
 16 unequipped birds have been regularly identified afterwards by their hair-dye painted number on
 17 their chest.

18 Bird feathering on recovery was intact and no physical damage on the bird or on the device was
 19 apparent. All loggers were still securely attached, even after the longest deployment of 25 days
 20 (Table 2). Our recovery rate for November (90%) is similar (z-test, p-value > 0.05) to those of previous
 21 studies (Table 2). The recovery rate from December 2018 (30%), despite being higher, is statistically
 22 similar to what Robertson⁵⁶ recorded for deployments performed in December on the opposite side
 23 of Antarctica (near Australia's Mawson Station) with a loss rate of 89%. The probability to recover a
 24 device deployed in December is significantly lower (z-test, p-value < 0.05) than in November.

25

26

27

1 b) Long-term deployment: back-glued loggers

2 Our study is the first to report recapture of emperor penguins after a whole-winter deployment
3 (January to November). Identified by the number painted on their chest (Additional file 9), 4 of the 8
4 birds equipped in January 2018 were resighted and recaptured in November 2018 (Table 2). All of
5 them had lost the devices on their back. Instead, there was a line of missing/broken feathers (Fig. 3).
6 No injury was detected.

7 Signals from all ARGOS devices were lost during the winter. The mean transmission period was $150 \pm$
8 30 days (range 118-201 days, Table 2), significantly exceeding the previous average deployment
9 durations of 66⁴² (p-value > 0.05, ANOVA) and 114 days⁴³ (p-value < 0.05, ANOVA) from all previous
10 similar studies.

11

12 c) Long-term deployment: back-taped-epoxied loggers

13 Three of the 8 juveniles equipped in January 2019 transmitted until their annual moult in January
14 2020. None of the birds did return to their native colony for moult; an observation congruent with
15 the conjecture that juveniles of 1.5-years of age do not come back to moult at their birth colony for
16 the first year^{44,72}. This tracking period of a full year, from January 2019 to January 2020 (Table 2) is
17 the longest documented deployment duration for the genus *Aptenodytes*. None of the 5 remaining
18 birds were spotted on colony despite visual search in summer 2019/2020. One device stopped
19 transmitting after 73 days while the four others lasted between 142 and 185 days resulting in an
20 average deployment duration of 233 ± 108 days. This mean deployment duration is longer than any
21 previously reported (p-value > 0.05, ANOVA, see Table 2 for mean $\pm$ sd values) but not significantly
22 compared to Labrousse et al.⁴⁴ (p-value < 0.05, ANOVA).

23

24

25

26

1 d) Long-term deployment: leg-banded loggers

2 Our study is the first to perform a year-round deployment and data collection on emperor penguins.

3 The 4 adults recaptured without their back-mounted loggers were still carrying their leg bracelet

4 mounted TDR, providing an unprecedented record of an entire year of high frequency (1 Hz) depth

5 and temperature logs for emperor penguins.

6 For all recaptured birds, the leg-bracelet mounting did not present any damage, the bracelet and the

7 TDR were at the same position of their deployment, suggesting that the device did not rotate around

8 the leg during the deployment period. However, all recaptured birds had lost a few feathers

9 especially on the inside part of the leg and showed signs of abrasion in the form of a slight reddening

10 of the skin and peeling under the bracelet area. Two of them had small sore spots on their tarsi. No

11 limping was observed before or after removal. An illustrated comparison between an equipped and

12 an unequipped leg after recovery can be found in the Additional file 14.

1 Discussion

2 To our knowledge, two of the four deployment methods presented in this study are new
3 developments for this species. These two methods allowed for the longest documented deployment
4 duration for this species. The description of those methods, paired with an exhaustive
5 documentation, aims to facilitate and enhance future research on this species.

7 Capture and handling

8 All capture techniques presented in this study yield minimal colony disturbance regardless of the
9 period of the breeding cycle. The described handling is safe for birds and handlers, and only a
10 minimal number of trained personnel is required. We recommend the use of the corral if no member
11 in the field team is accustomed to handling a crook or a hook on at least one penguin species.

12 Deployments

13 a) Short-term deployment: back-taped loggers

14 Our study is the first to report the deployment of GPS devices on emperor penguins. GPS devices
15 have already been deployed on penguins^{87,94}, yet never on emperor penguins on which only ARGOS
16 devices^{62–64,95} or dive-pattern-analysis related loggers^{56,64,95} have been deployed during the late
17 chick-rearing period, presumably due to a combination of technical and logistical constraints. The
18 methods presented herein allow the deployment of high-resolution data acquisition loggers with a
19 high probability of recovery once the phenology of the colony has been assessed, for instance by the
20 size and moulting stage of chicks. At Atka Bay, the best deployment period is in November with a
21 logger recovery rate of 90%. The low recovery rate (38%) during the 2017-2018 season can be
22 explained by logistical issues we encountered and not the deployment technique. An unexpected late
23 on-site arrival led to late deployment of 11 loggers in December 2017, compared to 4 in December
24 2018, and consequently to a substantial loss of devices.

1 To optimise the recovery rate of devices deployed at the end of the breeding season, we recommend
2 to deploy devices on adults with medium-sized chicks at the very beginning of chick moult.
3 Supported by the secure attachment of the presented technique, we furthermore suggest increasing
4 deployment time rather than to recover loggers and redeploy them.

5

6 b) Long-term deployment: back-glued loggers

7 Our study is the first to document the recapture of a long-term equipped emperor penguin and thus
8 able to assess (i) the state of the bird, (ii) the state of devices, and (iii) provide evidence explaining
9 the loss of signal from communicating-satellite-relayed loggers reported in previous studies. Until
10 now, five studies had performed long-term deployments on emperor penguins right after the moult
11 (Table 2), all using ARGOS platforms and cyanoacrylate glue to attach the logger directly to the back-
12 feathers of the birds. None of the birds were resighted, perhaps partly due to the logistical
13 possibilities to reach the colony in the following years at other study sites. Two sets of deployments
14 were made on adults ^{42,43}, three on chicks ^{40,41,44}.

