Avian rucksacks for science: In search for minimum-impact tagging procedures for birds.

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How to cite:

Vandenabeele, Sylvie Paule (2013) *Avian rucksacks for science: In search for minimum-impact tagging procedures for birds..* thesis, Swansea University.
http://cronfa.swan.ac.uk/Record/cronfa42920

Swansea University
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Avian rucksacks for science:

In search for minimum-impact tagging procedures for birds.

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Biology and Environment
University of Montpellier, France

Submitted to Swansea University in fulfilment of the requirements for the degree of Doctor of Philosophy

March 2013

Á ma famille

Que j'espère rendre fière

'Fais de ta vie un rêve, et d'un rêve, une réalité.'

— Antoine de Saint-Exupéry, *Le Petit Prince*

ABSTRACT

Voltaire wrote “With great power comes responsibility”, a quote which can easily be applied to scientists nowadays whose work effectively shapes the life of billions of living beings, operating through various disciplines from medicine through to ecology. To help scientists working with wild creatures, animal-attached electronic devices, commonly referred to as ‘tags’, have become indispensable tools, pushing the boundaries into the unimaginable enabling, for instance, information to be sent from animals into space and back via satellites. This ‘great power’ does indeed come with ‘responsibility’ however, as evidence piles up of the deleterious effects of tags on their animal carriers. The aim of this doctoral project is to provide scientists with an analytical framework within which to examine the effects of external tags on wild animals with a view to providing guidelines informing best practise in animal tagging. For that purpose, an integrative, multidisciplinary approach was undertaken which, from a theoretical to an experimental level, assessed the impact of tags on birds. With a main focus on marine birds, the results show that tag effects ranged from behavioural aberrations to compromised energetics, ultimately reducing both flying and swimming performance. This impact varied as a function of tag size, mass, shape, position and attachment, as well as being dependent on bird morphology and lifestyle. The length of time to which a bird is exposed to deleterious tag effects appears critical since these effects can snowball over time. Fortunately, and as reported in this thesis, there are simple rules which can be implemented to help minimise tag impact even for long-term studies, mainly through an optimised tag design and innovative attachment system. So, happily, this thesis shows that by careful thinking, we can benefit maximally from our ‘great power’ and thus ensure that our ‘responsibilities’ to wild animals are best informed.

DECLARATION

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

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Date ......30/03/2013.............

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This thesis is the result of my own investigations, except where otherwise stated. Where correction services have been used, the extent and nature of the correction is clearly marked in a footnote(s).

Other sources are acknowledged by footnotes giving explicit references.
A bibliography is appended.

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Signed .... (candidate)

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ACKNOWLEDGEMENTS / REMERCIEMENTS

Nombreuses ont été les fois où j'ai pu réfléchir à comment je ferais mes remerciements, réalisant que ce serait sûrement la partie la plus difficile à rédiger (bien que je ne puisse pas me plaindre vu que j'ai le choix d'écrire, pour une fois, dans n'importe quelle langue m'offrant ainsi la chance de m'exprimer le plus librement et judicieusement possible). Mais ça, c'était jusqu'à ce que mon père me suggère gentiment que la façon la plus originale serait certainement de ne pas employer le mot 'merci', ce qui, bien que parti d'un bon sentiment, n'a pas rendue la chose plus aisée... mais on n'aime les défis dans la famille alors je me lance !

Tout au long de ma thèse, en de maintes occasions, je réalisais que le rêve de ma vie, mes aspirations de petite fille, étaient enfin devenus réalité. Ce pourquoi je m'étais toujours battue, le but depuis si longtemps poursuivi était enfin à portée de mains et même littéralement entre mes doigts, me faisant parfois sentir comme si je pouvais de nouveau soulever des montagnes. J'écris « entre mes doigts » car, en effet, ces sentiments d'accomplissement et de force m'ont parcouru bien des fois dans ces situations aussi banales qu'extraordinaires où je me retrouvais à envelopper de mes mains ces boules de chaleur à plumes qui, soit dit en passant et comme Rory l'avait prédit, exercent depuis lors une réelle fascination sur ma personne (bien que ceux à écailles, à fourrure ou fait de 'gelée', que j'ai également pu rencontrer en chemin, ne m'ont pas laissé indifférente, loin de là). Cela est sans parler des situations incroyables et inattendues comme lorsque je me suis vue embarquée pour une expédition vers le sub-Antarctique en route pour rencontrer le mythique albatros hurleur et autres animaux fantastiques, sur une île tout droit sortie de récits d'aventures.

Cette thèse représente sans aucun doute le projet de ma vie et c'est sûrement pourquoi je me sens si effrayée et perdue de parvenir au bout. Mais je dois réaliser que c'est certainement le premier d'une longue liste de projets à venir! Cependant si ce doctorat a tant compté pour moi c'est autant pour son sujet, que je n'aurais pu espérer être plus inspirant et en total accord avec mes aspirations, que pour tout ce que cela m'a apporté d'autre et que jamais je n'aurais soupçonné. Ce fut un réel apprentissage de la vie riche de part ces inoubliables rencontres et découvertes faites au fil de voyages des plus extraordinaires.

Tout cela je le dois à un homme en particulier, Rory Wilson, qui a su m'accorder sa confiance dès les premiers instants et malgré un premier échange téléphonique plutôt hésitant (mais pas des moins enthousiaste selon lui). Il a toujours cru en moi et m'a ainsi offert l'incroyable chance de faire de mon rêve une réalité ! C'est cet homme, dont l'humilité n'a d'égal que l'humanité, qui un jour éclaira ma route qui, pour diverses raisons, s'était obscurcie au point de me perdre sur le chemin sinueux de l'avenir. You made me grow both humanely, on a personal level, and professionally. This whole PhD went beyond everything I could imagined and exceeded all expectations. My gratitude towards you is eternal. One last thing I wish (in addition to the certificate of Doctor of Philosophy indeed) is that, one day, you will also reckon I deserve this so hoped-for British citizenship (despite a rather recalcitrant accent I know). 'Diolch yn fawr' Rory (the deal was not to use the word 'merci' but no one said I couldn't use another language especially if it's to honour the country which welcomed me, Wales...).

Cet accomplissement, qui prend aujourd'hui la forme écrite d'un mémoire de thèse, je le dois aussi à toutes ces merveilleuses personnes, collègues, famille, amis qui m'ont épaulé tout au long de cette fabuleuse, autant qu'éprouvante, aventure. En particulier;

This achievement, which today takes the shape of a written thesis, I owe it also to all these wonderful people, colleagues, family, friends who supported me throughout this amazing, but also challenging, adventure. In particular;

Ma famille toute entière à commencer par mes parents, Pichouquette & Papou, qui malgré leurs doutes et leurs craintes m'ont toujours poussé à poursuivre mes ambitions et m'ont supportés dans tous les sens du terme et de toutes les façons qui soient, m'aidant à me relever quand parfois je tombais sur ce chemin de vie qui se veut souvent un peu pentu. Les autres membres de ma famille ne sont pas à oublier et malgré les distances, discordes, malentendus qui font que tous ne peuvent être ensemble unis, je suis heureuse et reconnaissante que certains aient pu faire la démarche de se rapprocher quand il le fallait dans le seul et unique but de m'aider.

Á tous, 'diolch o galon' pour cet amour inconditionnel que vous m'avez apportez depuis toujours dans les moments difficiles comme dans les moments de joie ;

- Mon clan de frères dont Seb qui m'a permis d'avoir l'esprit tranquille me disant que sa porte, et peut être même son clic clac, seraient toujours à ma disposition si je finissais chômeuse après ma thèse! Aurélien et Ilane pour me faire sentir être la grande la plus aimée qui soit & enfin Bruno, parti trop tôt, j'ose croire que tu aurais été fière de moi;
- Mes grands-parents présents ou au ciel particulièrement celle dont j'envie la sagesse autant que le talent d'écriture ;
- Magali pour son éternel soutien;
- Les gersois retrouvés pour mon plus grand bonheur ;
- Ainsi que tous autres membres apparentés connus ou inconnus.

My friends and colleagues;

Adam Grogan who made it happened, both financially and logistically. You are a truly supportive person and of really good advice, 'diolch' Adam;

Emily Shepard with who I shared my very first steps as a PhD student starting with a memorable cold week in Birmingham in company of dear (and of real character) feathered friends (with a special thought for Orange!);

Sabrina Fossette, my French twin ;) 'Diolch' for all these amazing moments we shared from stinging fieldwork and surfing, to funny as well as emotive episodes pendant lesquels tu a toujours été une Oreille attentive et sachant choisir les justes mots du réconfort;

Adrian Gleiss (see I put you just next to your 'chérie' so that you can stay together, since now you can't live without each other, at least that's what you declared few months ago, a moment I regret I couldn't share), 'diolch' for being such an enthusiastic and unique friend, we miss you here!

Vicky Fidler-Hobson always so thoughtful, 'diolch' for having shared both your shoulder and cuddly Kitty from time to time;

Lama Qasem and her supportive favorite quote “You'll be fine”. I can tell you (but only now) ‘diolch’ cos you were right and you will be fine too;

Martin Lilley, ‘diolch’ for all the wonders and discoveries throughout charming Wales, enchanting Greece, travelling in the air as well as in water, on cliffs and even ice;

The furious team of the very beginning, Serena Wright & Marion Soresina. I miss our silly, crazy though definitely ‘good for you’ moments;

Also ‘diolch arbennig’ to all the others members of ‘SMART’ team (or “trackers” as one call us), Owen, Jacques, Ed Pope, Ed Grundy, Mark Bolton, Prof. Graeme Hays, Gail Schofield, SEACAMS particularly Nicole Esteban and Daryn Taylor, APT and AQWA people, all the ladies over at Margam building and, finally, all the souls you can meet in these rather bleak basement corridors that I walk up and down an infinite number of times to reach what, sometimes, seemed to be the end of the world but was also just the perfect place to quietly and manically finish your PhD. A special time that I didn't face on my own, having shared this secluded place with Rebecca Scott. ‘Diolch’ Becky for having prevented me to sink into total insanity or, at least, for having showed enough solidarity to share this madness with me.

Amis des lieux privilégiés qui m'ont accueillis et vu ‘grandir’ dans un passé pas si lointain ; zanmi Madinina restés au pays ou expatriés dont ma Guizmo et mon parisien que je n'oublie pas, amis marseillais en particulier mes cousines, Sam & Stef, et leur petit (bien que très grand) protégé qui a tant compté et comptera toujours pour moi, sans oublier son ‘frère’ Yann Pérez-Garcia qui s'est modestement rebaptisé ‘l'étalon’ mais que je préfère surnommé ‘le beau gosse’; amis bretons et de Strasbourg avec une mention spéciale à Yan Ropert-Coudert sans qui je n'aurai sûrement jamais atterri chez les gallois (on se revoit dans le sub-Antartique côté ouest la prochaine fois!) et Sophie Steelandt, ma ‘jumelle’ des temps strasbourgeois (on refait de l'aquagym quand tu veux!);

Others collaborators and friends_from around the world that I have had the chance to meet during my wonders on our beautiful planet from musical New

Orleans to fascinating Sydney and bewitching Marion Island. From close to my current hometown Swansea to farther and farther away, a special mention to;

People at Mallydams RSPCA wildlife centre in particular Richard Thompson;

Jemima Parry-Jones and fantastic ICBP team (Adam, Holly, Mark, Simon, John, Robin…), 'diolch' for your kindness and genuine interest in my work;

Steve Votier, Sam Patrick and others from Plymouth University as well as all the kind people down in St Davids and Ramsey Island;

Martin Wikelski for your real and so driving enthusiasm, 'diolch' to you and all the friendly team of the Max Planck Institute, Wolfgang, Jesko, Andreas, David, Katarina, Davide, Riek, Bart, Nina, Dina, Elke, Jennyfer… (so many that I will not have enough space to write it all!) for having given me the chance to demonstrate the whole potential of our 'multipurpose' silicone harness;

Dankie to all those warm and unbelievably welcoming South African souls in particular Peter Ryan & the Marion Islanders, Otto & Jenny as well as Katta & Gerard for having made discover the place of my dreams that is beautiful Cape Town;

Without forgetting, at last, my winged friends with who I shared intense particular moments (not only painful ones I can assure you!) since, if they hadn't existed, this thesis may have not seen the light (or would have but only to be on a different perhaps 'boring' or 'smellier' species as Rory would say). 'Majestuous' animals which I learnt to respect and even admire.

* * * * *

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N.B. All specialised terms and abbreviations are defined at first mention throughout the main text.

Additional publications

During the course of my PhD, I have been involved in few other projects which sometimes lead to publications. Below is a list of these papers and manuscripts.

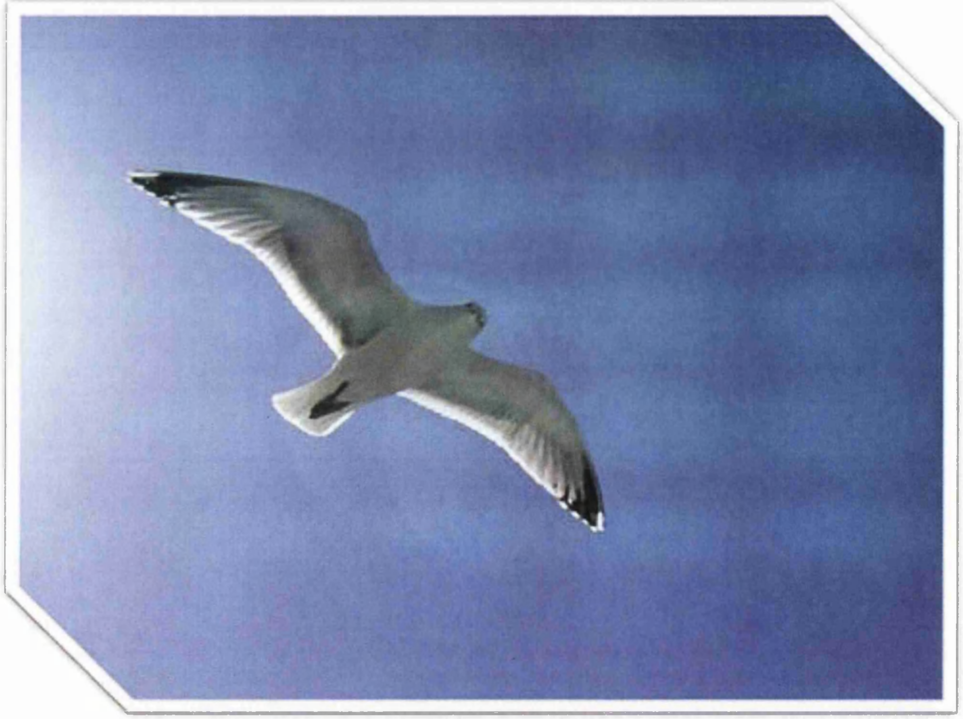
Dilley, B., Davies, D., Connan, M., Cooper, J., De Villiers, M., Swart, L., Vandenabeele, S. P., Ropert-Coudert, Y. & Ryan, P. G. Giant petrels as predators of albatross chicks. *Polar Biology (In review).*

Grogan, A., Wilson, R. & Vandenabeele, S. P. 2011. Implications of fitting monitoring devices to wild animals. *Veterinary Record,* 169, 613-613.

Patrick, S. C., Vandenabeele, S. P. & Votier, S. C. Animal-borne cameras capture individual differences in visual foraging cues. *PLoS One (In review).*

‘The gull sees farthest who flies highest’

— Richard Bach, *Jonathan Livingston Seagull*



Introduction

From folklore to reality

The myth of babies being delivered by storks is probably one of the most common stories associated with child birth in Europe and America (Margolis & Parker 1972, de Lys 1996, Burgess 2011). Several aspects of the stork's natural history may have contributed to the emergence of this belief. Not only do they live in watery areas where the souls of unborn children were believed to be kept (Burgess 2011) but also their large size and migratory behaviour certainly made this lore more plausible (Margolis & Parker 1972). It is also storks that were once believed to give lifts to smaller bird species, as experts found no other explanation for how creatures as tiny as wheatears could migrate cross-hemispheres.

Although it is unlikely that anybody has ever seen a stork with either a baby dangling from its beak or a wheatear clung on its back, the remarkable carrying feats of 'homing' pigeons, notably during the World War I, are well documented. These birds, fitted with capsules containing messages or even cameras mounted onto breast harnesses (Figure 1), were used to deliver and gather important information about the enemy and played a critical role in victory (Baumann 2001, Blechman 2007). Later, the carrier pigeons of the war years became penguins which, fitted with cameras and other electronic devices (Figure 2), came to be 'carriers' for technology to reveal details about their own lives underwater (e.g. Ponganis *et al.* 2000, Moll *et al.* 2007 and references therein) rather than of some enemy (Chapter 1).

The use of this remote-sensing technology to study animals actually started about 40 years ago, but now includes a broad variety of devices from radio to satellite transmitters and even multi-channel data loggers (Cooke *et al.* 2004, Ropert-Coudert & Wilson 2005). It has brought astonishing knowledge about the life of many free-ranging animals to light by allowing remote transfer, or recording, of information on animal location and movements, as well as detailing the surrounding environment (Ropert-Coudert & Wilson 2005, Rutz & Hays 2009). Animal telemetry is now unveiling the truth about the migration of even 'small' birds, showing that wheatears and the like are actually perfectly capable of covering remarkably long distances without having to "hitchhike" on larger birds (e.g. Egevang *et al.* 2010, Bairlein *et al.* 2012).

The revolution on animal-attached technology is mainly related to dramatic reductions in the weight and size of the devices, achieved through the miniaturisation of the electronic components, from memories to processors to batteries (Seegar *et al.* 1996, Ropert-Coudert & Wilson 2005), this being driven by constant consumer demand for brand new technology such as for mobile phones and other communication appliances. Further progress in animal-attached technology has more recently been focused on better ways to access the data while minimizing the disturbance caused mainly by capture and handling of study animals, couched primarily in terms of remote transmission so that data can be accessed from an equipped animal at a distance (Handcock *et al.* 2009, Tomkiewicz *et al.* 2010) without the animal even being aware. With much smaller and lighter devices, an increasing range of species is being equipped, including even the smallest songbirds, with, for example, tiny geolocators attached to the leg or back (Figure 3; Stutchbury *et al.* 2009, Bairlein *et al.* 2012).

The 40 year gap between the camera pigeons and the first deployment of cameras on penguins and the time since then has, therefore, seen incredible changes in our capacity to monitor the behaviour of free-living animals, but it is germane to ask whether we are still guilty over 'overloading' the bearers as was obviously the case for some of the World War I pigeons (Figure 1)? While men such as Charlie Chaplin clearly benefit from their "penguin suits", it is unlikely that this works the other way round (Figure 2; but see Cuthill *et al.* (1997) who showed that colour bands may enhance social status in zebra finches). In particular, although the advance of technology for animals has seen a reduction in size of units and their attachment mechanisms, we have also deployed units on ever smaller animals (Cooke *et al.* 2004, Wikelski *et al.* 2007), which raises questions about acceptable limits for our new 'carrier' pigeons encompassing ever more species.

The flipside of the coin

If we ignore, for the moment, the huge apparent benefits in the acquisition of data from equipped animals, animal-attached devices are still a source of potential harm and discomfort for the bearers. This issue was essentially overlooked at the onset of the approach, and although the situation has improved today, it is still of concern (Chapter 2). It is hard to blame the pioneers of this methodology for this as they, in their fervour, accessed the secret lives of wild animals for the very first time. Ultimately, however, we need to ensure that this approach actually meets the primary objective in describing the 'normal' behaviour of the animals.

Following the initial euphoria, a few reports began to consider the negative effects of animal-attached technology and, as a result, finally lead to the development of few basic, though essential, recommendations regarding best practice. Probably the most well-known of these recommendations is the "3% rule" suggested by Kenward (2001), based on the general observation that devices weighing more than 3% of the bird's body mass were likely to disrupt their behaviour. Although laudable, a main issue here is that this rule is not based on a real assessment of device effects and is, therefore, rather arbitrary, with the major limitation being that it cannot be successfully applied across all species given their variability in morphology and lifestyle (cf. Caccamise & Hedin 1985, Aldridge & Brigham 1988, Brown *et al.* 1999). A consequence of this is the huge fluctuation in the adopted value of this limit for device masses ranging from 1% to 10% of carrier body mass, depending on the species (e.g. 10% suggested by Richards *et al.* (1994) vs. 3% suggested by Kenward (2001)).

Scientists have also realised that the issue was not limited solely to the mass of the device. Another major issue linked with the utilisation of external devices on animals, and particularly relating to diving birds and mammals, is the resultant increased drag (Bannasch *et al.* 1994, Hazekamp *et al.* 2010, Pavlov & Rashad 2011). Long known to be important for fuel consumption in cars (Hucho 1978, Carr 1983), it took biologists much longer to appreciate the significance of this with regard to devices on animals (e.g. Wilson & Culik 1994, Watson & Granger 1998, Bowlin *et al.* 2010). Indeed, it transpires that drag is also a function of device placement as well as shape and this can be as critical in animals moving through the air as well as water (e.g. Bannasch *et al.* 1994, Ropert-Coudert *et al.* 2007, Bowlin *et al.* 2010) so that consideration of device effects only in terms of added mass is clearly simplistic. But there is more. There are subtle aspects of the detrimental effects of animal-attached devices related to, for example, the colour of the equipment (e.g. Burley *et al.* 1982, Wilson *et al.* 1990, Seamans *et al.* 2010) or the fact that antennae (aside from producing extra drag (Wilson *et al.* 2004) can also incite excessive preening and even disrupt reproduction (e.g. Paquette *et al.* 1997, Garrettson *et al.* 2000 A. Dixon pers. comm.).

More recently, and probably linked with the increasing need for long-term tracking studies to be conducted, was the added problem of device attachment. Methods which involve fixing devices to bird feathers using glue or tape have proven successful only over relatively short periods of time (Raim 1978, Wilson & Wilson 1989, Wilson *et al.* 1990, Johnson *et al.* 1991). As a result, researchers have turned to harnesses, and although ostensibly less cumbersome than those used on penguins in the past (see above), these attachment techniques are also clearly beset with problems (e.g. Schulz *et al.* 2001, Steenhof *et al.* 2006, Peniche *et al.* 2011). Perhaps the answer lies in a paradigm shift in harness material (Chapter 3).

The science behind animal tagging; towards objectivity in animal welfare

Animal welfare, a concept that has sat uncomfortably between emotive descriptors and objective science, has emerged as a platform for the consideration of device effects (Hawkins 2004, Grogan *et al.* 2011). Animal conservation is currently increasingly constrained by rules set up to avoid any unnecessary 'suffering' potentially linked with the use of tracking devices used on wild animals (Wilson & McMahon 2006, McMahon *et al.* 2012). The problem, however, lies in the approach adopted by animal welfare bodies which often advocate a hands-off attitude as a way to ensure that animal well-being is not compromised. Conversely, conservationists claim that the benefits obtained from tagging studies at a population level, for instance with the creation of marine protected areas defined using the identification of foraging grounds of endangered species (e.g. Le Corre *et al.* 2012, Scott *et al.* 2012), more than justify the potential detriment inflicted on just a few individuals.

Critically, somewhere between the fact that device effects can be fatal (e.g. Paton *et al.* 1991, Peniche *et al.* 2011, McIntyre & Bildstein 2012) and the observation that we can observe species go extinct without having the least idea why if we do not use tagging technology, there must be space for both individual animal welfare and species conservation in wildlife research. Indeed, animal welfare policy can, and should, provide the dimension required to ensure that research performed on wild animals, including animal conservation studies, can be conducted in an objective manner and, as such, is scientifically and ethically defendable (Wilson & MacMahon 2006). Indeed, animal welfare approaches can play a critical role by defining what is acceptable and what is not to allow wildlife practises to be undertaken without a universal ban. In fact, examples of farmed or laboratory animals are good illustrations of how animal welfare policy can successfully regulate practises so as to ensure that no unnecessary 'suffering' is caused (Hurnik 1988, Wolfensohn & Lloyd 2007).

The reason for such success in captive animal studies certainly lies in the length of time that we have been keeping animals in captivity (Klaits & Klaits 1974, Alves *et al.* 2012) and the glaringly obvious nature of detriment in animals that we can observe at any time. This gives animal welfare considerations a particularly robust basis for addressing ethical issues but also explains why it is still in its infancy in wildlife studies. Although science and welfare should be synonymous, Prof. Stuart Harrop alluded to differences between them when he noted during his talk at the Compassionate Conservation Symposium (University of Oxford, September 2010), that "science informs 'suffering' and ethics informs 'unnecessary' suffering" (Harrop 2010).

The aim of this doctoral project was to attempt to unite welfare concepts with the science of defining 'detriment' in wildlife issues relating to external tags, using seabirds as a primary model system. The ultimate aim is to adopt a scientific approach to inform appropriate guidelines for best practise in animal tagging studies. For this, the real extent and mechanisms of device effects on birds were assessed based on pure scientific disciplines such as physics, physiology and ecology by adopting a multi-step approach that ranged from pure theory to assessment of effects on birds in captivity before finally examining effects on free-living species (Figure 4).

A major part of this doctoral study focused on the development of a novel attachment system for long-term deployments of external tags on birds, a persisting challenge for most tracking studies (Chapter 3). This thesis also dealt with one of the most perceived deleterious effect of attached tags which is that of extra mass. Theoretical costs of flight models showed that it is simplistic to assume that a 3%

mass payload translates into a 3% energy 'payload' (cf. Kenward 2001, see above). Such models can, however, be very instructive in defining what such detriment may be for different species (Chapter 4). Device drag, also considered as important in modulating detriment, was measured in wind tunnel simulations of flight and swimming conditions, showing the critical nature of device placement and shape (Chapter 5). Data from this work were used to inform a study on captive cormorants and illustrate, using data derived from wild birds, the importance of movement speed and drag coefficient of the study animal in defining detriment related to device-induced drag and discuss the implications in terms of the ecology of the birds (Chapter 6). A captive bird study was also used to try to quantify the effect of antennae on the cost of swimming for guillemots (*Uria aalge*) (Chapter 7). Finally, an attempt was made to determine the importance of the precise position of device attachment on the flying efficiency of equipped gannets (*Sula bassana*) (Chapter 8).

From then to now and beyond

Although this study confirms that tagging can affect birds in many ways, it also shows that by applying simple rules, device effects can greatly be reduced. It also shows that tools (such as the Flight program developed by Prof. Pennycuick) are available for scientists to estimate the potential impact of the equipment and that recommendations, such as those made in this study, can be derived for most species. Indeed, given the diversity of tracking devices available and the potential variation in bird morphology and behaviour, it may be judicious, prior to any study, to attempt to define device effects and try to minimize them. This is easier now that software, such as that relating to Computational Fluid Dynamics, is available and can, for instance, help measure device-induced drag so that tags can be designed without having to access special facilities like a wind tunnel. From this, it is just one small step towards the fabrication of sleek and minimum impact tags while maintaining functionality. Chapter 9 describes how Computer Aided Design can inform 3D printing technology to build appropriate tag housings, using gannets, badgers and turtles as examples.

Such expertise and technology in 3D modelling can also greatly contribute to the future development of the tag attachment systems, such as the new harness proposed in Chapter 3. In fact, there is an increasing number of projects asking for appropriate Silastic®-based harnesses (as outlined in Chapter 3), which will necessitate such modern CAD and 3D printing approaches so as to be able to deal with the greater numbers of individuals and species. It is an exciting prospect that 3D scanners and printers could help build 3D moulds to produce harnesses rapidly and accurately while accounting for the variation in size and morphology encountered amongst the different bird species. A few obvious improvements of this long-term attachment system are still wanting, with, for instance, the necessity to incorporate a drop-off system before this project may be considered adequately useful for long-term device deployment. With tags designed to be of minimum impact attached using such harnesses, we may aspire to a more complete merging of science and welfare so that robust, morally defendable data can be acquired using animal-attached tags to inform us of the secret lives of animals for blue-skies research and conservation issues alike (Synopsis chapter).

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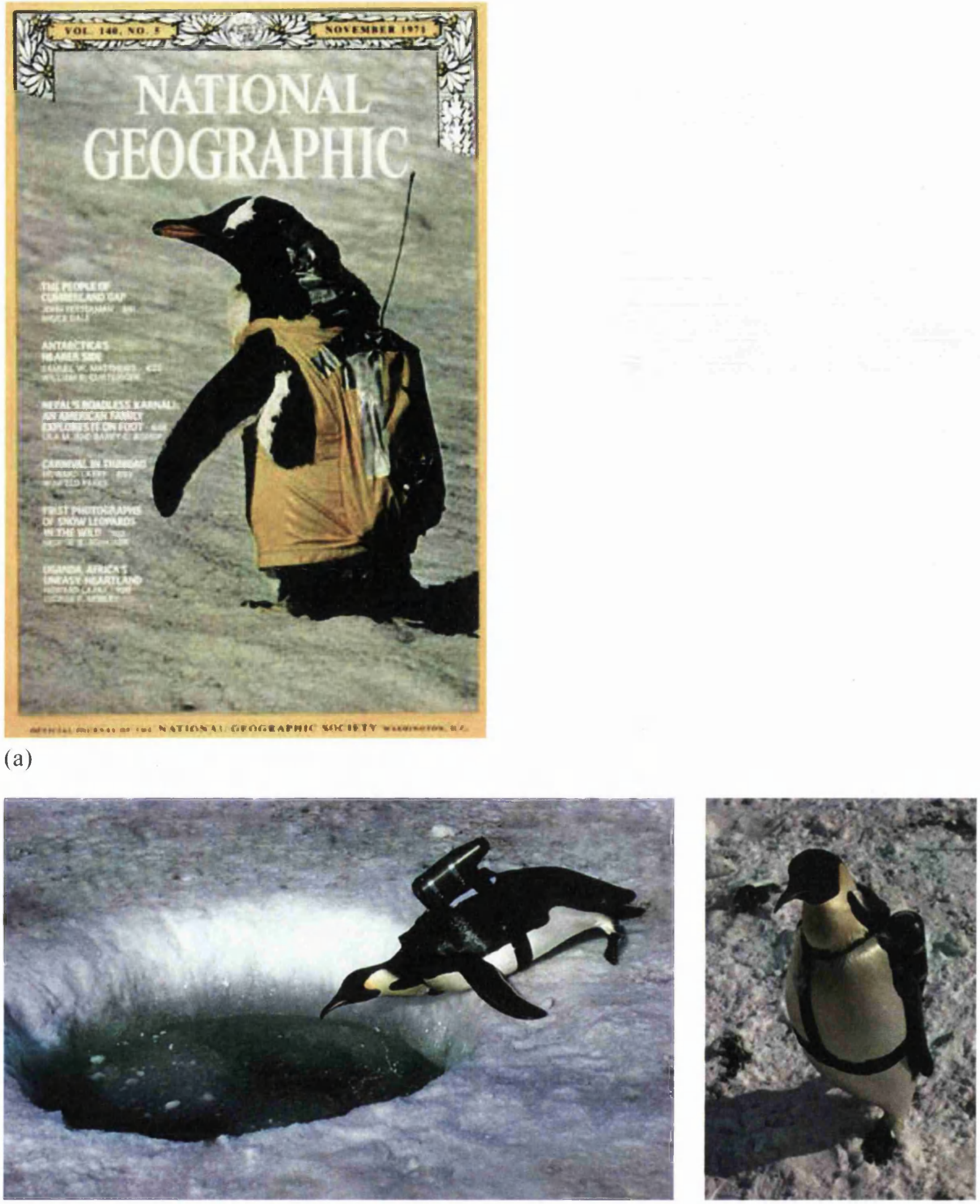
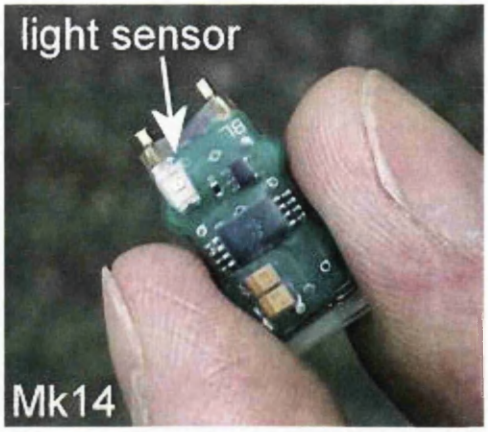
Figure 1. Archive photos of homing pigeons during World War I and II carrying encapsulated messages attached to the back or leg (top) or harnessed with a camera (bottom) as a way to deliver and collect strategic information during the conflict. (Sources from left to right: Getty Images, National Humane Review April 1918, German Federal Archive).



(b)

Figure 2. (a) Front page cover of the National Geographic magazine issue from November 1971 showing a gentoo penguin (*Pygoscelis papua*) wearing a radio backpack and (b) photos of an emperor penguin (*Aptenodytes forsteri*) fitted with a Crittercam camera.
(Source: National Geographic website).



(a)

(b)

Figure 3. (a) Photo of miniature light level geolocator produced by Biotrack and (b) image of a Pacific Golden plover (*Pluvialis fulva*) fitted with a geolocator to its leg so as to retrace its migratory route (Johnson *et al.* 2011). (Source: photo (a) accessible on Biotrack website, photo (b) credit to Wally Johnson).

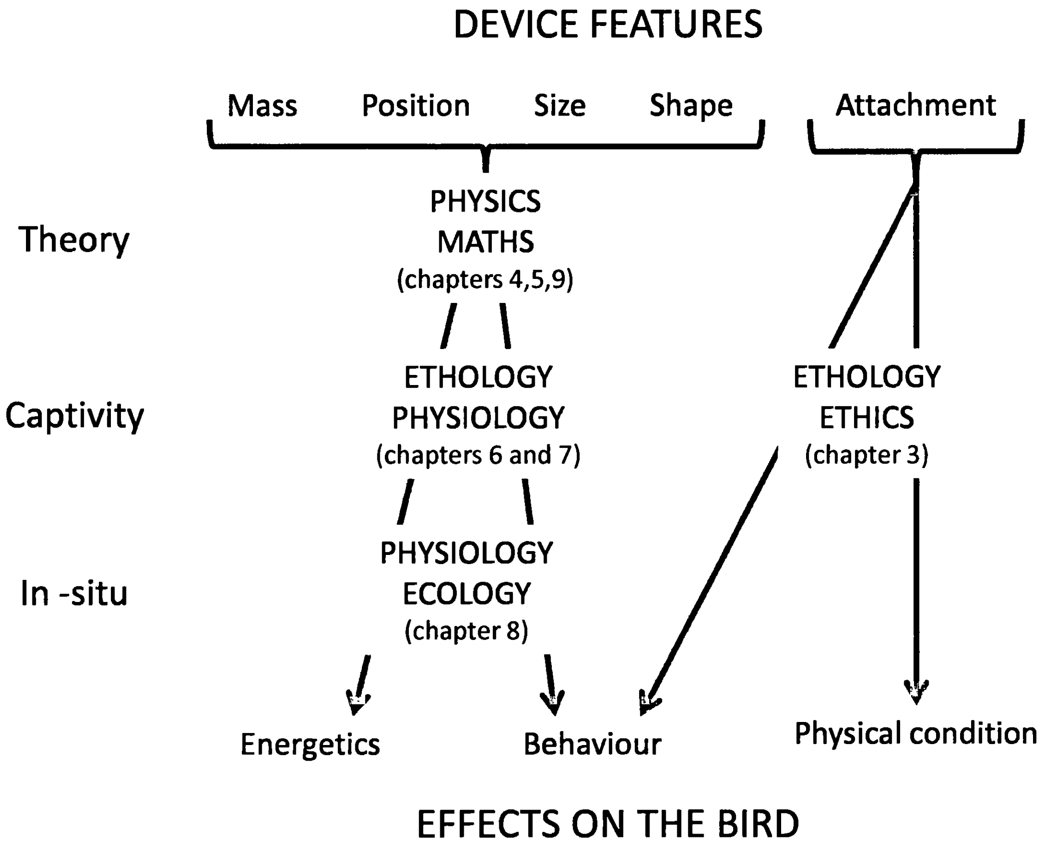
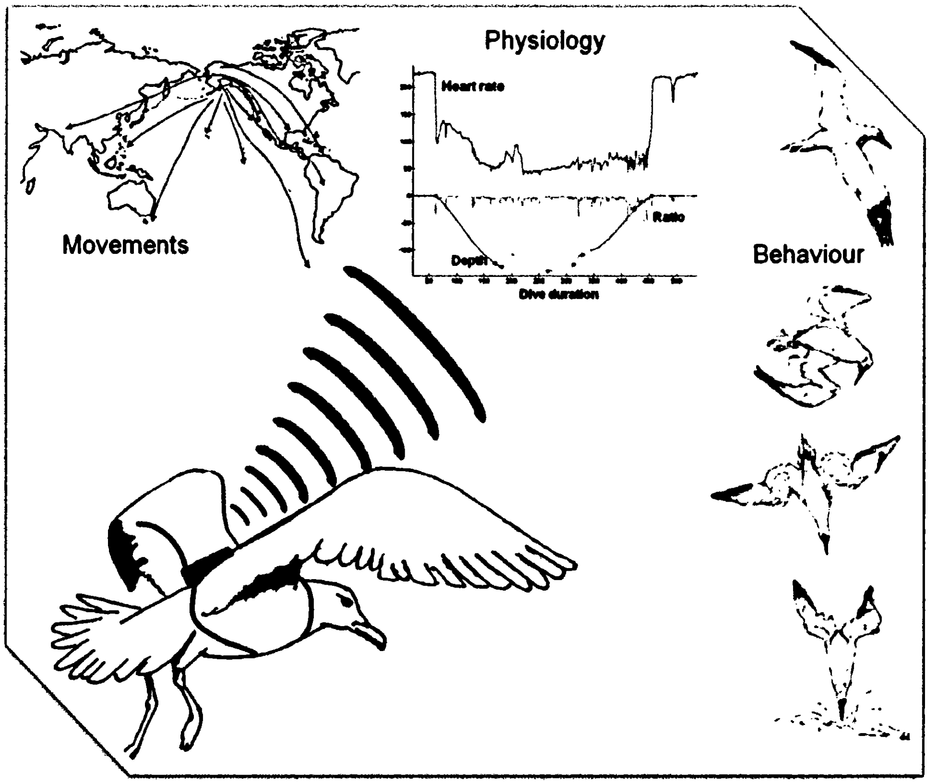


Figure 4. Schematic chart illustrating the multi-step and multidisciplinary approach undertaken in this doctoral study to address the issue of the potential negative impact of tracking device on birds.