15 Our results show that both glued devices, the ARGOS transmitter and the small accelerometer, which
16 vary in size and weight (Additional file 1), were lost in the same manner on all birds. We speculate
17 that the cyanoacrylate glue rigidifies the feathers, which then become brittle and break with either
18 the continuous birds' movements and/or their attempts to remove the device. Wilson et al. ⁷⁷ also
19 observed this device-sized hole in the feather layer after winter deployment on four Magellanic
20 penguins (*Spheniscus magellanicus*) using epoxy instead of cyanoacrylate glue. In our study, five of
21 the eight ARGOS signals were lost while birds had been on fast ice at the breeding site for several
22 weeks. The longest duration of deployment (201 days, Table 2) was recorded for the only bird that
23 did not spend any extended time on ice. When the birds remain on the fast ice at their breeding
24 colony, they are exposed to extremely cold temperatures, below -50°C in Atka Bay ⁹⁶. We assume
25 that such cold temperature could have two different effects. Either the cyanoacrylate induced brittle

1 feathers become very weak when exposed to such cold temperatures and, therefore, are easier to
 2 break during the penguins' movement, or the brittle feathers do not provide the proper isolation
 3 against the cold, thus altering the heat transfer and/or thermoregulation of the bird (as observed on
 4 pup grey seals (*Halichoerus grypus*) by McCafferty et al.⁹⁷). This could lead to the animal preening
 5 their feathers fiercely and thereby removing the logger by breaking/removing the brittle glued
 6 feathers. In addition, blizzards may have caused the accumulation of ice around the loggers,
 7 amplifying the above effects and tearing the device off^{42,45}. However, we suggest that the huddling
 8 behaviour of emperor penguins^{67,98} would prevent ice accumulation in the middle of the winter.
 9 Another possible explanation could be the timing of deployment. Devices were attached just at the
 10 end of the moult, a time when feathers may not yet be fully developed despite a meticulous bird
 11 selection process (Additional file 10). Their growth after deployment could potentially have added
 12 some slack and thus reinforced the pull on the feather shafts, ultimately leading to their breakage
 13 after few months. The loss of back feathers undoubtedly leads to a diminution of insulation that
 14 causes a greater heat loss. The resulting increase in energetic needs reduces fasting capabilities and
 15 forces the birds to compensate by finding more prey items when they return at sea to forage in order
 16 to replenish their reserves while accumulating food for their chick. As body reserves management is
 17 critical, especially for this species, any significant heat loss is likely to impact breeding success.

18 In tagging procedures, the ethical principle of *Refinement* from the Three Rs³², i.e. the use of
 19 methods which decrease any adverse effect, should apply. It is likely that the device loss we recorded
 20 also happened during previous deployments that used this technique. We consider that the loss of
 21 the device and resulting consequences for the birds are unacceptable and that our findings combined
 22 with the ones from Wilson et al.⁷⁷ should prevent further use of glue directly on the birds feathers
 23 for long-term deployment on penguins as it is currently practiced. We propose an alternative
 24 technique that has not yet been shown to induce such damage. The tape does not include acrylamide
 25 glue and is therefore less likely to brittle the feathers.

26

1 c) Long-term deployment: back-taped-epoxied loggers

2 To investigate the distribution at-sea according to the age-class we employed the back-taped-
3 epoxied technique on juveniles. So far, this age-class had only been tagged using the back-glued
4 method (Table 2).

5 Three of the juveniles (40%) retained their device for an entire year, thus achieving the longest
6 duration of back-mounted logger deployment possible in penguins. The previous longest durations
7 recorded for juvenile emperor penguins were of 344, 298 and 271 days ⁴⁴ with one bird (6% of the
8 deployments) approaching the one year length duration. The mean duration of our long-term
9 deployments (233 ± 108 days) with the taped-epoxied technique is longer than any previously
10 reported on juvenile or adult emperor penguins (Table 2). Therefore, we are confident that the
11 technique presented is a significant improvement for tracking of penguins and understanding their
12 activities at sea, even if the contribution of a possible gain resulting from the evolution of
13 technologies is not measurable.

14 Some of the previous studies using glue on juveniles approached long-term attachment duration,
15 with only one of the 48 juveniles exceeding 10 months of equipment. The lack of recovery of ARGOS
16 devices deployed on juveniles can be explained (i) by the fact that the birds moult outside their
17 original colony ^{62,73–75}, or by the loss of devices as suggested by our results on adults. Electronic
18 failure or bird predations are also alternative hypotheses ⁴². Nevertheless, in addition to the possible
19 loss of feathers and insulation previously discussed, the glue has the potential to cause thermal skin
20 burns ⁹⁹. Juveniles are more vulnerable than adults as their foraging skills (including their ability to
21 dive, to capture prey, and to find productive feeding grounds) are not yet fully developed, and their
22 experience to escape predators is also minimal ^{100–102}. The additional cost mentioned above induced
23 by a glued device may negatively impact the survival of the juveniles during their first months in their
24 new marine environment that they experience for the first time. As a result, for studies requesting
25 the deployment of back-mounted devices on penguins for long-term duration, the use of glue on

1 feathers should be entirely avoided, and we recommend to use instead a mix of Tesa® tape strips
2 (feathers' side) and epoxy (on the strips covering the device) to reinforce adhesion.

3 We could not show that this attachment will last on adult emperor penguins as long as for juveniles.
4 An early departure from the field due to logistical constraints prevented us to deploy this new
5 technique on fully moulted adult emperor penguin. Adult emperor penguins experience very harsh
6 environmental conditions on the sea ice, especially at their breeding site, during winter with
7 temperatures below -50°C and wind speeds above 150 km/h at Atka Bay ⁹⁶. Average deployment
8 durations on adults are less than six months (Table 2) and need to be improved to cover the entire
9 breeding cycle and justify the impacts on the birds' welfare. We are convinced that new techniques
10 should be tested such as the promising one presented in this study for juveniles.