Chapter 1:

Technological innovation in archival tags used in seabird research

Rory P. Wilson & Sylvie P. Vandenabeele



RPW and SPV searched the literature and wrote the manuscript.
Marine Ecology Progress Series (2012) 451, 245-262

Abstract

The first archival tags were used on seabirds in the 1960s. Since that time, when recording systems were primitive, various technological advances, culminating in solid state devices, have provided the seabird research community with extraordinarily sophisticated and powerful tags. This work documents the progress and development of archival tags used on seabirds, highlighting major advances and the insights that these have provided into seabird behavioural ecology before examining the current limitations to our capacities and speculating on what the future will bring in this exciting and dynamic field.

Keywords: archival tags, seabirds, ecology, behaviour, loggers

Introduction

Man's terrestrial nature means that we are not well adapted to study most marine animals in their natural environment. Debatably though, seabirds are easier than most marine animals. Being virtually all flighted, they are generally highly conspicuous, even at sea, and have incited comment and fascination for years (e.g. Murphy 1936). In addition, many seabirds are colonial and so constitute an obvious part of the landscape in some areas of the world's coastal regions. Against this, the volant species travel fast, and often range far out to sea, which makes them problematic to follow, while the flightless species tend to be inconspicuous at sea and are hard to study because they are such adept divers. Little surprising, therefore, that early studies of seabirds were almost entirely devoted to their life in the colony (e.g. Stonehouse 1975) even though documentation of the behaviour of birds at sea was considered to be pivotal to understanding their ecology and role in ecosystems (Croxall 1987).

Ironically, the same features that lent themselves to the study of seabirds on land made them natural subjects for the deployment of automatic recording devices to determine their at sea behaviour. In 1965, Gerald Kooyman and colleagues attached the first depth recorder to a free-ranging marine mammal, the Weddell seal *Leptonychotes weddelli* (Kooyman 1965), documenting that this animal could dive hundreds of metres deep and demonstrating the power of recording technology to elucidate the behaviour of elusive animals at sea. Aside from their size, however, marine mammals were problematic because recovery of deployed devices necessitates that equipped animals return to a predictable location, something that most marine mammals do not, but that all nesting seabirds do, precisely. During these early archival tag years, the biggest disadvantage that seabirds had over marine mammals for the technology was their considerably smaller mass. However, the penguins, whose heaviest representative, the Emperor Penguin *Aptenodytes forsteri,* at *ca.* 32 kg (Williams 1995) were a substantial departure from the seabird norm. It is therefore likely to be no coincidence that the first seabird equipped with archival tag technology was indeed this bird (Kooyman *et al.* 1971), that it was the technology pioneer Gerald Kooyman who did it, and that for a few years following that, the only loggers deployed on seabirds were on the large, robust, colonial, ground-nesting and flightless penguins (Kooyman *et al.* 1982, Adams & Brown 1983, Lishman &

Croxall 1983, Wilson & Bain 1984). This is not to say that penguins are exempt from deleterious device effects, as extensive literature shows (Ropert-Coudert *et al.* 2000b, 2007, Beaulieu *et al.* 2010). Indeed, device size and mass has been, and will always be, problematic for seabirds, with unacceptable behavioural and physical changes induced by tags acting as the ultimate deterrent for their use (see later).

Since Kooyman's early work, archival tag technology for seabirds has advanced dramatically. This approach now allows seabirds to be followed virtually whenever and wherever they go to sea and thereby eliminates many of the biases of land- or ship-based observations, which are so dependent on environmental conditions to be accurate (Duffy 1983, Schneider & Duffy 1985). Archival tag technology has enabled us to measure everything from the size of individual prey items swallowed (Wilson *et al.* 1992a, 1995c) to the space use by migrating birds over years (González-Solís *et al.* 2007, Egevang *et al.* 2010). This paper looks back at the developments in seabird-attached logging technology over the 40 years since Kooyman (1971) first published on the diving capacities of the Emperor Penguin and attempts to highlight important developments and how these have enabled us to chisel away at the at-sea secrets of these most conspicuous yet most elusive of marine animals.

In order to be concise and contained, this review will focus on recording units (also known as archival tags or loggers) although few brief references are made to transmitting devices, which have had their own particular developmental history which is described very briefly here. Transmission telemetry started with VHF tags simply giving position via triangulation, achieved from two spatially different receiving stations (cf. Kenwood 1987). Signal attention and 'line of sight' operating conditions limit the distance over which this telemetry can be used (Kenwood 1987), both of which are problematic in the marine environment because radio-waves are not transmitted through seawater, giving no reception of signals from diving birds, and birds on the sea surface may have signals attenuated by the swell. Nonetheless, authors have tracked seabird movement using this approach (Sirdevan & Quinn 1997, Whittier *et al.* 2005,) and even used the cessation of signals during diving to deduce dive/pause intervals (Wanless *et al.* 1993). Although the problem of seabirds ranging too far from land to be tracked by land-based receiving stations (Adams *et al.* 2005) could sometimes be solved by researchers following in boats or aircraft

(Heath & Randall 1989, Hébert *et al.* 2003, Romano *et al.* 2004), clearly, some birds cover such large tracts of ocean so fast that this too, has its limitations. This problem was partially solved when researchers were able to use Platform Transmitter Terminals (PTTs) which transmit to orbiting satellites using the Argos system (Taillade 1992) so that position could be derived from anywhere on the planet (e.g. Jouventin & Weimerskirch 1990). The Argos system is limited, however, in the number of positional fixes that can be taken per day (e.g. Georges *et al.* 1997) and positional accuracy is variable, being generally no better than a few hundred metres at best (see, e.g. Weimerskirch *et al.* 1992, Brothers *et al.* 1998, Wilson *et al.* 2002). These two limitations have been largely mitigated now by Global Positioning Systems (GPS) which derive position in the tag using radio-waves from orbiting satellites (von Hünerbein *et al.* 2000, Hulbert & French 2001). Calculated bird positions are good to within a few metres (Grémillet *et al.* 2004, Ryan *et al.* 2004) and updated positions can be derived at any time (except when the bird is underwater) so the only real limitation on temporal or spatial resolution is the size of the battery package size because appreciable amounts of power are needed to determine position (Rose *et al.* 2005, Meyburg & Fuller 2007). Most applications of GPS technology on seabirds use this radio-transmission technology with loggers to store the positional data which are retrieved when the bird is recaptured at the colony (e.g. von Hünerbein *et al.* 2000, Freeman *et al.* 2010) and so represent a hybrid of transmission telemetry and the logging approach.

Developmental stages

Tags on animals and the problems of recording

There are two concepts that were important in the development of archival tag technology for seabirds, one was that animals could carry any sort of foreign body, something that had evolved in the carrier pigeon era and was routinely adopted by researchers using VHF telemetry by the 1960s (Cochran & Lord 1963, Kenward 1987, 2001), and the other was that the foreign body carried could actually record information autonomously. Although modern technology accepts this as given, in the first half of the 20th century, data, of any sort, was generally stored by ink on paper. In the biologists' realm, notebooks and ink chart recorders were at the core of this.

Although such methods are inappropriate for wild animals, it is unsurprising that Gerry Kooyman's first depth recorder for Weddell seals used an analogous method, recording data using a scriber on a rotating drum which had been covered by carbon from smoke, with the scriber actually scratching a trace in the smoked layer (Kooyman 1965).

An in-depth view of seabird foraging

Although penguins are large seabirds, the first attempts to record data from them at sea had to involve a much smaller system than that developed for seals by Kooyman and colleagues. Per Scholander had proposed using an ingenious system developed by Lord Kelvin in the mid 1880's (Scholander 1940 - cited in Kooyman 2004 and 2007) for recording depth by ships where a plumb line was used to assess the likelihood of running aground while navigating in uncharted areas. Here, an air-filled capillary tube, closed at one end, acts as a depth gauge because with increasing depth (and therefore pressure), water is forced into the air-filled space, travelling up the tube, being expelled again when the depth decreases. If the capillary tube is dusted with a water soluble dye, the system shows the maximum depth attained over any period of time (Figure 1). Kooyman *et al.* first used this on penguins in the 1960s (Kooyman *et al.* 1971) and it has been used on a large variety of seabirds many times since (e.g. Montague 1985, Burger & Wilson 1988). The system is, in fact, still being used today, particularly on the smaller species such as storm petrels *Hydrobates pelagicus* (e.g. Albores-Barajas *et al.* 2011).

Despite its limitations, this first recording system for seabirds at sea revealed penguins to be able to dive to depths that far exceeded previous beliefs and demonstrated that these birds must have remarkable physiological mechanisms to allow them to withstand the complications of very high pressures and to breath-hold for the presumed extended periods of time necessary to reach those depths (Kooyman 1975, Kooyman *et al.* 1982). Over time, this was realised for other, much smaller, species because the 'dusted capillary tube depth gauge' is so small, robust and cheap, that it could be deployed on a large range of diving seabird species. As with the first penguins, it has demonstrated that diving seabirds tend to exceed our expectations substantially. For example, 180 g Cassin's Auklets *Ptychoramphus* *aleuticus* can dive to 43 m (Burger & Powell 1990) while 420 g Wedge-tailed Shearwaters *Puffinus pacificus* can dive to 66 m (Burger 2001).

The recording of a single maximum depth in diving seabirds over a specified period of time has profound physiological implications but may give a very biased view of ecologically relevant depths (Burger & Wilson 1988, Whitehead 1989). In a further developmental step, in order to determine the norm, rather than the extremes of depth use, the capillary tube system was modified by placing a radioactive bead of phosphorus on the water-air interface and it was placed on X-ray film sealed inside a waterproof sachet (Wilson & Bain 1984). The position of the phosphorus, a measure of depth, exposed the adjacent film, darkening it more the longer it spent at any site. Careful densitometer readings at various places showed the total amount of time that the device spent at any depth (Wilson & Bain 1984) (Figure 2a). This specific approach was only ever used on the African Penguin *Spheniscus demersus* (Wilson 1985) but it did spawn the development of depth gauges using light on film rather than radioactivity (Wilson *et al.* 1989) (Figure 2b). These systems showed that, although the maximum depths reached by diving seabirds may be exceptional (for an extensive compilation see the Penguiness book online database of diving records at *http://polaris.nipr.ac.jp/~penguin/penguiness/*), the time spent at depth tended to decrease with increasing depth (Wilson *et al.* 1991a, Chappell *et al.* 1993, Wanless *et al.* 1993, Zimmer *et al.* 2010). This is due to two things; that diving birds tend to terminate their dives at shallow depths more often than deep, but also that the accumulated time underwater is biased towards greater time at shallower depths because birds always have to start and finish their dives at the surface, travelling through the surface waters, even if they are foraging at greater depths (Zimmer *et al.* 2010). The accumulation of time underwater for transit, rather than foraging, meant that even time-at-depth recording devices could not easily ascribe time underwater specifically to foraging or transit.

A solution to this was demonstrated elegantly by a Japanese researcher, Yasuhiko Naito, who built a modified, very miniature analogue to the Kooyman *et al.* (1965) Weddell seal continuous dive recorder (Figure 2c). A diamond-tipped stylus scratched an ultra-thin line (<8 µm) on carbon-coated paper (<10 µm thick) as it wound from one spool to another, with time, with the stylus moving across the film width with depth, creating a trace that effectively mirrored the depth use over time for periods of days (the original system used for birds had a very slow scroll rate [0.024 mm/min] and so had deployment periods of up to 20 days) (Naito *et al.* 1990) (Figure 2c). This system was deployed extensively on a large number of penguins (e.g. Williams *et al.* 1992, Croxall *et al.* 1993, Watanuki *et al.* 1997) and cormorants (e.g. Croxall *et al.* 1991, Kato *et al.* 1992) (Figure 3) and did much to create the important concept of the 'dive profile', effectively a graphical representation of depth on the y-axis (usually with increasing depth descending) and time on the x-axis (Simeone & Wilson 2003, Halsey *et al.* 2007). The ability to record depth continuously had profound consequences for our understanding of seabird behaviour underwater. Not only did researchers realise that dives typically consisted of a descent, bottom and ascent phase (Naito *et al.* 1990) but that dives were variously grouped into types according to the shapes they made in the dive profile (cf. Leboeuf *et al.* 1988, Wilson 1991). In fact, this process continues today using much more sophisticated logging systems but ones which, as far as depth is concerned, are actually little better than the original Naito *et al.* (1990) unit. U-shaped, V-shaped and W-shaped dives have been documented (Croxall *et al.* 1993, Wilson *et al.* 1996) with the steepness of the vertical arms in the dive profiles indicating rates of change of depth, a measure of the putative 'interest' of birds in the different water strata. Transit can be reasonably differentiated from foraging in loggers that record depth continuously and there seems little doubt now that small undulations in the depth profile of the bottom phase are generally due to prey pursuit and/or capture (e.g. Charrassin *et al.* 2001, Simeone & Wilson 2003, Bost *et al.* 2007, Hanuise *et al.* 2010).

The continuously-recording depth gauge not only gave useful information about the way seabirds used depth, it also provided fundamental data about the periods spent at the surface between dives. The relationship between dive depth and dive duration had been examined by simple observation by Dewar as long ago as 1924 (Dewar 1924) as had, later, the relationship between dive duration and surface pause (e.g. Cooper 1986) but both study types were conducted from convenient vantage points which, by being primarily from the coast, implicated birds diving in shallow water, which was not necessarily the norm. The continuously recording depth gauge allows researchers to examine the durations of all dives, how they relate to depth, and how long it takes birds to recover from the dives before they dive again (cf.

Burger *et al.* 1993, Wanless *et al.* 1993). Such work can examine dive performance and surface pauses from a physiological standpoint, and may attempt to formalize processes affecting the rate of oxygen uptake and carbon dioxide removal (Croll *et al.* 1992, Burger *et al.* 1993), as well seeking explanations for the commonly observed accelerating surface duration with dive duration (Ydenberg & Forbes 1988, Ydenberg & Guillemette 1991, Wanless *et al.* 1993) by invoking anaerobic dives and the production of lactate (Boyd 1997, Kooyman & Ponganis 1997, 1998).

Finally, by their very nature, continuously recording depth gauges allow examination of depth use over a range of temporal scales. Thus, researchers have been able to examine how dives may vary over the course of foraging trips and how they relate to ecological variables, notably time of day (e.g. Williams *et al.* 1992).

The interface with electronics

The first fully electronic devices used on seabirds were crude but, nevertheless, heralded a fundamental change in the way information from seabirds was recorded. An ingenious development where the system could be constructed by biologists rather than electrical engineers involved a simple modification of quartz watches. David Cairns and colleagues prepared the watches so that seawater short-circuited the progression of the liquid crystal-displayed time before fitting them to guillemots (*Uria sp.*) in such a way that the time display could be seen (Cairns *et al.* 1987b). By careful observation of the birds at their colonies, noting the displayed time when the auks left the colony and returned, these workers could determine the time spent underwater during the foraging trip (Cairns *et al.* 1987a).

In a further development, Wilson and Achtleitner (1985) built an electronic counter into a propeller system which, when placed on an African Penguin, rotated with distance as the birds swam, giving a single value at the end of the foraging trip of how far the bird had travelled over the whole foraging trip.

With the development of electronics, single data points rapidly became superseded by the capacity of devices to store multiple data points, even if, in the first instance, they could not do so in a continuous temporal manner, as did Naito et al's (1990) depth gauge. The interface between old-style data recording and the more sophisticated solid-state devices which recorded parameters as a proper function of time was a multiple maximum depth recorder, first used by Kooyman *et al.* (1982). This unit simply recorded the number of dives that a bird exceeded a certain depth threshold. There were nominally 5 depth thresholds and these were set in an attempt to cover the whole depth range exploited by the species. Its first use was on penguins smaller than those from the genus *Aptenodytes,* chinstrap penguins *Pygoscelis antarctica* (Lishman & Croxall 1983), and although it served to demonstrate remarkable diving capacities in some of the smaller penguin species, it was rapidly eclipsed by more advanced systems that recorded data with a proper time base.

Solid-state technology

By the end of the 1980s, the electronics consumer industry had produced accessible, accurate, quartz-based clocks and memory chips, both elements that could be built into seabird loggers to record parameters as a proper function of time. This development also signalled the time when most biologists stopped inventing devices themselves, leaving the increasingly complicated task to electronic engineers. From that moment on, the capacities of seabird archival tags have followed well-defined trends, mirroring demands for enhanced sophistication by the consumer market in, for example, ever smaller mobile phones with increasing functionality, with the result that seabird tags have become smaller while delivering increasingly detailed information about bird activities at sea.

Changes in capacities in solid-state devices

The primary constraint limiting seabird archival tag performance is size and/or mass so the adoption of 'better' systems primarily reflects the availability of technology that performs a specific function while being minimally sized and requiring reduced power to run it while impacting the seabird carrier minimally. The inception and subsequent widespread use of surface-mounted technology (Prasad 1997) reduced the size of components used within circuits but minimal power use was, and still is, particularly important because the lower the power required, the smaller the battery needed. Even today, batteries in seabird loggers are a major part of the overall volume and mass. Nonetheless, solid-state systems in seabird loggers have shown a dramatic decrease in power consumption over the last two decades while continually increasing performance. For example, it takes energy to write data into a memory but seabird loggers with roughly comparable batteries used e.g. 16 kb memories in 1992 (Wilson *et al.* 1993) and today use 1 Gb (Wilson *et al.* 2008). Likewise, current drain was such that few solid-state seabird devices used in the 1990s could be deployed for more than a week or two (e.g. Kooyman *et al.* 1992, Jouventin *et al.* 1994) whereas today some of the smallest, such as some light geolocation tags weighing less than 5 g, can operate over years (Afanasyev 2004), and thus give insights into the movements of some species over the full annual cycle (e.g. Phillips *et al.* 2006, González-Solís *et al.* 2007, Guilford *et al.* 2009) (Figure 4). The power requirements of the various sensors have also decreased, which means that deployment durations can be increased and/or that the recording frequency can be increased. The first solid-state seabird loggers to record with a proper time base typically stored data once every 10 or 15 s (e.g. Wilson *et al.* 1993). This rather crude timescale as a measure of bird behaviour is, in many ways, analogous to protocols used by behavioural ecologists involving instantaneous scans of their study animals (e.g. Van Oort *et al.* 2004, O'Driscoll *et al.* 2008). The value of the data depends critically on the duration of the behaviour relative to the sample interval. Where behavioural sequences have durations similar to that of the scan interval, the study can only document the percentage time engaged in this activity or its incidence over the course of the day rather than giving details of its precise length (cf. Boyd 1993, Wilson *et al.* 1995b). More particularly, since sensors in seabird loggers actually return values of some parameter, such as depth, rather than a binary-type return, such as 'the bird is underwater', sampling interval is critical in defining the form of the behaviour. This is amply illustrated by the effect of the temporal resolution on the definition of the dive profile. Sampling at intervals of 10 s would give 19 points for the mean dive length of a king penguin *Aptenodytes patagonicus* of ca. 190 s (Moore *et al.* 1999) but only two for the little Penguin *Eudytpula minor* with mean dive duration of 21 s (Bethge *et al.* 1997) and miss most dives made by Peruvian boobies *Sula variegata* at around 2-3 s (Ludynia *et al.* 2010). So, not only would a sampling regime of 10 s be inadequate to define the descent, bottom and ascent phases of most dives made by little penguins but, where surface intervals are shorter than 10 s (cf. Bethge *et al.* 1997), this temporal resolution would not be enough to actually define even the length of most dives because adjacent dives would tend to run together (Wilson *et al.* 1995b).

The descriptions of dive durations and dive profiles are affected by more than just the temporal resolution, however. The resolution of the actual recorded information, something that has also improved over the years, critically affects both. It is notable that many authors detailing information on the dive durations and depths of penguins disregard any dives that do not exceed 3 m (e.g. Bost *et al.* 1994, Moore *et al.* 1999, Radl & Culik 1999, Falk *et al.* 2000, Deagle *et al.* 2008). This may be, in part, a perception that such 'surface' dives are irrelevant for actual feeding, something that is certainly not true for Adélie *Pygoscelis adeliae,* Chinstrap *Pygoscelis antarctica,* Gentoo *Pygoscelis papua* or African penguins (unpubl. data), though may be for the habitually deeper diving species such as the king and emperor penguins (e.g. Rodary *et al.* 2000, Zimmer *et al.* 2008b). However, in reality, it is more likely to be due to a combination of the ability of the recording system to resolve depth accurately and the drift that transducers display about values recorded when the bird is at the water surface. Assuming perfect transducer functioning, 8-bit resolution will only give a depth reading to the nearest *ca.* 2 m if the maximum recordable is 500 m. With increasing resolution, however, researchers should be able to give more credence to near-surface dives, which is important for proper understanding of seabird foraging ecology. Aside from potentially being used for foraging, near-surface dives are commonly used by penguins for commuting (Williams *et al.* 1992, Bengtson *et al.* 1993, Wilson 1995) and, as such, constitute an appreciable proportion of both their time and energy allocation while at sea. This latter is particularly pertinent because buoyancy effects due to the compression of air with depth make near surface swimming particularly energetically expensive (Wilson *et al.* 1992b).

Although depth use by seabirds is probably the most examined aspect of their marine ecology using logger technology, the increase in temporal and absolute resolution that has come with developments in the solid-state industry has enabled us to resolve a suite of ever smaller, and more fleeting changes in seabird behaviour which, far from being trivial, can be pivotal for understanding their ecology. For example, when initially proposed, the measurement of stomach temperature to determine when endothermic seabirds ingest ectothermic prey took place once every

8, 16 or 32 s (Wilson *et al.* 1992a), resulting in a very coarse time-based resolution of prey swallowing. Arguably, better temporal resolution would not have helped because of the delay in heat-state transfer between prey and device anyway (Wilson *et al.* 1995c), but higher sampling frequencies for temperature sensors enabled researchers to move the transducers from the stomach to the oesophagus and thus not only determine precisely when prey was ingested, but also be able to resolve much smaller prey items than the stomach system (Ancel *et al.* 1997, Ropert-Coudert *et al.* 2000a, Charrassin *et al.* 2001, Hanuise *et al.* 2010) (Figure 5). Our capacity to sample parameters with every greater accuracy and higher frequencies has led to a capacity to ask questions that were unthinkable just a decade or two ago and which, depending on recording frequency, relate to entirely different aspects of seabird biology. For example, low frequency measurement (e.g. *ca.* 1 Hz) of acceleration can give information on body posture and thus allude to behaviour (Yoda *et al.* 1999) allowing the time/behaviour budget of penguins to be resolved (Yoda *et al.* 1999, Yoda *et al.* 2001). Higher frequencies (e.g. *ca.* 30 Hz) allow resolution of faster events (Ropert-Coudert & Wilson 2004), such as foot-strokes in shags (Watanuki *et al.* 2005) and flipper beats in penguins, which has allowed authors to examine how seabirds invest effort in swimming with respect to depth and consequent changes in buoyancy (e.g. Sato *et al.* 2002a, Watanuki *et al.* 2003) or how cormorants modulate wing beat frequency as a function of meal size (Sato *et al.* 2008). Even higher recording frequencies of acceleration (*ca.* 300 Hz) show the complexity of processes such as the wing beat (e.g. Figure 6). Although, as yet, not examined critically, the higher frequency wave signals within the major heave signal that corresponds to the wing beat (Figure 6) are presumably due to particular muscular, bone/joint configurations and wing morphology (Pennycuick 1990, 1996) and may indicate food load, feather condition or flight conditions (Figure 6).

Sensor development

The advances in recording frequency, sensor resolution and power consumption would have had little impact on our understanding of seabird ecology if they had not been accompanied by a substantial development of various miniature, low-power sensors. Such transducers are powerful, and have enabled recording of particular data that have led to two primary lines of research philosophy. One approach uses the specific function of the transducer in its own right, while the other uses it as a proxy for something else. For example, temperature transducers have disclosed fascinating information on temperature *per se*: Measurement of seabird internal temperature (Woakes *et al.* 1995) has, *inter alia*, stimulated debate about, for example, deep body temperature cooling to enhance diving capacity (Handrich *et al.* 1997) and measurements showing the overall flexibility of seabird body temperatures have led to propositions that the costs of homeothermy may be offset by storing muscle-generated heat (Wilson & Grémillet 1996), while measurement of external temperature (Koudil *et al.* 2000, Watanuki *et al.* 2001) has enabled researchers to define the environment in which birds operate and the metabolic consequences of this (Croll & McLaren 1993, Handrich *et al.* 1997, Enstipp *et al.* 2006, Niizuma *et al.* 2007). The proxy approach has, however, used changes that occur in environmental temperature to infer seabird behaviour, such as when birds are on the water or flying (e.g. Tremblay *et al.* 2003). In a further development, this has been combined with bird geographic position (often derived using transmission technology) to map the temperature properties of seabird foraging areas in 2- (Weimerskirch *et al.* 1995) or 3-dimensions (e.g. Charrassin *et al.* 2004).

Sensors that respond to light are an excellent example of the value of measuring a parameter as a proxy for some other process. Although the measurement of environmental light has been useful to determine burrow use in hole-nesting species (Wilson *et al.* 1995a) and to define the conditions of ambient light under which visual predators, such as penguins can operate (Wilson *et al.* 1993, Zimmer *et al.* 2008a), its most widespread and revealing use has been in helping determine seabird position by allowing determination of day length and local mid-day, as a function of Julian day, giving latitude and longitude, respectively (Wilson *et al.* 1992b, Hill 1994). This Global Location Sensing or Geolocation technique (*op cit.*) has spawned a large number of studies that have revealed the extraordinary distances that some species may travel during the annual cycle (e.g. Shaffer *et al.* 2006, Egevang *et al.* 2010). Latterly, in a recent example of a double proxy, Green *et al.* (2009b) even reconstructed the routes of macaroni penguins *Eudyptes chrysolophus* using internal loggers which could not record light but could document a proxy for it. Here, Green *et al.* (2009b) recorded dive depth over time of day because macaroni penguins only swim as deeply as they can see, so the changes in light at the water surface, which were themselves a proxy for bird position, were reflected in the changing depth use of the foraging birds.

The work by Green *et al.* (2009b) was based on implanted devices. This has been, and likely always will be, the province of a select few. Today, researchers, and particularly physiologists, use a variety of implanted devices to measure parameters such as the concentration of lactate in the blood as well as the more conventional body temperature (Ponganis 2007, Ponganis *et al.* 2010). Essentially pioneered for seabirds by Pat Butler (Butler & Woakes 1979 and references therein), the implantation approach, which has had a particular strength in using sensors to measure the electrical activity associated with heartbeats (generally referred as 'heart rate') without having to deal with signal noise coming from skeletal muscles (Kuroki et al 1999), has necessitated a high degree of sophistication in the electronics. Indeed, heartbeat rate researchers were already using complex electronics to transmit heartbeat rate from seabirds in 1982 (Butler & Woakes 1982) and to store data in 1995 (Woakes *et al.* 1995), a time when many researchers using external tags were still using mechanical systems. Although useful as a direct measure, recordings of heartbeat rates in diving seabirds were important in fuelling discussions about the general applicability of brady- and tachycardia (Butler & Jones 1997, Kooyman & Ponganis 1998) and the more general value of heartbeat rate as a proxy for metabolic rate (Butler 1993). The general finding that heartbeat rate increases with increasing metabolic rate (Bevan & Butler 1992, Bevan *et al.* 1994, Green *et al.* 2001), coupled with the fact that implanted loggers can be kept in place for months (Butler *et al.* 1998, Guillemette *et al.* 2002, Green *et al.* 2004), has meant that researchers have been able to allude to the metabolic costs of specific activities such as flight (e.g. Weimerskirch *et al.* 2000) and diving (e.g. Froget *et al.* 2004) as well as the more generic costs of incubation (e.g. Weimerskirch *et al.* 2002), brooding (e.g. Green *et al.* 2002) and chick-rearing etc. (e.g. Bevan *et al.* 2002). Indeed, this technique has even recently been used to derive food consumption by macaroni penguins throughout the annual cycle (Green *et al.* 2009a), something that is currently impossible by any other means.

Over the last few years metabolic rate, at least that associated with movement, has become accessible using another proxy, and one that can be derived using tri-axial acceleration transducers in externally-attached devices (Wilson *et al.* 2006). Here, body movement is quantified by the dynamic acceleration which correlates linearly with rate of oxygen consumption (Gleiss *et al.* 2011 and refs therein), and this relationship seems to hold, in cormorants at least, irrespective of whether birds are swimming, diving or walking (Gómez-Laich *et al.* 2011). An advantage of accelerometry over heartbeat rate as a proxy for metabolic rate lies in the short time periods over which the energy expenditure can be determined so that, for example, not only can the cost of the descent, bottom phase and ascent of dives be estimated, in penguins for example, but so too can the cost of pursuit of individual prey (Wilson *et al.* 2010) which will inevitably lead to standard behavioural ecology cost/benefit analyses with quantification approaching, or exceeding, those used in experimental manipulation of terrestrial birds (Shepard *et al.* 2009). Importantly, since accelerometer signals also code for animal behaviour (Yoda *et al.* 2001, Watanabe *et al.* 2005, Shepard *et al.* 2008b, Sakamoto *et al.* 2009a), the same transducers can provide information on the timing, incidence, extent, intensity and energetic cost of behaviours. Determination of the activity-specific metabolic rate of free-living seabirds has long been problematic (cf. Nagy *et al.* 1984, Birtfriesen *et al.* 1989, Furness & Bryant 1996) but this is changing due to tri-axial accelerometer loggers. Combination of these with other transducers, such as depth (e.g. Shepard *et al.* 2008b) or altitude (e.g. Weimerskirch *et al.* 2005), should help us put the behaviour into an ecological context so that modellers, given the suite of behaviours that seabirds have at their disposal and their costs, can examine the consequences of adopting particular strategies.

Considered combination of sensors in seabird archival tags can yield more than the simple sum of each of the sensors. An example of this is in dead-reckoning, or vectorial calculation of animal movements (Wilson & Wilson 1988, Wilson *et al.* 1991b), made possible by geomagnetic sensors which allow derivation of bird heading during travel (Shiomi *et al.* 2008). Using this together with estimates of speed (e.g. Ropert Coudert *et al.* 2002, Ropert-Coudert *et al.* 2006, Shepard *et al.* 2008a) the movements of seabirds can be determined with very fine (relative; sub-metre (Wilson *et al.* 2002b) resolution (e.g. Quillfeldt *et al.* 2011), even when they are underwater (Wilson 2002, Shiomi *et al.* 2008, 2010) where the more commonly used GPS systems (which rely on radio-signals from satellites) cannot function. The seamless nature of dead-reckoned tracks with their high temporal resolution (Wilson *et al.* 2007) means that they have particular potential for determining behaviour from the precise form of the track. Currently, the most sophisticated behavioural analyses associated with seabird tracks are based around using some metric, such as first passage time (Johnson *et al.* 1992), to examine Area Restricted Search (ARS) (Fauchald & Tveraa 2003, Pinaud & Weimerskirch 2005, Suryan *et al.* 2006). Although the concept of ARS is clearly fundamental to the way some seabirds forage, the spatial resolution of tracks and the ability to determine bird behaviour are critical in identifying what is genuinely ARS and what is possibly just a change in travel mode (e.g. flight to paddling) resulting in a decrease in translocation rate. This can result either from a change in search strategy or just be a consequence of the bird resting at the sea surface. Fine scale dead-reckoning tracks coupled with transducers that code for behaviour, such as accelerometers, will do away with this uncertainty and allow us to examine ARS as a function of travel mode and, therefore, scale, in an unbiased manner.

Beyond derivation of bird heading during travel, sensors for determining magnetic field strength have also been used to create proxies for a number of important activities by equipping birds with the sensors on a body part adjacent to another that moves with respect to it, on which a minute magnet is placed. The position of the moving body part (e.g. the lower mandible in the beak, the wing, the cloaca) with respect to the immobile part (e.g. the upper mandible or body) is given by the magnetic field strength perceived by the sensor (Figure 7). High sampling rates (typically > 10 Hz) allow such systems to determine, for example, every single breath that seabirds take (Wilson *et al.* 2003), when they defaecate (Wilson *et al.* 2004) and when and how much birds consume (Wilson *et al.* 2002a). This approach has led to estimates of consumption that far exceed that projected, at least for the Magellanic penguin *Spheniscus magellanicus* (Wilson *et al.* 2007). It has also strengthened the idea that some diving seabirds anticipate their proximate dive depth and inhale accordingly, so as to have near neutral buoyancy at operating depths (Sato *et al.* 2002b, Wilson & Zimmer 2004). In addition, this technology has indicated that some penguins load their bodies with oxygen according to the perceived likelihood of prey consumption based on the number of prey they have caught in the previous dive (Wilson 2003). As powerful as this approach may appear to be, its substantial weakness is currently the link between the sensor and the logger, which takes the form of a cable which can be easily broken (Bost *et al.* 2007, Liebsch *et al.* 2007, Hanuise *et al.* 2010). This will change when loggers become small enough to be fitted to the body part that is currently just the site for the sensor.

Finally, following the pioneering work of Marshall (1998), who used cameras on pinnipeds, cetaceans and turtles, some seabird researchers have been using miniature cameras on free-living birds to give a visual picture of the environment around the animals (e.g. Takashi et al 2004, Watanuki et al 2008, Sakamoto et al 2009) (Figure 8). Although currently limited to taking pictures relatively infrequently (e.g. once every 15 s), and therefore subject to analogous sampling frequency problems of the early loggers, this approach is fundamentally different from any other logger system because it allows researchers to look outside the bird. Previously, the closest that workers have come to examining the environment has been in bird-borne transducers that sample directly at the bird/environment interface, with all the associated problems (Wilson *et al.* 2002b). The range of camera loggers is dictated only by the opacity of the medium through which the birds are moving so they have been used underwater to assess which substrate types shags *Phalacrocorax aristotelis* forage over (Watanuki *et al.* 2008) and to allude to prey-predator interactions(Takahashi *et al.* 2008) as well as to look at intra-specific (Takahashi *et al.* 2004) and inter-specific foraging associations (Sakamoto *et al.* 2009b) and even to assess interactions with shipping (Grémillet *et al.* 2010). A disadvantage of this approach lies in the non-standardization of the visual field, which varies according to the transparency of the medium (particularly in water), but also according to how much of the visual field is taken up by portions of the bird (particularly the head). The restrictions on the visual field of the camera means that non-documentation of an event, such as the presence of e.g. a vessel (Grémillet *et al.* 2010) does not mean that one is not there although documentation of it is obvious proof that it is. This will require a new conceptual approach to be most powerful although careful use of fish-eye lenses may mitigate the problem to some extent. A final drawback of camera systems is that many man-hours are currently required to examine the data, the vast majority of data stored being worthless. Sophisticated analytical software should make this task more manageable in the future.