11

12 d) Long-term deployment: leg-banded loggers

13 We developed and tested a leg-band TDR mount to enable year-round deployments on adult
14 emperor penguins. The deployed leg-band TDR mount collected high frequency (1 Hz), pressure and
15 temperature data during the whole year. This data will allow a detailed analysis of foraging activities
16 and water column exploitation over a full year for the same birds.

17 Leg-band mounted devices had already been deployed on penguins ^{11,30,54,55,103-105}, but not yet on the
18 emperor penguin species, which can walk over long distances on sea ice ⁶⁵. Often, the condition of
19 the birds at retrieval are not mentioned, however, some of the studies reported similar leg irritations
20 ^{30,105} (Raclot personal communications; Houstin, Fournier and Le Bohec, unpublished observations) as
21 the ones we observed in this study. Such irritations might be due to the fact that emperor penguins
22 can walk over long distances on sea ice to reach the water ⁶⁵. The commonly accepted flying bird
23 banding technique is also known to cause unintentional damage like sores, inflammation, or even
24 loss of feet in extreme cases ¹⁰⁶⁻¹⁰⁸, thus the irritations observed here can be considered as a minor
25 impact.

1 We suggest that the use of non-continuous heat-shrink tubing and the glue around the head of the
2 rubber cable tie created a small ledge in the otherwise smooth surface that irritated the birds' leg-
3 skin. From this observation, we have designed an improved version for the second season (Additional
4 file 13), which could not be tested due to early departure from the field site. The continuous heat-
5 shrinkable sheath in the updated bracelet attachment will likely reduce friction between the leg and
6 the bracelet and ideally avoid skin irritation. If feathers are still lost, we expect the tibiotarsus to be
7 less irritated and the occasional development of sores prevented. To prevent the formation of glue
8 flakes, glue will only be applied inside the cable tie's closure, with parsimony, and not around the
9 whole head.

10 At retrieval, the mounting did not show any damage or sign of wear and is expected to last several
11 years before the elastomeric cable tie breaks. Consequently, before deploying such a system, a
12 strategic plan for its retrieval is crucial. Emperor penguins are non-nesting seabirds, breeding freely
13 on sea ice within a mobile colony ¹⁰⁹, makes the recapture of birds difficult, especially after more
14 than one year when the annual moult removed any externally painted-markings. Due to their PIT-tag,
15 all birds manipulated can be life-long identified by automatic Radio-frequency identification (RFID)
16 detection systems, without requiring recapture or visual observation ^{110–112} and without long-term
17 deleterious effects of flipper-banding for life ^{35,37,38}. Such automatic detection systems have been
18 successful at detecting emperor, Adélie and king (*Aptenodytes patagonicus*) penguins over the last
19 years at the Pointe Géologie archipelago and Crozet and Kerguelen archipelagos (Le Bohec, Houstin,
20 Chatelain and Courtecuisse, unpublished observations, ¹¹³). Such a system will be deployed at Atka
21 Bay colony starting in summer 2021-2022 to improve our retrieval ratio of 50%, compared to the
22 retrieval rate for nesting birds that is between 60 and 90% ^{11,30,104,105,114,115}. This technological
23 improvement will allow in the years to come to recapture birds even after several years of
24 deployment like for nesting birds ³⁰ (Raclot personal communications; Houstin and Le Bohec,
25 unpublished observations).

1 Specifically, with this bracelet technique, multi-year deployments might be considered. Scientific
 2 programs running in Antarctica are not always able to return several years in a row, and this
 3 technique of deployment offers some flexibility. Solutions still need to be developed for
 4 communicating devices that need to get out of water regularly to send or receive telemetry (GPS,
 5 ARGOS) or for biologgers that would record too noisy data when positioned on the leg. However, for
 6 small data loggers, that are able to record environmental variables (*e.g.* hydrostatic pressure, water
 7 conductivity and temperature, environmental luminosity) on a multi-year scale ^{102,116}, the leg-band
 8 technique appears as a high potential alternative.

1 Conclusion

2 Ethical concerns raised by the use of measuring devices on wild animal are not new ²⁸ and a recent
3 review ¹¹⁷ addressed the current pros and cons on attachment issues. To ensure data is of exemplary
4 quality from a scientific and ethical point of view, the potential deleterious effects of deployment
5 procedures (capture-attachment-recapture) must be assessed and mitigated. Our study provides
6 highly detailed procedures to capture/recapture and externally attach telemetry devices on emperor
7 penguins. We, therefore, consider this study as a significant advancement by (i) stating clearly the
8 impact of using glue for biologging device attachment on emperor penguins, (ii) helping to assess
9 long-term loggers loss reasons (notably ARGOS transmitters), (iii) presenting two promising
10 attachment techniques of biologging devices on emperor penguins in detail, and (iv) explicitly
11 providing techniques to capture and handle emperor penguins with a limited amount of disturbance
12 as well as a maximum of safety and efficiency. This publication is intended to serve as a resource to
13 facilitate future research on this iconic species.

14 This study aims also to encourage researchers and journals to give more exposure to fieldwork
15 methodology in scientific publications not specifically methodology oriented, in particular to
16 techniques developed and tested but not successful in the field. We are convinced that too much
17 time and resources are allocated to the development of techniques already tested but not shared
18 because of their failure. Tests, errors and failures are inherent of research and should be, to some
19 extent, valued as significant results; a practice that would benefit to both scientists and animals.

1 **Abbreviations**

2 GPS: Global Positioning System; TDR: Time-Depth Recorder; ARGOS: Advanced Research and Global
3 Observation Satellite; MPA: Marine Protected Area; PIT: Passive Integrated Transponder; VHF: Very
4 High Frequency; Acc: Accelerometer; CLS: Collecte Localisation Satellites; GLS: Global Location
5 Sensor; RFID: Radio-frequency identification.