Software development

The problems of data analysis from camera loggers are not unique to camera systems. The large amounts of data gathered by multiple-channel loggers are increasingly necessitating special software to deal with them to an extent that it even necessitates on-board processing. On-board data treatment is common for GPS tags to perform real-time calculation of the animal location (e.g. Yasuda & Arai 2005, Handcock *et al.* 2009) and appears essential when using animal-borne video systems (e.g. Moll *et al.* 2009). This is in comparison to post-processing when the data have been extracted from the device which, from data analysis to visualisation, usually necessitates the use of different specific software. Standard spreadsheets such as Excel (*http://office.microsoft.com/en-us/excel/*), with its maximum number of graphable points currently being 32,000, are unhelpful given that the basis for most seabird data recording systems is graphical. OriginLab (*http://www.originlab.com/*) and IGOR-Pro (*http://www.wavemetrics.com/*) are vastly superior programs for this but, given the relatively complex computations necessary to derive, for example, a dead-reckoned track from geomagnetic, pressure and speed data (Shiomi *et al.* 2008), the seabird community really needs bespoke software. Some tag manufacturers such as Wildlife Computers (*www.wildlifecomputers.com*) provide special software for e.g. analysis of depth traces but the increasing number of different applications such as behavioural or energetic analysis from accelerometers makes this an ever-expanding task. The R-environment (*www.r-project.org*) and Matlab (*www.mathworks.com*) are applicable, and allow people to share analytical protocols, but both will have to deal with many millions of data and may simply not be fast enough. The approach taken by Sakamoto *et al.* (2009) may set a trend in providing freeware, in this case Ethographer which works in IGOR Pro, to help determine behaviours (*http://sites.google.com/site/ethographer/download*) for the seabird community. We may hope so. The future will determine whether the faster processors in computers will allow even programs like IGOR Pro to function rapidly enough with the increasingly larger datasets or whether we will have to revert to bespoke software written in a highly efficient computer language such as C++ (Grundy *et al.* 2009). Finally, complex data require complex analysis, but that this can be greatly facilitated by software that visualizes the data in a revealing manner. Spherical scatter plots represent such an approach, and are the basis behind a program called CRYSTAL BALL (Grundy *et al.* 2009), which translates the three acceleration axes into a graph that can display 6 or 7 dimensions all in one moveable image without being over-facing (Figure 9). Certainly, the future will need more of this.

The future

Smaller size, bigger capacity

The future of archival tags in seabird research is set to follow the trends already set. Devices will become ever smaller and ever more powerful with respect to what they can record so that, ultimately, even the smallest seabirds such as storm petrels (Hydrobatidae) can be equipped with units that will detail the minutia of their lives. Critically, reduction in size and mass will also help reduce deleterious device effects (cf. Bowlin *et al.* 2010, Vandenabeele *et al.* 2011). Some of the analytical work will be processed on-board but much will be left to a suite of, hopefully coherent, programs for the community.

The future will see increasing detail into the lives of seabirds coupled with a more holistic approach, as researchers realise that it is possible to determine bird activities precisely, as well as their costs (both in terms of energetics and time – cf. Shepard *et al.* 2009 - and their consequences). Understanding how the environment, biotic and abiotic, affects seabirds as well as modelling out the costs and benefits of different strategies available to birds, must be one of the primary goals in a changing world where prediction is becoming paramount. We have never had such extraordinary capacity for acquiring difficult knowledge about the lives of enigmatic seabirds. Let us hope that our ability to use the data is on a par with the technology that lets us acquire it.

A sober moment – the flipside of gadgets

The euphoria of discovery using animal-attached tags must be tempered with the certainty that seabirds with attached devices do not behave in a manner identical to unequipped conspecifics (Paredes *et al.* 2005, Ropert-Coudert *et al.* 2007, Beaulieu *et al.* 2010, Saraux *et al.* 2011). Even discounting ethics, which we should not (Hawkins 2004), the value of data acquired by animal-attached devices depends critically on either the data being representative or at least allowing us to determine what is representative. In our desire for knowledge, and demonstration of exciting discovery, which may enhance our own publication record, we will have to walk the line between deployment of the unacceptably large (e.g. Wilson *et al.* 1986, Watanuki *et al.* 1992, Culik *et al.* 1994, Whidden *et al.* 2007) and the value of the data acquired, from a scientific, ethical and conservational perspective. Our teetering along this line in the past has brought us to where we are now, with a better understanding of seabirds at sea than ever before. We should not let the rush of advances cloud our judgement for the future either.

Acknowledgements

This work was partially funded by the RSPCA, the California Department of Fish and Game's Oil Spill Response Trust Fund through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis and the Rolex Awards for Enterprise. We are grateful to Steve Votier and Samantha Patrick from Plymouth University (UK) for their help acquiring data from gannets and for having shared some of their pictures. We are grateful to Yan Ropert-Coudert, Emily Shepard and Yasuhiko Naito for providing us with material for figures.

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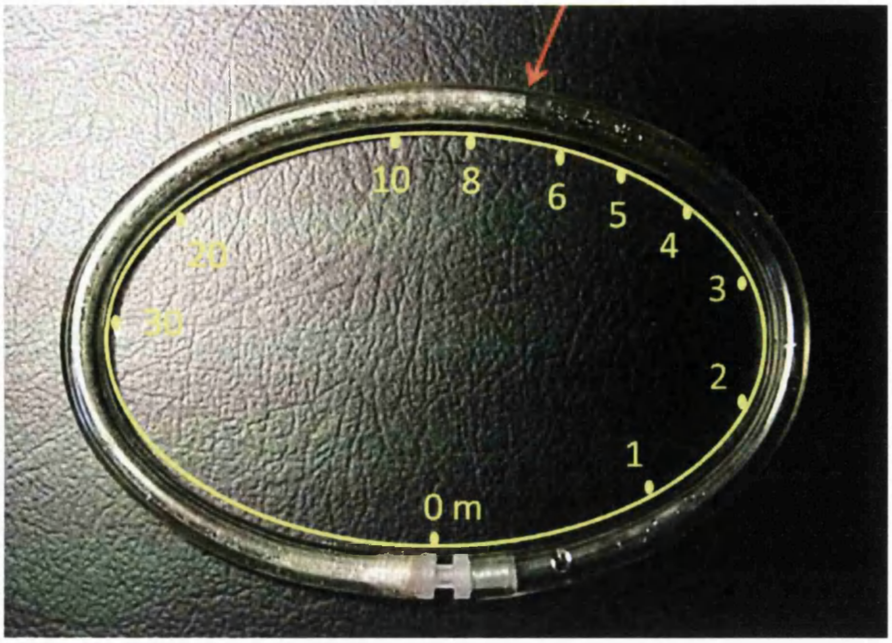

Figure 1. Capillary depth gauge with water soluble-dye showing the maximum dive depth of 7 m (arrow) reached by a crowned cormorant (*Phalacrocorax coronatus*).

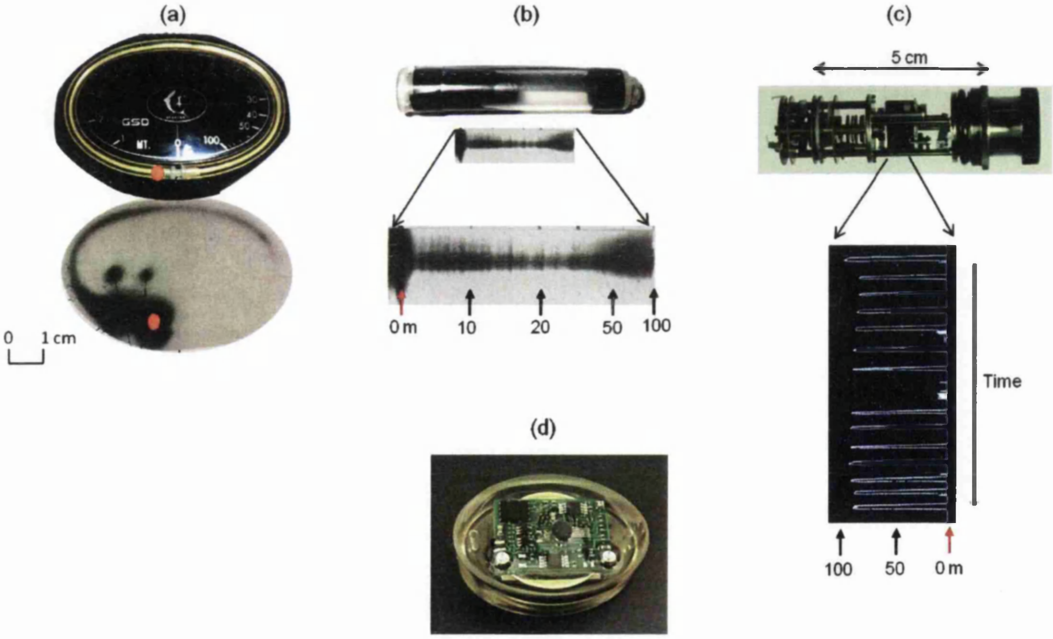

Figure 2. Four different generations of time-depth recorders used on seabirds; (a) a capillary depth gauge modified so that a radioactive bead exposes film (Wilson & Bain 1984) (b) a modified syringe fitted with light emitting diode to expose film (Wilson *et al.* 1989) (c) a compressible bellows system attached to stylus scribing on a rotating drum (Naito *et al.* 1990) and (d) a modern, solid-state depth gauge (Cefas G6, e.g. Elliott 2011). The red circles and arrow indicate 0 m depth.

Figure 3. Imperial shag *Phalacrocorax atriceps* wearing one of Yasuhiko Naito's early TDRs (see Figure 2c).

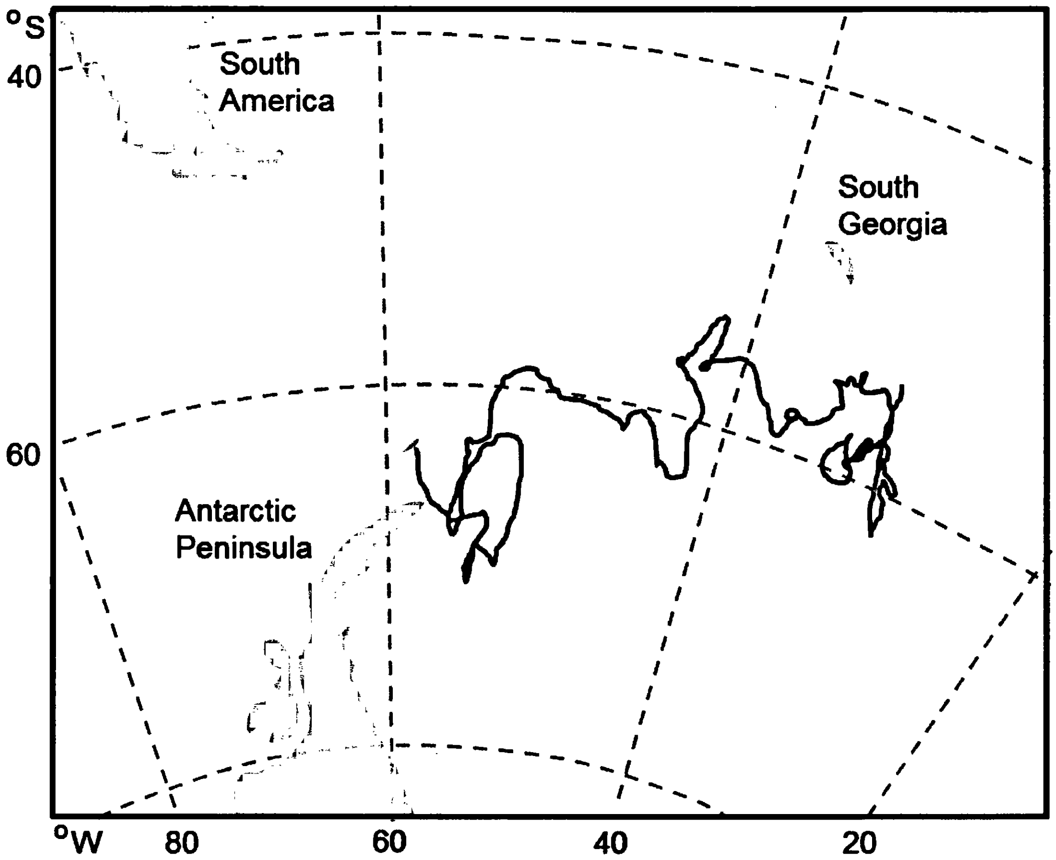

Figure 4. Post-breeding and over-winter movements of a chinstrap penguin *Pygoscelis antarctica* from King George Island (located at the most westerly part of the track) as determined using geolocation. This was the first multi-month (5) track obtained for a seabird using this technology. For more details see Wilson *et al.* (1998).

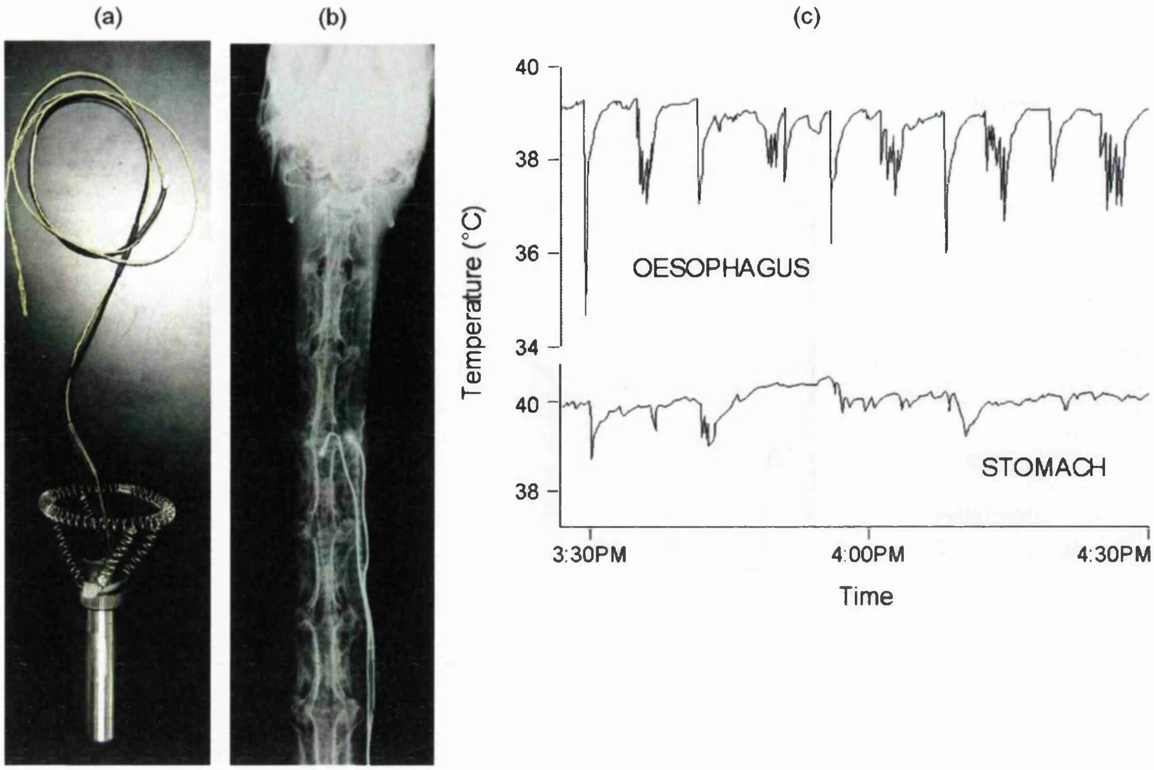

Figure 5. (a) Stomach temperature sensor housed within a titanium cylinder (with retaining spring to hinder regurgitation) combined with oesophageal temperature sensor, at the end of the wound cable. (b) shows an X-ray of the location of the oesophageal sensor in a king penguin (cf. Hanuise *et al.* 2010). (c) Prey ingestion indicated by drops in the temperature profile recorded by oesopageal and stomach thermistors (from Ropert-Coudert *et al.* 2001).

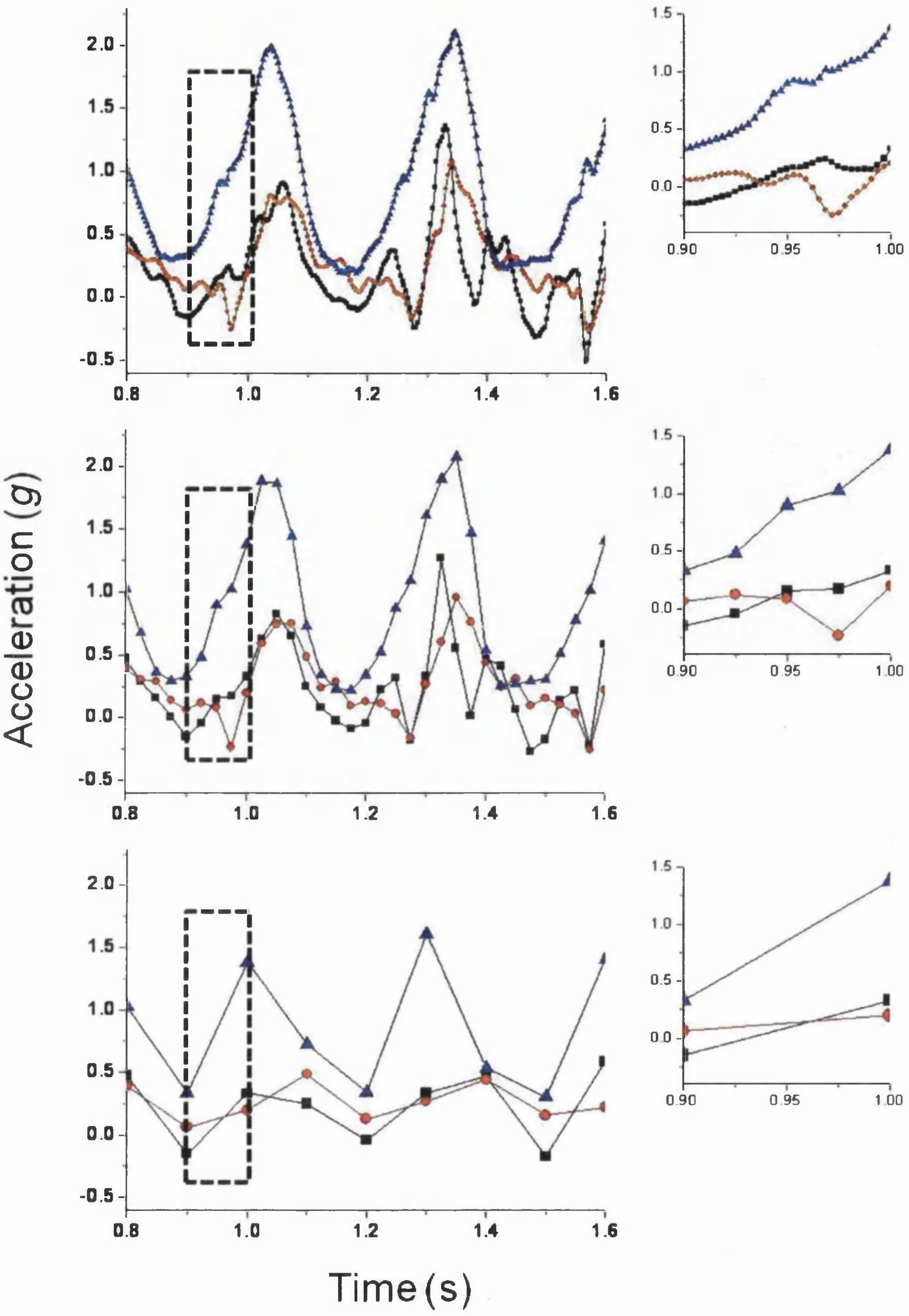

Figure 6. Acceleration signals (blue triangles - heave, red circles – surge, black squares – sway) recorded by a logger on a northern gannet (*Morus bassanus)* mounted dorsally showing two wing beats resolved at 320 Hz (top figure) and then subject to thinning so that they can be presented at apparent recording rates of 40 Hz (middle figure) and 10 Hz (bottom figure). The inserts to the right show a small (comparable) section from the three recording scenarios (dashed boxes) to illustrate how smaller amplitude, higher frequency wave patterns (perhaps due to the precise mechanisms of musculo-skeletal functioning during the wing beat cycle) are lost with decreasing recording frequency.

Figure 7. Imperial shag (*Phalacrocorax atriceps*) fitted with an intermandibular magnetic sensor unit that records beak openings.

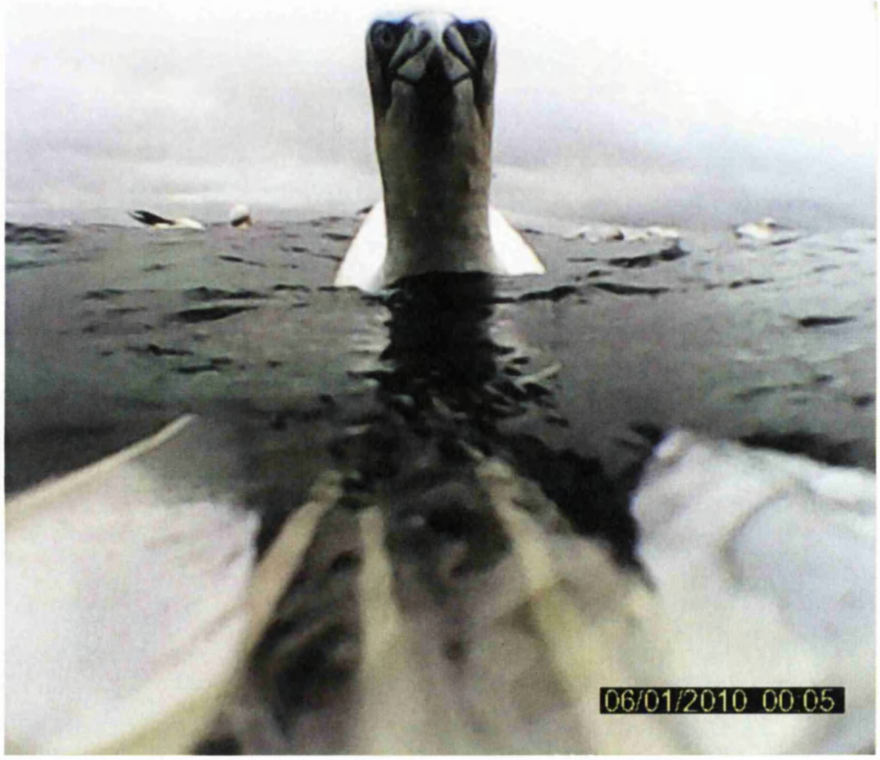

Figure 8. Pictures taken with a video camera place on the tail of a northern gannet (*Morus bassanus*) when sitting on the water with conspecifics around.

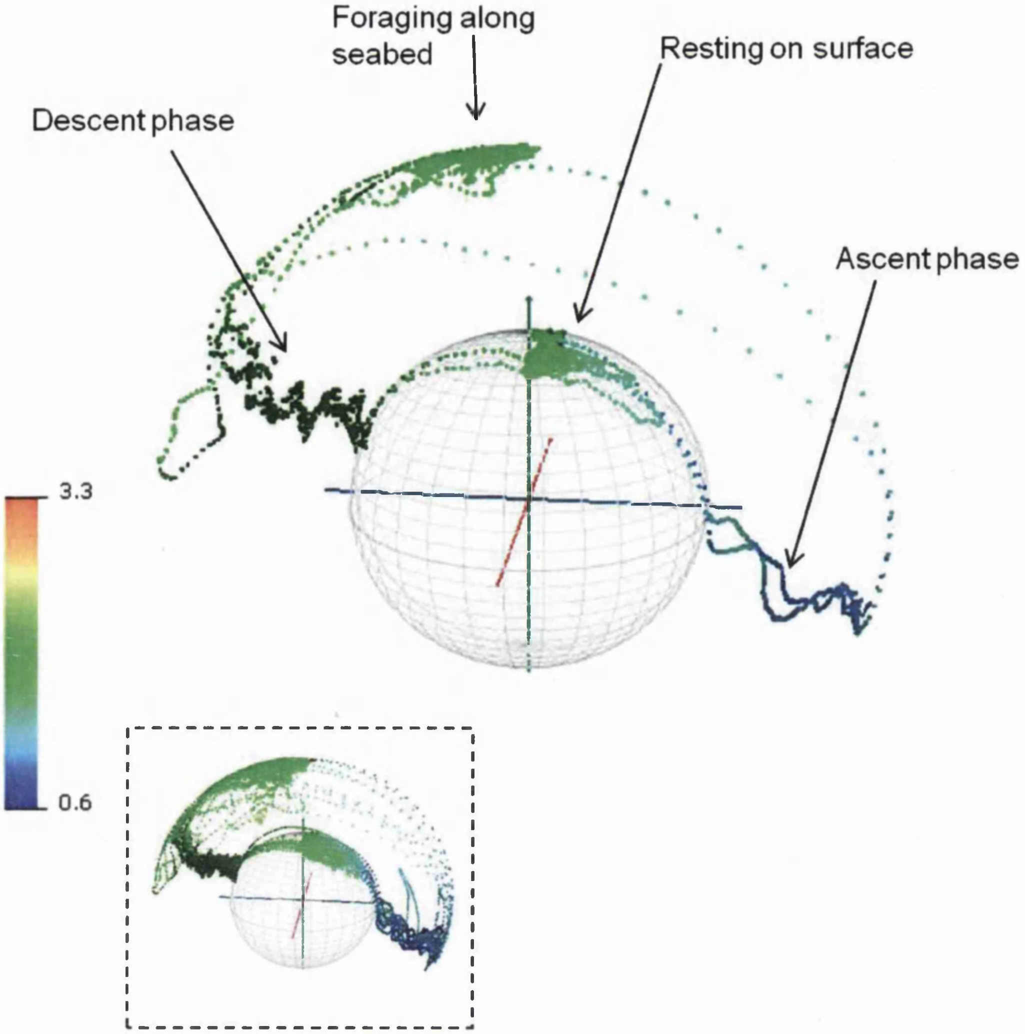

Figure 9. Screenshot of an output of a program (CRYSTAL BALL; (Grundy *et al.* 2009)) to visualize changes in behaviour adopted by an imperial cormorant *Phalacrocorax atriceps* during diving (the main figure shows two dives, the inset multiple dives). The position of the dots (one dot = one recording interval) on the outside of the globe indicates animal body angle (the axis indicated by the blue line bisecting the globe is the pitch, that by the red axis indicating the roll) so that points on the left hand side of the globe indicate head-down posture (e.g. descent – the green umbilical chord), those on the right hand side indicate 'head-up' posture (e.g. ascent – the blue umbilical chord), while those in the middle (concentrated around the 'North pole') indicate body angle deviating little from level. A measure of dive depth is given by the distance of the points into space, away from the globe (all points on the globe surface are from behaviours that occur when the bird is at the water surface). A measure of how hard the bird was working via dynamic body acceleration (cf. Wilson *et al.* 2006) is given by the colour. (red = most intense, blue = least intense).

Chapter 2:

Tags on seabirds; how seriously are instrument-induced behaviours considered?

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SPV reviewed the literature, analysed the gathered data and wrote the manuscript with contributions from RPW and AG

Animal Welfare (2011) 20, 559-571

Abstract

Equipping birds with tags (defined as any item externally attached to birds, including transmitters, loggers and flipper bands, or implanted devices such as transponders) gives particular insights into animal biology although researchers may not give systematic consideration of tag impact. We examined 357 papers published between 1986 and 2009 where tags (excluding rings attached to birds' legs) were used on seabirds, to examine the extent to which researchers considered deleterious effects. Fifty-one (14.3%) papers considered instrumentation effects in their abstract, 31 (60.8%) of which showed statistically significant effects on seabird biology. Of the total data set, 302 (84.6%) articles were classified as "indirect" (with no stated aim to assess the influence of the equipment used) and although most of these (237; 76.5%) did discuss instrumentation effects, although this accounted for less than a mean of 2% of the total length of the text. Despite a clear increase in the number of papers based on tagging technology for seabird study over the last 24 years, there has been no corresponding increase in documentation of the effects of devices on their bearers. We suggest mechanisms by which this issue might be addressed.

Keywords: animal welfare, device effects, seabirds, tags, tracking

Introduction

Seabirds play an important role in marine ecosystems by consuming significant quantities of prey (e.g. Duffy & Schneider 1994, Brooke 2004), thereby influencing the structure and the function of aquatic communities (Croxall 1987, Croll & Tershy 1998). Seabirds appear particularly sensitive to biological and physical changes in their environment (Cairns 1987, Montevecchi 1993), including habitat quality and degradation (Burger & Gochfeld 2004, Newman *et al.* 2007), and, as a result, have been used as indicators of ocean ecosystem status and change (Furness & Camphuysen 1997, Tasker & Furness 2003, Piatt *et al.* 2007). Our understanding of the role of seabirds in marine ecosystems and how they respond to change has been enhanced by tagging technology that has provided important insights into how they use their environment (Croxall 1987, Hunt & Schneider 1987, Monaghan 1996). However, using such tags raises ethical concerns (Wilson & McMahon 2006), including the extent to which the behaviour, physiology, or energetics of seabirds might be compromised by tags (Murray 2000, Hawkins 2004, Wilson & McMahon 2006).

Marine animals, particularly seabirds, are frequently used taxa in tracking and logging studies (Ropert-Coudert *et al.* 2009), primarily because they often operate far from land where direct observation is not easy. However, inability to observe animals carrying devices means that potential deleterious effects of devices may, therefore, not be obvious. Among the major potential effects that external units may cause on animals are behavioural disturbance (cf. Ropert-Coudert & Wilson 2004 for review), physical injuries (e.g. Buehler *et al.* 1995, Hatfield & Rathbun 1996, Troëng *et al.* 2006, Zschille *et al.* 2008, Goodman *et al.* 2009), and compromised energetics (e.g. Schmid *et al.* 1995, Godfrey & Bryant 2003, Wilson *et al.* 2004). Although such perturbations can be observed in both terrestrial and marine animals, external tags may impact aquatic species more, both because water conducts heat better than air so that compromised plumage insulation will have greater potential for heat loss (e.g. Hartung 1967, Jenssen 1994) and because species that move at any given speed are subject to higher drag underwater, due to the higher viscosity and density of the medium compared to air, which leads to projected higher rates of energy expenditure as a result of having to push external devices through the water (cf. Wilson *et al.* 1986, Culik & Wilson 1991).

This study focuses on seabirds and the potential deleterious effects of external units which are defined here as any effect observed on the foraging behaviour, the physiological condition, the time budget, the breeding success, the energetics or the survival rate of seabird individuals (Table 1). Cursory examination of the literature indicates that scientists vary in the emphasis given to the potential deleterious effects of tags, despite the fact that the validity of any work depends on animals behaving normally. Thus, we reviewed the literature systematically to assess the extent to which the effects of animal-attached devices and their attachment or implantation procedures have been reported in seabird studies hoping, through this, to define some perceptions of the scientific community to this issue.

Methods

Literature search

Papers published in peer-reviewed journals were searched using the web-based search engine "Web of Knowledge" (*www.isiknowledge.com*) and using the following key words: seabirds, devices, loggers, recorders, transmitters, instruments, PTTs, TDRs, GPS, transponders, harness, attachment, equipment, telemetry, radio, satellite, tracking, remote-sensing, tag, monitor, effect, impact, and influence. We included bird flipper bands but not leg rings in our search and did not consider their potential effects (cf. Calvo & Furness 1992, Nietfeld *et al.* 1994). Key words were used on their own as well as in various combinations such as 'satellite, tracking and seabirds.' Finally, we gathered papers that were cited in those found during our literature search. If neither the abstract nor a full-text copy of cited papers was available, the search engine Google scholar (*http://scholar.google.co.uk/*) was used in an attempt to locate missing papers. The oldest paper considered was published in 1986, the limit of the full-text catalogue we had available to us.

Paper classification

Based on the information provided in abstracts, papers were classified as either: (1) 'direct papers' that included assessment of the effects of equipment (or attachment methods) as a study objective, or (2) 'indirect papers' that focused primarily on some aspect of seabird biology (such as foraging behaviour, breeding success, or diving performance) using tagging technology, and where assessing of the possible effects of tags was not an explicit objective. For both categories of papers, we classified the results, irrespective of statistical significance and whether the impact of tags was considered positive or negative, into seven categories based on the type of deleterious effect: (i) foraging behaviour, (ii) diving behaviour, (iii) physiology, (iv) time budget, (v) breeding success, (vi) energetics, and (vii) mortality (Table 1). For each category, we noted whether tag effects were documented in the abstract and, if so, whether they were statistically significant.

Using the full-text version of indirect papers, we estimated the amount of text devoted to the effects of tags by measuring the relevant area of the paper and expressing it as a percentage of the total area of the text of the paper, excluding the literature cited section. We refer to this as the 'Instrumentation Effect Index' (IEI). All measurements were taken from PDF versions of papers in single-page view. We understand that this measure is imperfect because, for example, some studies may not have had suitable control birds to compare tagged and non-tagged individuals and that there is substantial variation in tag size relative to bird size that may affect the potential for perceived deleterious effects. However, we believe that IEI does provide a useful, if basic, indication which allows for standardized assessment of a large number of papers. In addition, we evaluated the content of the section on the effects of tags for each indirect paper. More precisely, paragraphs devoted to the effects of tags were, based on the information provided, classified in one or more of the five categories to assess the degree of documentation, ranging from category A (papers that cited tagging effects mentioned in other studies) to category E (where authors assessed the impact of the tags; Table 2). For papers classified into more than one category, the higher-level category (tending towards E) was used for calculation of the percentage of papers in each category (e.g. a paper classified into categories A and D was only classified in category D).

Statistical analysis

All the papers considered in the analysis were derived from single studies (i.e. no study was replicated in separate publications) so that each could be counted as an independent item. To examine possible changes in the documentation of tag effects over time, the number of direct and indirect papers was determined for each year and the correlation between the sum of direct and indirect papers and the years was tested using Spearman's rank statistic (r_s). In addition, the proportion of direct papers relatively to the total number of papers examined was calculated and the correlation with year was assessed. Lastly, Spearman's rank statistics were also used to examine the correlation between IEI and year using the raw data (i.e. the IEI calculated for each paper across years) and between the IEI mean for all papers in a given year and year.

We used chi-square tests (χ^2) to assess significant differences in the number of indirect papers between the following classes of IEI: 0%, $0 > \% \geq 1$, $1 > \% \geq 2$, $2 > \% \geq 3$, $3 > \% \geq 4$, $4 > \% \geq 5$, $5 > \% \geq 6$, $6 > \% \geq 7$, and $7 > \% \geq 8$ (to get a value above 5 and fulfill chi-square test obligations, classes $6 > \% \geq 7$ and $7 > \% \geq 8$ were combined). Change over time was analyzed by examining the correlation between the number of indirect papers and year. Where indirect papers were classified into categories according to the nature of information reported in the section devoted to the effects of the equipment (Table 2), these categories were compared using chi-square tests. Correlations between the IEI and the categories were assessed using Spearman's rank statistics. Mean IEI-values were calculated for the categories and compared across the categories using the Kruskal-Wallis test (H). Finally, the correlation between the categories of indirect papers and the year of publication was tested using Spearman's rank correlation. All the tests were performed using Minitab (MINITAB® Release 14.1 version 2003). A significance threshold of $P < 0.05$ was used for all analyses.

Results

We identified 357 studies involving the use of tags, ranging from transmitters to transponders (including flipper bands but not leg rings), on seabirds published in 65 peer-reviewed journals. Of these, 51 (14.3%) included information about instrumentation effects in the abstract. Of those 51 papers, 38 (74.5%) tested the effects of tags or attachment systems and were designated as direct papers (Table 3); the other 13 papers were indirect studies (i.e. studies involving the use of tags where the primary objective was not to assess tag effects).

Of the 51 articles analyzed from their abstracts, 30 (58.8%) focused on testing the effects of instrumentation on breeding success and 25 (49%) on foraging behaviour. Instrument effects on diving behaviour, physical condition, time budgets and energetics were assessed in about 20% of these papers (Figure 1A). Of these studies where investigators examined the effects of instrumentation on different aspects of the seabird biology, between 33.3% and 80% evoked statistically significant changes (Figure 1B). Significant effects were found for each category of seabirds' biology analyzed in this review, with 31 of 51 studies (60.8%) reporting significant effects in at least one category.

Of the 357 papers examined, only 42 (11.8%) were direct papers focused on the effects of tags or attachment systems used on seabirds. A significant change over time ($N = 23$, $r_s = 0.68$, $P < 0.001$) was found in terms of total number of papers collected (i.e. sum of direct and indirect papers) with a steadily increasing number of papers across the years (Figure 2). Given that result, the variation in the proportion of direct papers across years was evaluated and a significant decrease was obtained ($N = 23$, $r_s = -0.45$, $P < 0.001$; Figure 3). Considering the IEI of the indirect papers, there was no significant correlation with the date of publication irrespective of whether the data used were raw ($N = 309$, $r_s = -0.08$, $P = 0.18$,) or taken as a mean per year, ($N = 18$, $r_s = -0.15$, $P = 0.55$). The maximum IEI obtained was 8% for a paper published in 2004 (that of Bost *et al.* 2004). The average IEI, using all 310 indirect papers, was 1.2 % (sd = 4.4%, on arcsine transformed data).