6 **Declarations**

7 **Ethics approval and consent to participate**

8 The AWI long-term program “MARE” (*Monitor the health of the Antarctic maRine ecosystems using*
9 *the Emperor penguin as a sentinel*), to which this study belongs, and all procedures were approved by
10 the German Environment Agency (Umweltbundesamt-UBA permit no.: II 2.8 – 94033/100 delivered
11 on the 04/10/2017 and 04/10/2018), and conducted in accordance with the Committee for
12 Environmental Protection (CEP) guidelines.

13 **Consent for publication**

14 Written informed consent for publication was obtained.

15 **Availability of data and material**

16 All data generated or analysed during this study are included in this published article and its
17 supplementary information files will be available in the “Publishing Network for Geoscientific &
18 Environmental Data” (PANGAEA, <https://www.pangaea.de/>).

19 **Competing interests**

20 The authors declare that they have no competing interests.

21 **Funding**

22 This study was funded by the Centre Scientifique de Monaco with additional support from the LIA-
23 647 and RTP1-NUTRESS (CSM/CNRS-University of Strasbourg), by The Penzance Endowed Fund and
24 The Grayce B. Kerr Fund in Support of Assistant Scientists and by the Deutsche

1 Forschungsgemeinschaft (DFG) grants ZI1525/3-1 in the framework of the priority program “Antarctic
2 research with comparative investigations in Arctic ice areas”.
3 Logistics and field efforts were supported by the Alfred Wegener Institute (AWI) within the
4 framework of the program MARE.

5 **Authors’ contributions**

6 AH and CLB conceived the ideas and designed the methodology and protocols. AH, CLB, DZ, SR, BF,
7 AW conducted fieldwork. AH, DZ and CLB led writing of manuscript. VPB, DC, AA, JF gave conceptual
8 advice. All authors contributed substantively to the drafts and gave final approval for publication.

9 **Acknowledgements**

10 We thank the Alfred Wegener Institut Helmholtz-Zentrum für Polar- und Meeresforschung, Logistics
11 Department, the overwinterers and campaigners at Neumayer Station III for their invaluable support
12 in 2017-2018 and 2018-2019 seasons.

13 We are very grateful to Prof. Patrick Rampal for support in initiating the project, to Dr. Laurent Godet
14 (CNRS) for lending his VHF antennas and receivers, and to Dr. Olaf Eisen (AWI) for his invaluable help
15 with fieldwork and related activities.

16 We warmly thank 'Galileo' and 'ProSiebenSat.1 TV Deutschland GmbH' for their shooting in the field
17 and providing Additional files 3 and 5.

1 REFERENCES

- 2 1. Rutz, C. & Hays, G. C. New frontiers in biologging science. *Biology Letters* **5**, 289–292 (2009).
- 3 2. Marker, L. L., Dickman, A. J., Mills, M. G. L., Jeo, R. M. & Macdonald, D. W. Spatial ecology of
4 cheetahs on north-central Namibian farmlands. *Journal of Zoology* **274**, 226–238 (2008).
- 5 3. Kays, R., Crofoot, M. C., Jetz, W. & Wikelski, M. Terrestrial animal tracking as an eye on life
6 and planet. *Science* **348**, aaa2478–aaa2478 (2015).
- 7 4. Fortin, D. *et al.* Wolves influence elk movements: behavior shapes a trophic cascade in
8 yellowstone national park. *Ecology* **86**, 1320–1330 (2005).
- 9 5. Ropert-Coudert, Y., Beaulieu, M., Hanuise, N. & Kato, A. Diving into the world of biologging.
10 *Endangered Species Research* **10**, 21–27 (2009).
- 11 6. McIntyre, T. Trends in tagging of marine mammals: a review of marine mammal biologging
12 studies. *African Journal of Marine Science* **36**, 409–422 (2014).
- 13 7. Bograd, S., Block, B., Costa, D. & Godley, B. Biologging technologies: new tools for
14 conservation. Introduction. *Endangered Species Research* **10**, 1–7 (2010).
- 15 8. Clarke, J. *et al.* Sex differences in Adelie penguin foraging strategies. *Polar Biology* **20**, 248–
16 258 (1998).
- 17 9. Sato, K. *et al.* Buoyancy and maximal diving depth in penguins: do they control inhaling air
18 volume? *The Journal of experimental biology* **205**, 1189–1197 (2002).
- 19 10. Wilson, R. P. *et al.* Remote-sensing systems and seabirds: their use, abuse and potential for
20 measuring marine environmental variables. *Marine Ecology Progress Series* **228**, 241–261
21 (2002).
- 22 11. Bost, C. A., Thiebot, J. B., Pinaud, D., Cherel, Y. & Trathan, P. N. Where do penguins go during

- 1 the inter-breeding period? Using geolocation to track the winter dispersion of the macaroni
- 2 penguin. *Biology Letters* **5**, 473–476 (2009).
- 3 12. Weimerskirch, H. *et al.* Lifetime foraging patterns of the wandering albatross: Life on the
- 4 move! *Journal of Experimental Marine Biology and Ecology* **450**, 68–78 (2014).
- 5 13. Chimienti, M. *et al.* Taking movement data to new depths: Inferring prey availability and patch
- 6 profitability from seabird foraging behavior. *Ecology and Evolution* **7**, 10252–10265 (2017).
- 7 14. Pistorius, P. *et al.* At-sea distribution and habitat use in king penguins at sub-Antarctic Marion
- 8 Island. *Ecology and Evolution* **7**, 3894–3903 (2017).
- 9 15. Massom, R. A. *et al.* Fast ice distribution in Adélie Land, East Antarctica: Interannual variability
- 10 and implications for emperor penguins *Aptenodytes forsteri*. *Marine Ecology Progress Series*
- 11 **374**, 243–257 (2009).
- 12 16. Zimmer, I., Wilson, R. P., Beaulieu, M., Ancel, A. & Plötz, J. Seeing the light: Depth and time
- 13 restrictions in the foraging capacity of emperor penguins at pointe géologie, Antarctica.
- 14 *Aquatic Biology* **3**, 217–226 (2008).
- 15 17. Ancel, A. *et al.* Foraging behaviour of emperor penguins as a resource detector in winter and
- 16 summer. *Nature* **360**, 336–339 (1992).
- 17 18. Hussey, N. E. *et al.* Aquatic animal telemetry: A panoramic window into the underwater
- 18 world. *Science* **348**, 1255642–1255642 (2015).
- 19 19. Carter, M. I. D., Bennett, K. A., Embling, C. B., Hosegood, P. J. & Russell, D. J. F. Navigating
- 20 uncertain waters: a critical review of inferring foraging behaviour from location and dive data
- 21 in pinnipeds. *Movement Ecology* 1–20 (2016). doi:10.1186/s40462-016-0090-9
- 22 20. Culik, B. & Wilson, R. P. Energetics of under-water swimming in Adélie penguins (*Pygoscelis*
- 23 *adeliae*). *Journal of Comparative Physiology B* **161**, 285–291 (1991).