Of 310 indirect studies analyzed from the full-text version (5 of the 315 indirect articles were not available in full-text version), most (207; 66.8%) had an IEI less than, or equal to, 1% (Figure 4). Only 6.8% had an IEI >4% while approximately 40% had no section dedicated to the effects of instrumentation. Most indirect papers collected were classified into categories C, D and E with most (70; 36.3%) in category E (Figure 5). There was a correlation between the qualitative categories (Table 2) and the corresponding IEI of the indirect papers ($N = 193$, $r_s = 0.32$, $P < 0.001$) with the IEI increasing across the categories from A to E (Figure 6). The mean IEI was significantly different between the categories ($N = 193$, $H = 22.65$, $df = 4$, $P < 0.001$; Figure 7). In each case, the higher mean IEI was apparent in the categories with the greatest degree of documentation of instrument effects. No correlation was found between the categories in which the indirect papers were classified and the year of publication of these papers (N = 193, $r_s = -0.7$, $P = 0.30$).

Discussion

Our study is an attempt to examine how scientists perceive potential problems caused by attaching, or implanting, instruments to seabirds. Periodic checks of this nature are important in helping define how we might better research practice as well as moving forward in the 'reduction, refinement and replacement' policy implemented within many governmental agencies specifically for laboratory animal science but, in fact, equally applicable for wild animals (Griffin & Gauthier 2004). A weakness in the approach we have taken relates to biases inherent in the published literature. Primary in this, perhaps, is the pressure on researchers to publish significant results in papers favoured to be concise by editors which would tend to diminish the likelihood of studies reporting the effects of tags. Nonetheless, we believe that, by combining both a quantitative and qualitative analysis, this review represents a reasonable statement of the information gathered during the last 24 years about the impact of tags on seabirds. Among the most noteworthy results is that almost 61% of the papers examined from their abstract reported significant effects of the equipment on seabird behaviour or condition. Equally striking is the fact that, of the 315 indirect papers examined, only 13 (4.1%) provided information about the effects of the equipment in their abstract (of which the majority (53.9%) reported significant impacts).

Despite the editorial and publishing pressure misgivings, we find that it is of concern that most of the indirect studies (62.3%) devoted less than 2% of the total text to the effects of the equipment. It is encouraging, however, that the length of text devoted to the effects of tags was clearly positively correlated to the nature of information given (Figure 6) with the most serious implications being considered at greater length. Inconsistencies in the type of information reported in indirect papers presumably stem partly from differences in the ability of the authors to assess potential tag effects (e.g. absence of control birds or limited equipment) but may equally reflect the level of interest paid to this issue. Based on this assumption, and as it might be expected, papers with longer sections on the instrumentation effects (categories with mean IEI>2%) were also those which manifest greater concern for animal welfare issues by detailing direct assessment of the impact of instrumentation used. It is encouraging to notice that this relates to the majority (36.3% of category E and 25.9% of category D) of the indirect papers. However, it is also encouraging to note that categories of indirect papers with a mean IEI of less than 2% did not completely ignore the subject but expressed concern in a variety of different ways. Typically, this concern ranged from simple cognizance of potential tag effects by citing literature on the topic (category A) to reference to previously conducted and comparable studies where effects were tested (category C) (although many such studies often indicated that the work complied with the regulations established to minimize the disturbance imposed on their study birds (category B)). Reference to the literature may also act as a measure reducing the amount of space perceived necessary to deal with the instrumentation effects since citation of previous studies where no effects were found may be taken as reason enough to consider the issue no further. This may be acceptable practice but only in the case of papers such as those of category C which have carefully considered device effects by using appropriate citations. Overall though, while such papers demonstrate a clear awareness of tag effects, they cannot be considered the most reliable documentation. Nonetheless, it is valuable that authors sometimes noted that they were unable to test the effects of the equipment, and that further studies were needed. The matter is complicated by the problems of having to separate the effects of animal handling, which, in itself may produce aberrant behaviour (e.g. Wilson & McMahon 2006), from that induced by the equipment. Despite this, we would argue that, although an appreciable part of the problem is due to insufficient consideration being given, it is also due to the problems associated with attempting to document changes in multiple possible parameters and having no time and resources to do so. It is therefore inappropriate to consider that all studies with a paucity of information reflect lack of consideration. How can we equate limited resources to robust scientific assessment of our protocols? Perhaps some elements of seabird well-being are more sensitive to tags than others so that these might be given study priority for best use of limited resources.

Among the papers reporting the effects of equipment in their abstracts, most (80.4%) considered breeding success or foraging behaviour. Breeding success is relatively easy to assess due to the availability of some obvious and reliable measurable indicators (e.g. clutch size, chick growth, chick survival etc.) and its documentation may be a consequence of this (cf. Cherel *et al.* 2000, Forero & Hobson 2003, Quillfeldt *et al.* 2005). Although more onerous to document, researchers have shown particular interest in foraging behaviour, possibly because seabirds have been shown to be so important for understanding trophic relationships in marine ecosystems (e.g. Iverson *et al.* 2008). Importantly though, significant instrumentation effects have been reported in every category of seabird biology considered in this review. The different proportions of effects reported (Figure 1B) might, however, reflect researcher investment rather than representing the importance of animal responses. This problem could be mitigated by thorough and systematic work by scientists using a direct approach. Indeed, we would suggest that funding bodies should consider supporting such work so that proper guidelines can be postulated rather than workers having to allude to recommendations on some aspects of the tags which currently act as pointers, such as a streamlined shape (Bannasch *et al.* 1994, Culik *et al.* 1994) or a weight which should not exceed 3% of the bird's body mass (Kenward 2001). Unfortunately, there are few papers of this type to which scientists can refer, the best known being White & Garrott (1990), Kenward (2001) or Hawkins (2004). Even these publications, however, do not always give specific and appropriate guidelines based on clearly-defined research. An example is the widely adhered to "3% rule" suggested by Kenward (2001). Here, we note that, although a number of studies have detected no negative effects of externally-attached devices on birds when they are less than 3% of the body mass (e.g. Garthe *et al.* 2003, Igual *et al.* 2005, Tremblay & Cherel 2005), energy expenditure for flight depends critically on bird mass and wing characteristics (Pennycuick 1975, Norberg 1995, Rayner 1995, Rayner *et al.* 2008), a factor which is not built into this recommendation. Thus, larger birds and/or those with higher wing loadings are much less likely to accommodate extra mass within their normal power requirement costs for flight (Pennycuick 1975, Pennycuick *et al.* 1989, Ellington 1991). The difficulties of determining power costs for flight (Rayner & Ward 1999, Rayner 2009) make proper testing of such generalizations problematic. However, mass is not the only important parameter, as illustrated by the recent study of Saraux *et al.* (2011) who report a reduction of 39% in reproductive success and 16% in survival rate over ten years in king penguins *Aptenodytes patagonicus* wearing seemingly innocuous flipper bands, considered likely to result from the extra drag caused by the tag. This study also shows that the time scale over which device effects are considered is also important.

Our study has shown no apparent change in the amount of documentation of tag effects on seabirds over time since 1986, whether in terms of the proportion of direct and indirect papers published or the length and content of the section devoted to the impact of instrumentation in the indirect papers. This is cause for concern because there has been a steady increase in the number of indirect papers published over the past 24 years while over the same period, the number of direct papers remained low (the number of direct papers from 1990 to 2009 was between zero and five per year). This is the case despite Murray in 2000, pointing out a lack in the assessment of marking effects (including external devices) on animals including birds. He reported that in 90% (215 out of 238) of the papers surveyed, the marking effects were not considered or at least not reported as such. Given the increase in public concern relating to animal welfare (de Boo & Knight 2005) this is perhaps surprising, especially as other authors have reported an increasing use of animal-attached techniques in research since the sixties (Ropert-Coudert *et al.* 2009, Barron *et al.* 2010). This is probably because the technology is being increasingly miniaturized (Kooyman 2004, Hays *et al.* 2007) and affordable making it applicable to an ever wider variety of species (Naito 2004, Davis 2008). Indeed, this might explain why Barron *et al.* (2010) alleged that researchers do not seem to be getting better at minimizing the effects of the tags on their animal carriers noting that instrumentation impacts do not appear to change across years.

The mismatch between the increase in use of tagging technology and constant, low documentation of tag-induced deleterious effects is not restricted to birds (Murray 2000, Withey *et al.* 2001, Godfrey & Bryant 2003) although there is high variance in researchers studying different groups. For example, Godfrey and Bryant (2003) reported that investigators studying mammals were less likely to test the effects of radio tags than those studying birds and fish.

Given the extent to which tags are being used across diverse animal taxa (e.g. Cooke *et al.* 2004, Ropert-Coudert*et al.* 2009), and the trend for increasing use, our study is clearly limited in that it considers only seabirds. However, our work with direct studies has identified that aberrant instrumentation effects are usual, even if the topic seems to be controversial, and that a non negligible part (73, 37.8% corresponding to categories A, B and C together) of the indirect studies using tagging technology on seabirds do not consider tag effects adequately, although part of this must be due to authors preferring not to invest resources in evaluating instrumentation effects where previous comparable studies have already done so. Importantly though, the suite of factors in bird biology that may be affected by attachment of tags (see e.g. Wilson & MacMahon (2006) for some examples) means that no studies to date can be considered comprehensive, even those documented here as 'direct', so complacency is perhaps inappropriate. Although efficient work on animals would obviously be impeded by perpetual and onerous consideration of tag effects for every study, we believe the problem needs further consideration by the scientific community. A way round this dilemma might be for explicit studies to be undertaken on representative species from target taxa where attachment techniques, protocols and tags design are examined carefully, so that recommendations may be proposed to which future researchers can adhere. In parallel with this, other studies using tagging technology on animals could determine, in a more or less indirect way, the impact of instrumentation as it has been done by the papers ranked in category D. This approach should not require an elaborate protocol specifically designed to achieve this goal and could be achieved through simple examination of changes in some critical aspects of the bird's life (e.g. foraging behaviour, parental investment…) that may be due to the equipment, as part of the experiment. For other aspects which could be critical to examine such as the survival rate, it can however be more challenging mainly because it is often not possible to determine the fate of tagged birds which have not been resighted/recaptured or which devices have stopped transmitting. Publishing such information should help fill out the paucity of information about the effects of tags and highlight how methods may be improved. For this to be really viable, however, funding bodies need to be aware of the importance of the problem and support direct studies on the effect of tags on their animal carriers. Although scientists have a role to play in the refinement of the animal tagging methods, we believe it is also the tag manufacturers' responsibility to ensure they supply with the most appropriate equipment. Their contribution could be to support or even to conduct studies to assess the impact of their devices. Ideally, these companies could also develop manuals explaining how to make the best use of their equipment. Such a combination of effort and expertise should help ensure that animals tagged in the future will be minimally compromised. This should help lead to a robustness and transparency in the ethics of ecological research that is comparable to that of other disciplines such as molecular biology or medicine (Braun *et al.* 1998, Ives *et al.* 2007).

Acknowledgements

We thank the RSPCA which made this study possible by providing financial support. This study was also supported in part by the California Department of Fish and Game's Oil Spill Response Trust Fund through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis who have proven themselves to be an organization that does indeed support studies on the direct effects of tags. Finally, the support and comments of friends and family is always greatly appreciated especially for an author facing, for the first time, all the stress involved in writing a first scientific paper.

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Table 1. Main categories used to classify the data on the effects of devices and attachment systems reported on seabirds and presentation of some parameters included in each category.

Categories	**Foraging behaviour (FB)**	**Diving behaviour (DB)**	**Time budgets (TB)**	**Physiological condition (PC)**
Parameters	Parameters linked with the foraging trip such as trip duration, number of trips per day or per bird, foraging direction headed during the trip, proportion of diurnal and nocturnal trips, and mean distance covered, meal mass and composition.	Parameters linked with the dives performed such as number of diving bouts, number of dives, depth and duration of the dives, surface duration between two consecutive dives or bouts, dives shapes, swimming speed and time spent by the bird during the descent, ascent and bottom phases of the dives	Proportion of time allocated to normal activities compared to device-induced behaviours (pecking, excessive preening or other comfort behaviours such as flapping or bathing, nest desertion)	Parameters linked with birds' body condition or physiology such as body mass change, hormone levels, feather loss.
Categories	**Breeding success (BS)**	**Energetics (E)**	**Mortality rate (MR)**	
Parameters	Adult return rate, fledging mass, chick provisioning, chick growth, chick survival, nest attendance, parental investment.	Heart rate, metabolic rate, energy expenditure, rate of oxygen consumption.	Mortality rate or survival rate	

Table 2. Main categories used to classify the indirect papers according to the nature of information provided on the impact of the equipment. The categories are sorted from A to E in ascending order in terms of perceived importance.

A	Use of citations considering the potential impact of the equipment on the birds. Example: *"Large transmitters or recording devices may cause flying birds to alter their behaviour or subject them to risk of injury"* Citation from Anderson *et al.* (1991).
B	Use of citations to support the fact that the equipment and procedure used are within the recommended specifications. Example: *"The total mass of the equipment was 100 g, or 0.8–1.2% of the bird mass, well below the 5% threshold beyond which behavioural disruptions are likely to occur in flying birds."* Citation from Weimerskirch *et al.* (2005).
C	Use of citations of previous studies that have purposely and acutely tested the effects on the same or similar species and using the same or similar equipment. Example: *"Deployment of these geolocators on Cory's shearwaters has no detectable short-term effect on the birds."* Citation from Felicisimo *et al.* (2008).
D	Use of simple observations or basic comparisons with the normal situation or data reported from other studies (though no directed protocol to assess the effects and no statistical tests) on different aspects of the bird's life (e.g. date of return to the colony, preening behaviour frequency…). Example: *"The birds did not appear to be adversely affected by the transmitter; they flew, walked, and behaved normally."* Citation from Fraser *et al.* (2002).
E	Use of a specific protocol to test the effects of the devices with comparisons between the control and the tagged birds or different groups of tagged birds. Example: *"The mean duration of foraging trips was not significantly different between equipped birds and control birds."* Citation from Ropert-Coudert *et al.* (2004).

Table 3. Classification and distribution of the papers collected and analyzed in this review.

Papers focused on the effects of equipment	Results on the effects of instrumentation in the abstract	Numbers of papers	Designation
Yes	Yes	38	Direct papers
Yes	No	4	
No	Yes	13	Indirect papers
No	No	302	

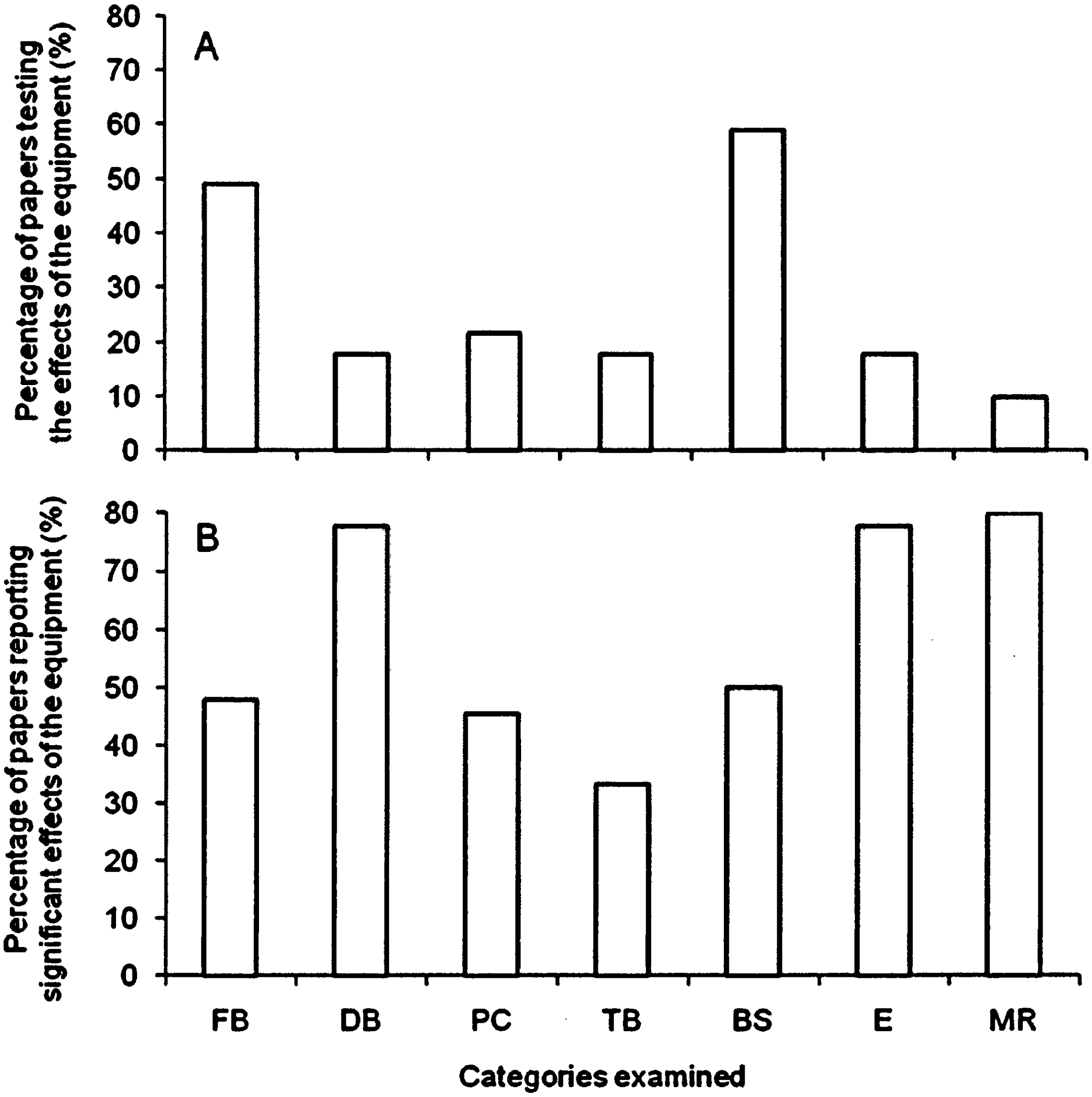

Figure 1. (A) Percentage of the 51 direct and indirect articles that documented in their abstracts the testing of the effects of instrumentation on defined categories of seabird biology.