- 1 21. Beaulieu, M. *et al.* Can a handicapped parent rely on its partner? An experimental study
2 within Adélie penguin pairs. *Animal Behaviour* **78**, 313–320 (2009).
- 3 22. Ropert-Coudert, Y., Wilson, R., Yoda, K. & Kato, A. Assessing performance constraints in
4 penguins with externally-attached devices. *Marine Ecology Progress Series* **333**, 281–289
5 (2007).
- 6 23. Vandenabeele, S. P., Wilson, R. & Grogan, A. Tags on seabirds; how seriously are we
7 considering instrument-induced behaviors? *Animal Welfare* **20**, 559–571 (2011).
- 8 24. Ropert-Coudert, Y. *et al.* Impact of externally attached loggers on the diving behaviour of the
9 king penguin. *Physiological and Biochemical Zoology* **73**, 438–444 (2000).
- 10 25. Wilmers, C. C. *et al.* The golden age of bio-logging: how animal-borne sensors are advancing
11 the frontiers of ecology. *Ecology* **96**, 1741–1753 (2015).
- 12 26. CCAMLR. *Ecosystem Monitoring Program Standard Methods*. (2014).
- 13 27. Kenward, R. E. A Manual for Wildlife Radio Tagging. *The Auk* **118**, 812–815 (2001).
- 14 28. Wilson, R. P. & McMahon, C. R. Measuring devices on wild animals: what constitutes
15 acceptable practice? *Frontiers in Ecology and Evolution* **4**, 147–154 (2006).
- 16 29. Casper, R. M. Guidelines for the instrumentation of wild birds and mammals. *Animal*
17 *Behaviour* **78**, 1477–1483 (2009).
- 18 30. Ratcliffe, N. *et al.* A leg-band for mounting geolocator tags on penguins. *Marine Ornithology*
19 **42**, 23–26 (2014).
- 20 31. Williams, H. J. *et al.* Optimizing the use of biologgers for movement ecology research. *Journal*
21 *of Animal Ecology* 1365-2656.13094 (2019). doi:10.1111/1365-2656.13094
- 22 32. Russel, W. M. S. & Burch, R. L. *The principles of humane experimental technique*. (London:

- 1 Methuen & Co. Ltd., 1959).
- 2 33. Wanless, R. M. & Oatley, T. B. Sixth review of data held by the central data bank for antarctic
3 bird banding , july 1987 – june 1996. *Bird Banding* (2000).
- 4 34. Jackson, S. & Wilson, R. P. The potential costs of flipper-bands to penguins. *Functional Ecology*
5 **16**, 141–148 (2002).
- 6 35. Gauthier–Clerc, M. *et al.* Long–term effects of flipper bands on penguins. *Proceedings of the*
7 *Royal Society of London. Series B: Biological Sciences* **271**, 423–426 (2004).
- 8 36. Saraux, C. *et al.* Reliability of flipper-banded penguins as indicators of climate change. *Nature*
9 **469**, 203–206 (2011).
- 10 37. Dugger, K. M., Ballard, G., Ainley, D. G. & Barton, K. J. Effects of flipper bands on foraging
11 behavior and survival of adélie penguins (*Pygoscelis adeliae*). *The Auk* **123**, 858 (2006).
- 12 38. Le Maho, Y. *et al.* An ethical issue in biodiversity science: The monitoring of penguins with
13 flipper bands. *Comptes Rendus - Biologies* **334**, 378–384 (2011).
- 14 39. Wilson, R. P., Grant, W. S. & Duffy, D. C. Recording devices on free-ranging marine animals:
15 does measurement affect foraging performance? *Ecology* **67**, 1091–1093 (1986).
- 16 40. Wienecke, B., Raymond, B. & Robertson, G. Maiden journey of fledgling emperor penguins
17 from the Mawson Coast, East Antarctica. *Marine Ecology Progress Series* **410**, 269–282 (2010).
- 18 41. Thiebot, J.-B., Lescroël, A., Barbraud, C. & Bost, C.-A. Three-dimensional use of marine
19 habitats by juvenile emperor penguins *Aptenodytes forsteri* during post-natal dispersal.
20 *Antarctic Science* **25**, 536–544 (2013).
- 21 42. Kooyman, G. L., McDonald, B. I. & Goetz, K. T. Why do satellite transmitters on emperor
22 penguins stop transmitting? *Animal Biotelemetry* **3**, 54 (2015).

- 1 43. Goetz, K., McDonald, B. & Kooyman, G. Habitat preference and dive behavior of
2 non-breeding emperor penguins in the eastern Ross Sea, Antarctica. *Marine Ecology Progress*
3 *Series* **593**, 155–171 (2018).
- 4 44. Labrousse, S. *et al.* First odyssey beneath the sea ice of juvenile emperor penguins in East
5 Antarctica. *Marine Ecology Progress Series* **609**, 1–16 (2019).
- 6 45. Kooyman, G. L. & Ponganis, P. The icing of external recorders during the polar winter.
7 *Memoirs of National Institute of Polar Research. Special issue* **58**, 183–187 (2004).
- 8 46. Hays, G. C. *et al.* Translating marine animal tracking data into conservation policy and
9 management. *Trends in Ecology & Evolution* **34**, 459–473 (2019).
- 10 47. Hindell, M. A. *et al.* Tracking of marine predators to protect Southern Ocean ecosystems.
11 *Nature* **580**, 87–92 (2020).
- 12 48. Block, B. Physiological ecology in the 21st century: advancements in biologging science.
13 *Integrative and Comparative Biology* **45**, 305–320 (2005).
- 14 49. Costa, D. P., Breed, G. A. & Robinson, P. W. migrations: implications for ecology and
15 conservation. *Annual Review of Ecology, Evolution, and Systematics* **43**, 73–96 (2012).
- 16 50. Cooke, S. Biotelemetry and biologging in endangered species research and animal
17 conservation: relevance to regional, national, and IUCN Red List threat assessments.
18 *Endangered Species Research* **4**, 165–185 (2008).
- 19 51. Small, C. & Taylor, F. Analysis of albatross and petrel distribution within the CCAMLR
20 Convention Area: Results from the global Procellariiform tracking database. *CCAMLR Science*
21 **13**, 143–174 (2006).
- 22 52. CCAMLR. *Report of the Twentieth Meeting of the Scientific Committee*. (2009).

- 1 53. Hays, G. C. *et al.* Key questions in marine megafauna movement ecology. *Trends in Ecology &*
2 *Evolution* **31**, 463–475 (2016).
- 3 54. Thiebot, J.-B. *et al.* Adélie penguins' extensive seasonal migration supports dynamic Marine
4 Protected Area planning in Antarctica. *Marine Policy* **109**, 103692 (2019).
- 5 55. Takahashi, A. *et al.* Migratory movements and winter diving activity of Adélie penguins in East
6 Antarctica. *Marine Ecology Progress Series* **589**, 227–239 (2018).
- 7 56. Robertson, G. G. Some field techniques for ecological research on emperor penguins. *Marine*
8 *Ornithology* **19**, 91–101 (1991).
- 9 57. Zimmer, I. Constraints on Foraging and their Consequences for Emperor Penguins PhD. (2007).
- 10 58. Cockrem, J. F., Potter, M. A., Barrett, D. P. & Candy, E. J. Corticosterone responses to capture
11 and restraint in emperor and Adélie penguins in Antarctica. *Zoological Science* **25**, 291–298
12 (2008).
- 13 59. Kooyman, G. L. *et al.* Heart rates and swim speeds of emperor penguins diving under sea ice.
14 *The Journal of experimental biology* **165**, 161–180 (1992).
- 15 60. Williams, C. L., Meir, J. U. & Ponganis, P. J. What triggers the aerobic dive limit? Patterns of
16 muscle oxygen depletion during dives of emperor penguins. *Journal of Experimental Biology*
17 **214**, 1802–1812 (2011).
- 18 61. Ponganis, P. J., Van Dam, R. P., Marshall, G., Knowler, T. & Levenson, D. H. Sub-ice foraging
19 behavior of emperor penguins. *Journal of Experimental Biology* **203**, 3275–3278 (2000).
- 20 62. Zimmer, I. *et al.* Foraging movements of emperor penguins at Pointe Géologie, Antarctica.
21 *Polar Biology* **31**, 229–243 (2007).
- 22 63. Zimmer, I. *et al.* Dive efficiency versus depth in foraging emperor penguins. *Aquatic Biology* **8**,

- 1 269–277 (2010).
- 2 64. Watanabe, S., Sato, K. & Ponganis, P. J. Activity time budget during foraging trips of emperor
3 penguins. *PLoS ONE* **7**, e50357 (2012).
- 4 65. Kirkwood, R. & Robertson, G. The foraging ecology of female Emperor penguins in winter.
5 *Ecological Monographs* **67**, 155–176 (1997).
- 6 66. Rodary, D., Bonneau, W., Le Maho, Y. & Bost, C. A. Benthic diving in male emperor penguins
7 *Aptenodytes forsteri* foraging in winter. *Marine Ecology Progress Series* **207**, 171–181 (2000).
- 8 67. Prévost, J. Ecologie du manchot empereur. in *Expéditions polaires françaises*, (ed. Hermann
9 Press) 204 (1961).
- 10 68. Fretwell, P. T. *et al.* An emperor penguin population estimate: the first global, synoptic survey
11 of a species from space. *PLoS ONE* **7**, e33751 (2012).
- 12 69. Ancel, A. *et al.* Looking for new emperor penguin colonies? Filling the gaps. *Global Ecology*
13 *and Conservation* **9**, 171–179 (2017).
- 14 70. Orians, G. . & Pearson, N. . On the theory of central place foraging. in *Analysis of ecological*
15 *systems* (eds. Horn, D., Staris, G. & Mitchell, R.) 155–177 (Columbus: Ohio State University
16 Press, 1979).
- 17 71. Stonehouse, B. *The Emperor Penguin breeding behaviour and development - FIDS Scientific*
18 *Report*. (1953).
- 19 72. Mougin, J. . & Van Beveren, M. *Structure et dynamique de la population de Manchots*
20 *empereurs de la colonie de l'archipel de Pointe Géologie, Terre Adélie*. (1979).
- 21 73. Kooyman, G. L., Hunke, E. C., Ackley, S. F., Van Dam, R. P. & Robertson, G. Molt of the
22 emperor penguin: Travel, location, and habitat selection. *Marine Ecology Progress Series* **204**,

- 1 269–277 (2000).
- 2 74. Kooyman, G. L., Siniff, D. B., Stirling, I. & Bengtson, J. L. Moulting habitat, pre- and post-moulting
3 diet and post-moulting travel of Ross Sea emperor penguins. *Marine Ecology Progress Series* **267**,
4 281–290 (2004).
- 5 75. Wienecke, B., Kirkwood, R. & Robertson, G. Pre-moulting foraging trips and moulting locations of
6 Emperor penguins at the Mawson Coast. *Polar Biology* **27**, 83–91 (2004).
- 7 76. Bannasch, R., Wilson, R. P. & Culik, B. Hydrodynamic aspects of design and attachment of a
8 back-mounted device in penguins. *The Journal of Experimental Biology* **194**, 83–96 (1994).
- 9 77. Wilson, R. P. *et al.* Long-term attachment of transmitting and recording devices to penguins
10 and other seabirds. *Wildlife Society Bulletin* **25**, 101–106 (1997).
- 11 78. Thiebot, J.-B., Lescroël, A., Pinaud, D., Trathan, P. N. & Bost, C.-A. Larger foraging range but
12 similar habitat selection in non-breeding versus breeding sub-Antarctic penguins. *Antarctic*
13 *Science* **23**, 117–126 (2011).
- 14 79. Le Maho, Y., Delclitte, P. & Chatonnet, J. Thermoregulation in fasting emperor penguins under
15 natural conditions. *American Journal of Physiology-Legacy Content* **231**, 913–922 (1976).
- 16 80. Jouventin, P., Barbraud, C. & Rubin, M. Adoption in the emperor penguin, *Aptenodytes*
17 *forsteri*. *Animal Behaviour* **50**, 1023–1029 (1995).
- 18 81. ATS. General guidelines for visitors to the Antarctic (Attachment to Resolution 3). (2020).
- 19 82. Wilson, R. P. & Wilson, M. T. J. Tape: a package-attachment technique for penguins. *Wildlife*
20 *Society Bulletin* **17**, 77–79 (1989).
- 21 83. Ropert-Coudert, Y., Kato, A., Naito, Y. & Cannell, B. L. Individual diving strategies in the little
22 penguin. *Waterbirds: The International Journal of Waterbird Biology* **26**, 403–408 (2003).

- 1 84. Chiaradia, A., Ropert-Coudert, Y., Kato, A., Mattern, T. & Yorke, J. Diving behaviour of Little
2 Penguins from four colonies across their whole distribution range: bathymetry affecting diving
3 effort and fledging success. *Marine Biology* **151**, 1535–1542 (2007).
- 4 85. Pichegru, L. *et al.* Diving patterns of female macaroni penguins breeding on Marion Island,
5 South Africa. *Polar Biology* **34**, 945–954 (2011).
- 6 86. Le Vaillant, M. *et al.* How age and sex drive the foraging behaviour in the king penguin. *Marine*
7 *Biology* **160**, 1147–1156 (2013).
- 8 87. Poupart, T. A. *et al.* Variability in the foraging range of *Eudyptula minor* across breeding sites
9 in central New Zealand. *New Zealand Journal of Zoology* **44**, 225–244 (2017).
- 10 88. Wilson, R. P. *et al.* Southern rockhopper penguin *Eudyptes chrysocome* chrysocome foraging
11 at Possession Island. *Polar Biology* **17**, 323–329 (1997).
- 12 89. Pütz, K. *et al.* Post-fledging dispersal of king penguins (*Aptenodytes patagonicus*) from two
13 breeding sites in the South Atlantic. *PLoS ONE* **9**, e97164 (2014).
- 14 90. Williams, T. D. *The Penguins: Spheniscidae. The penguins. Bird families of the world.* (Oxford
15 University Press, 1995). doi:10.2307/1521878
- 16 91. Wienecke, B. & Robertson, G. Foraging space of emperor penguins *Aptenodytes forsteri* in
17 Antarctic shelf waters in winter. *Marine Ecology Progress Series* **159**, 249–263 (1997).
- 18 92. Labrousse, S. *et al.* Dynamic fine-scale sea icescape shapes adult emperor penguin foraging
19 habitat in east Antarctica. *Geophysical Research Letters* **46**, 11206–11218 (2019).
- 20 93. Kooyman, G. L. & Ponganis, P. J. The initial journey of juvenile emperor penguins. *Aquatic*
21 *Conservation: Marine and Freshwater Ecosystems* **17**, S37–S43 (2007).
- 22 94. Trathan, P. *et al.* Linear tracks and restricted temperature ranges characterise penguin

- 1 foraging pathways. *Marine Ecology Progress Series* **370**, 285–294 (2008).
- 2 95. Sato, K., Shiomi, K., Marshall, G., Kooyman, G. L. & Ponganis, P. J. Stroke rates and diving air
3 volumes of emperor penguins: implications for dive performance. *Journal of Experimental*
4 *Biology* **214**, 2854–2863 (2011).
- 5 96. Wikipedia contributors. Neumayer-Station III. (2021). Available at:
6 https://en.wikipedia.org/w/index.php?title=Neumayer-Station_III&oldid=1024176365.
7 (Accessed: 25th May 2021)
- 8 97. McCafferty, D. J., Currie, J. & Sparling, C. E. The effect of instrument attachment on the
9 surface temperature of juvenile grey seals (*Halichoerus grypus*) as measured by infrared
10 thermography. *Deep Sea Research Part II: Topical Studies in Oceanography* **54**, 424–436
11 (2007).
- 12 98. Gilbert, C., Robertson, G., Le Maho, Y., Naito, Y. & Ancel, A. Huddling behavior in emperor
13 penguins: Dynamics of huddling. *Physiology and Behavior* **88**, 479–488 (2006).
- 14 99. Walker, K. A., Trites, A. W., Haulena, M. & Weary, D. M. A review of the effects of different
15 marking and tagging techniques on marine mammals. *Wildlife Research* **39**, 15 (2012).
- 16 100. Wanless, S., Frederiksen, M., Daunt, F., Scott, B. E. & Harris, M. P. Black-legged kittiwakes as
17 indicators of environmental change in the North Sea: Evidence from long-term studies.
18 *Progress in Oceanography* **72**, 30–38 (2007).
- 19 101. Orgeret, F., Weimerskirch, H. & Bost, C.-A. Early diving behaviour in juvenile penguins:
20 improvement or selection processes. *Biology Letters* **12**, 20160490 (2016).
- 21 102. Enstipp, M. R. *et al.* Apparent changes in body insulation of juvenile king penguins suggest an
22 energetic challenge during their early life at sea. *The Journal of Experimental Biology* **220**,
23 2666–2678 (2017).

- 1 103. Thiebot, J.-B. & Pinaud, D. Quantitative method to estimate species habitat use from light-
2 based geolocation data. *Endangered Species Research* **10**, 341–353 (2010).
- 3 104. Ballard, G. *et al.* Responding to climate change: Adélie Penguins confront astronomical and
4 ocean boundaries. *Ecology* **91**, 2056–2069 (2010).
- 5 105. Dunn, M. J., Silk, J. R. D. & Trathan, P. N. Post-breeding dispersal of Adélie penguins
6 (*Pygoscelis adeliae*) nesting at Signy Island, South Orkney Islands. *Polar Biology* **34**, 205–214
7 (2011).
- 8 106. Pierce, A. J., Stevens, D. K., Mulder, R. & Salewski, V. Plastic colour rings and the incidence of
9 leg injury in flycatchers (Muscicapidae, Monarchidae). *Ringing and Migration* **23**, 205–210
10 (2007).
- 11 107. Griesser, M. *et al.* Causes of ring-related leg injuries in birds - evidence and recommendations
12 from four field studies. *PLoS ONE* **7**, (2012).
- 13 108. Costantini, D. & Møller, A. P. A meta-analysis of the effects of geolocator application on birds.
14 *Current Zoology* **59**, 697–706 (2013).
- 15 109. Richter, S. *et al.* A remote-controlled observatory for behavioural and ecological research: A
16 case study on emperor penguins. *Methods in Ecology and Evolution* **9**, 1168–1178 (2018).
- 17 110. Gendner, J.-P. *et al.* Automatic weighing and identification of breeding penguins. In *4th*
18 *European international conference on wildlife telemetry*, Ilis Horwood Ltd 29:30 (1992).
- 19 111. Gendner, J.-P., Gauthier-Clerc, M., Le Bohec, C., Descamps, S. & Le Maho, Y. A new application
20 for transponders in studying penguins. *Journal of Field Ornithology* **76**, 138–142 (2005).
- 21 112. Le Bohec, C. *et al.* Population dynamics in a long-lived seabird: I. Impact of breeding activity
22 on survival and breeding probability in unbanded king penguins. *Journal of Animal Ecology* **76**,
23 1149–1160 (2007).

- 1 113. Cristofari, R. *et al.* Climate-driven range shifts of the king penguin in a fragmented ecosystem.
2 *Nature Climate Change* **8**, 245–251 (2018).
- 3 114. Thiebot, J.-B., Cherel, Y., Trathan, P. N. & Bost, C. A. Inter-population segregation in the
4 wintering areas of macaroni penguins. *Marine Ecology Progress Series* **421**, 279–290 (2011).
- 5 115. Thiebot, J.-B. *et al.* Mates but not sexes differ in migratory niche in a monogamous penguin
6 species. *Biology Letters* **11**, 1–4 (2015).
- 7 116. Enstipp, M. R. *et al.* The dive performance of immature king penguins following their annual
8 molt suggests physiological constraints. *The Journal of Experimental Biology* **222**, jeb208900
9 (2019).
- 10 117. Forin-Wiart, M.-A., Enstipp, M. R., Le Maho, Y. & Handrich, Y. Why implantation of bio-loggers
11 may improve our understanding of how animals cope within their natural environment.
12 *Integrative Zoology* **14**, 48–64 (2019).

1 Additional files list

2 Additional file 1 (.pdf): Table S1. General information on the loggers deployed including the logger

3 type, name, dimensions and weight, as well as the manufacturers name and location

4 Additional file 2 (.mp4): Movie S1. PIT-tagging of an adult emperor penguin

5 Additional file 3 (.mp4): Movie S2. Capture of an adult-chick pair

6 Additional file 4 (.mp4): Movie S3. Weddell seal disturbance on the emperor penguin colony

7 Additional file 5 (.mp4): Movie S4. Release of an adult-chick pair

8 Additional file 6 (.mp4): Movie S5. Capture of a single adult with the crook

9 Additional file 7 (.mp4): Movie S6. Adult emperor penguin handling

10 Additional file 8 (.mp4): Movie S7. Back-taped GPS deployment

11 Additional file 9 (.pdf): Fig. S1. Marking of an emperor penguin with a painted number

12 Additional file 10 (.mp4): Movie S8. Back-taped TDR deployment

13 Additional file 11 (.pdf): Fig. S2. Adult emperor penguin at the end of its moult

14 Additional file 12 (.mp4): Movie S9. Back-taped-epoxied logger deployment - epoxy spreading

15 Additional file 13 (.pdf): Slideshow S1. Leg-banded TDR mounting manual

16 Additional file 14 (.pdf): Slideshow S2. Leg-banded TDR deployment and recovery

17

18

19

1 Figures

2

3 **Fig. 1** Required tools to capture emperor penguins. **a** An adult-chick pair inside the corral. **b** A 3 m
4 long bamboo stick at the top, one of the panel of the corral (a 50 cm ruler is placed just above it to
5 facilitate scaling) in the middle, and the crook at the bottom. Photo © CNRS-IPHC / CSM.

6

Fig. 2 Pictures of the different deployments performed. **a** Adult emperor penguin equipped with back-taped loggers (a TDR in the middle of the back and a GPS underneath). The green line on the bird's belly is non-permanent marking. **b** Adult emperor penguin equipped with back-glued loggers (an accelerometer in the middle of the back and ARGOS satellite transmitter underneath) and a leg-banded logger on its right foot. **c** Juvenile emperor penguins both equipped with a back-taped-epoxied logger. Photo © CNRS-IPHC / CSM.

1
2 **Fig. 3** Back of the 4 penguins having lost their back-glued loggers during the winter. Photo © CNRS-
3 IPHC / CSM.