Keys: FB = foraging behaviour; DB = diving behaviour; PC = physical condition; TB = time budgets; BS = breeding success; E = energetics and MR = mortality rate. (B) Percentage of the studies shown in (A) reporting statistically significant effects of instrumentation for the defined categories.

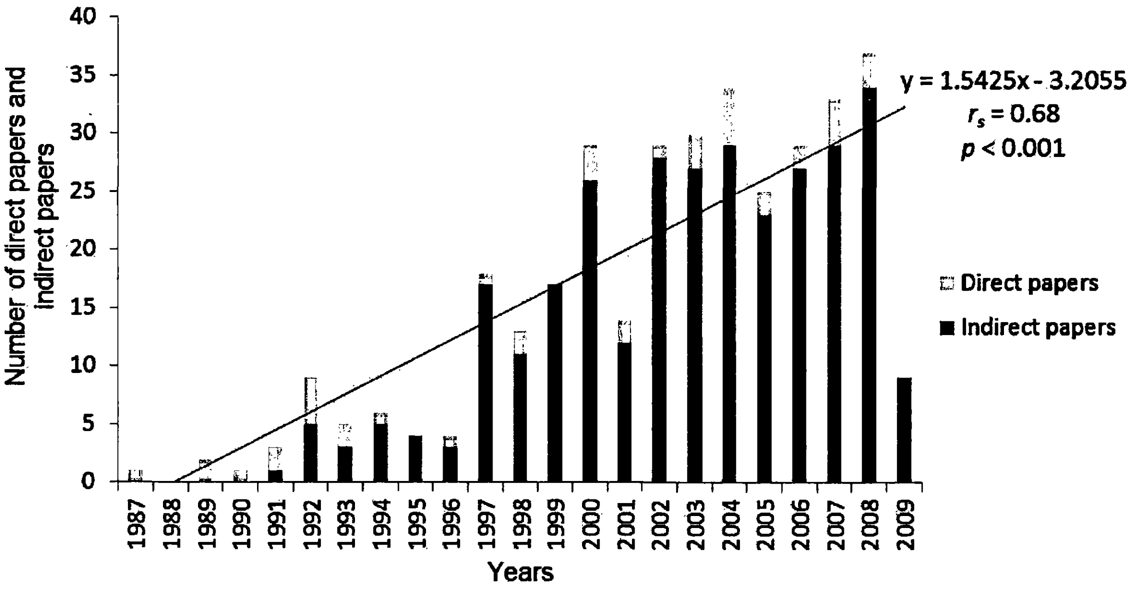

Figure 2. Number of direct (pale grey) and indirect (dark grey) papers collected documenting seabird study using tags as a function of year.

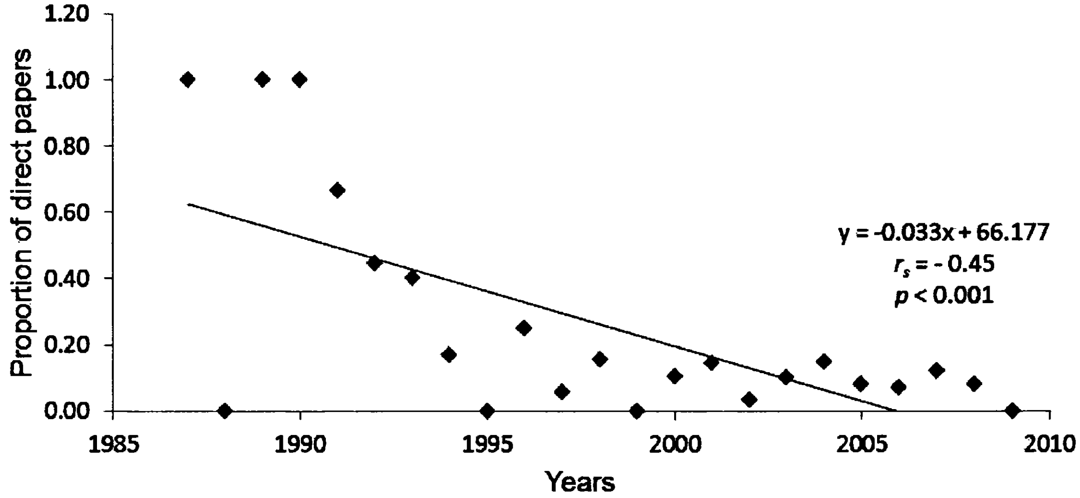

Figure 3. Proportion of direct papers relatively to the total number of papers examined as a function of year.

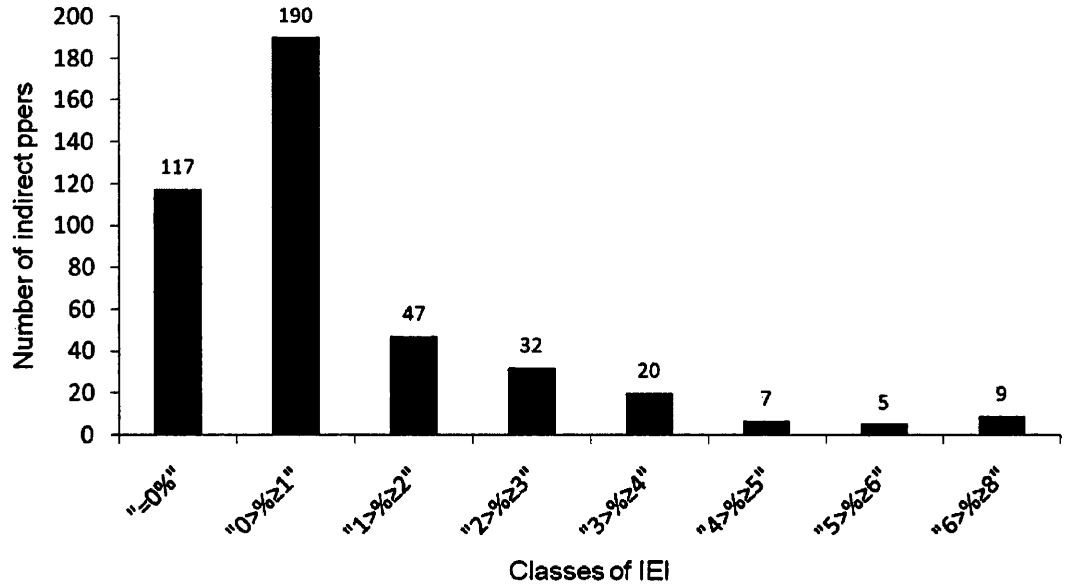

Figure 4. Number of indirect papers as a function of the percentage lengths of text dedicated to discussing instrument effects.

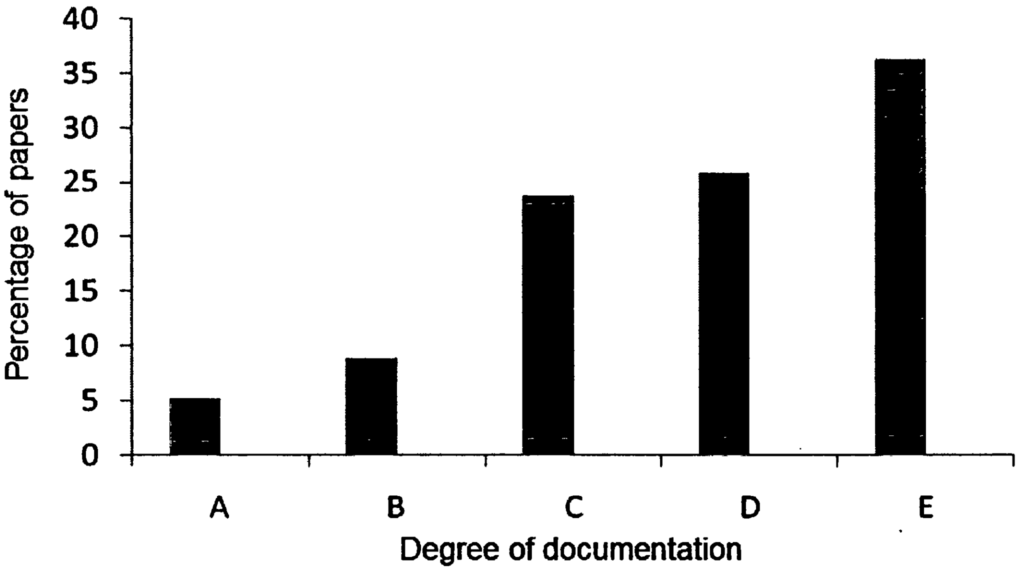

Figure 5. Percentage of indirect papers in each of the categories elected according to the degree of documentation of device effects (see Table 2).

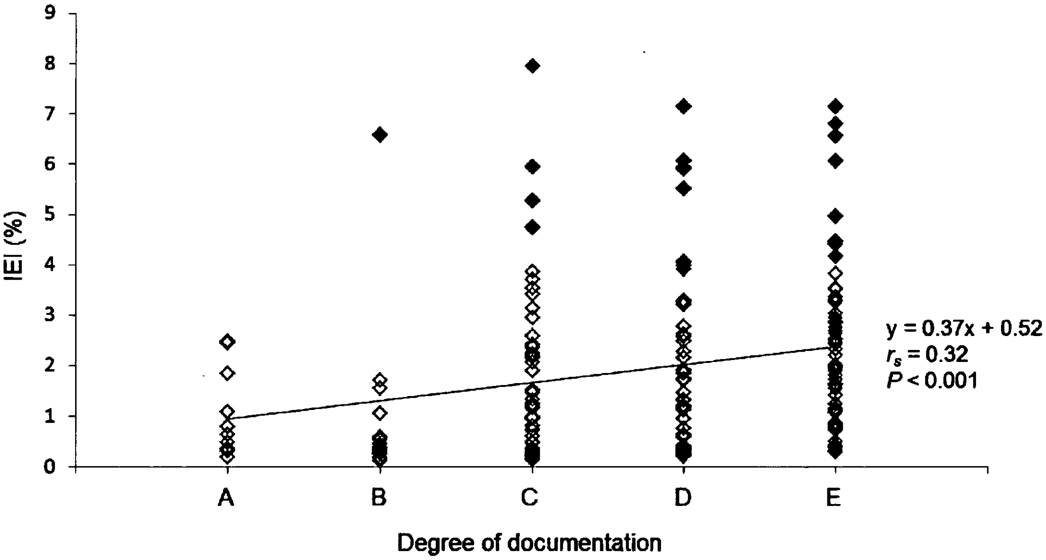

Figure 6. Percentage of text devoted to the tag effects (IEI) for each indirect paper as a function of the respective degree of documentation of device effects (see Table 2). The papers with an IEI greater than 0% but less than, or equal to, 4% are represented by squares with gray outlines and those with an IEI greater than 4% by black-filled squares. The regression line was performed including all the data points.

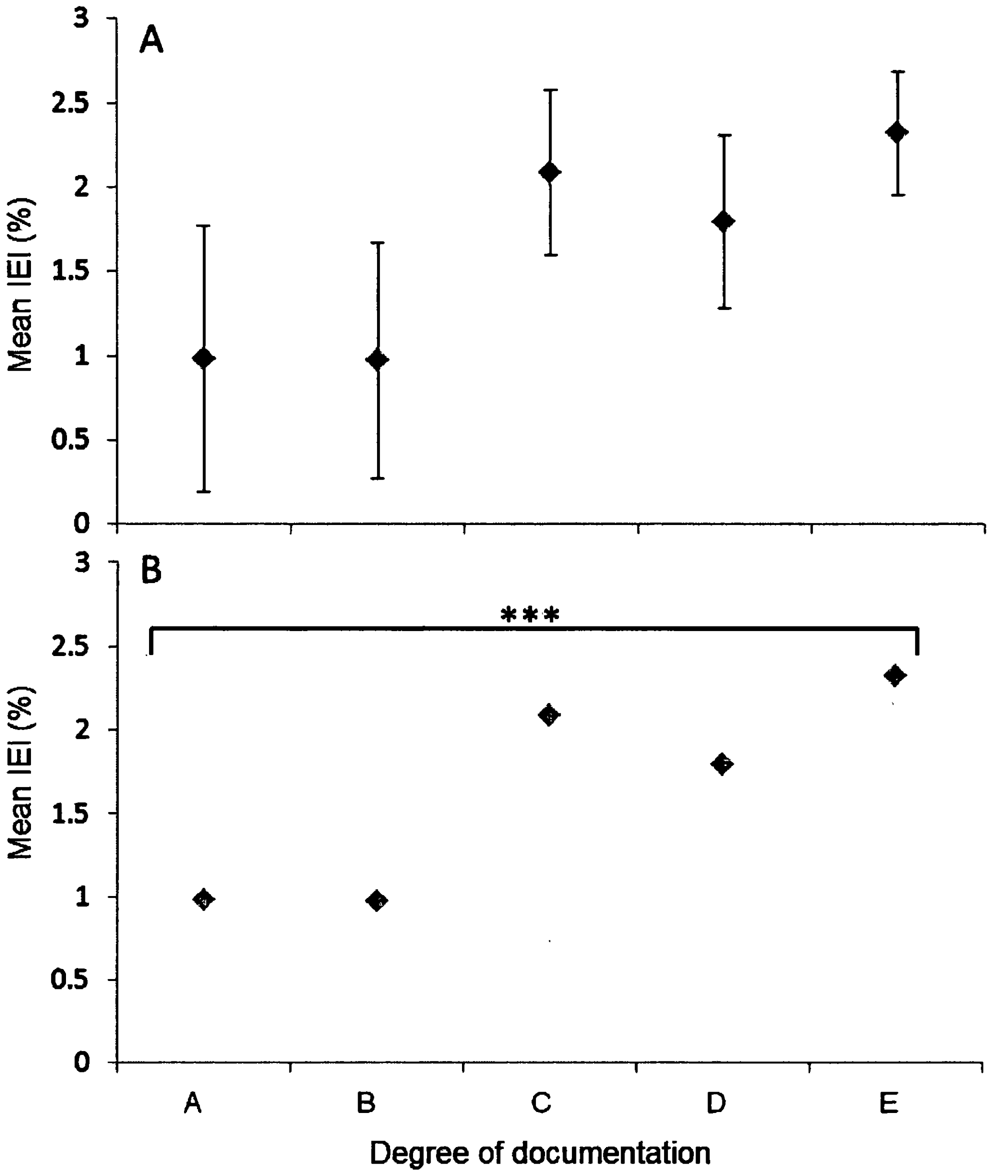

Figure 7. (A) and (B) Mean percentage IEI as a function of the degree of documentation of device effects categories (see Table 2). In A vertical bars show standard errors calculated using arcsine transformed data. In B, the stars indicate a significant difference between the categories (Kruskal-Wallis test, N = 193, $H = 22.65$, df = 4, $P < 0.001$).

Chapter 3:

The devil in the detail; does assessment of long-term bird movement depend on a gentle touch and an eye in the sky?

Preface

The following chapter deals with the development of a silicone harness as a novel method to attach tags on birds over long-term periods with minimal impact. This has led to multiple tests being conducted, first in a laboratory, and then on captive and finally wild birds. It started in 2009, with some trials still running at the time of writing including the deployment of harnesses on captive birds of prey and one harness fitted on a wild wandering albatross (*Diomedea exulans*), due to return to land to breed at the end of this year when it will be recaptured and checked.

Initially, I attempted to submit this work as a journal article but due to its rather technical aspect, editors and reviewers suggested that it would be more appropriate to try to publish it as a short note. Stemming from this, a letter summarising the latest results of the captivity tests was accepted for publication in the journal Frontiers of Ecology and the Environment. Although, it appeared appropriate to have this work published as a brief note rather than a detailed article, assuming it to be in accordance with the disclosure clause of the pending patent application (submitted December 2011), both the note (chapter 3a) and article (chapter 3b) versions are presented in this thesis.

SPV conducted the trials in collaboration with the RSPCA Wildlife Centre in Hastings (UK) and the Max Plank Institute in Radolfzell (Germany). SPV, RPW and MW wrote the letter version while SPV, AG and RPW wrote the article version.
Peer-reviewed letter in Frontiers in Ecology and the Environment (In press)

Chapter 3a: New tracking philosophy for birds

Sylvie P. Vandenabeele, Rory P. Wilson & Martin Wikelski

Peer-reviewed letter

In 1835 the English poet William Wordsworth wrote "*Resplendent Wanderer! followed with glad eyes, Where'er her course; mysterious Bird! To whom, by wondering Fancy stirred*", capturing both our intrigue of bird movement and our helplessness to determine it. But things have since changed. Minute leg rings allow for banded individuals to be resighted by observers, thereby demonstrating avian dispersal capacities (Salomonsen 1956). But leg-ring sightings are subject to chance and only provide point locations in space with unknown trajectories between them. This problem was partially solved by "geolocation" (Wilson *et al.* 1992), in which miniature data loggers on leg rings record light intensity against Greenwich Mean Time, thereby allowing daily determination of latitude and longitude (e.g. Shaffer *et al.* 2006). As with leg rings, however, the miniature loggers must be recovered to retrieve the data. With the inception of radio (very high frequency [VHF]) telemetry, researchers were able to pinpoint the location of transmitter-equipped individuals without recapture; furthermore, when such transmitters (e.g. Platform Transmitter Terminals [PTTs]) communicated with satellites, global coverage of bird movements was available (e.g. Jouventin & Weimerskirch 1990). Such devices are unlikely to ever work on leg-rings, however, being too big, and with any ventral positioning potentially hindering tag-satellite communication (but see Krapu *et al.* 2011). Ideally, these devices should be positioned dorsally, although physical attachment in this position is challenging. Methods to tape (Wilson & Wilson 1989a) and glue (Raim 1978; Sykes *et al.* 1990) tags to dorsal feathers work well until the feathers are molted, limiting deployment duration to weeks (Warnock and Warnock 1993), and harnesses have an inconsistent performance history (Rappole and Tipton 1991), with some reports pointing to behavioral anomalies (Perry 1981), feather wear or skin abrasion (Buehler *et al.* 1995), and even mortality (Peniche *et al.* 2011).

The problem with harnesses may lie in their conception as being able to withstand all possible environmental conditions as well as unwelcome attention from the bird itself, which explains why Teflon® is popular despite its mixed success (Steenhof *et al.* 2006). Here, we tried a fundamentally different approach, fashioning a harness from a soft, elastic, hypo-allergenic, silicone-based compound called Silastic® (Dow Corning Corporation, Midland, MI) that is designed to sit directly on the skin under the plumage (Figure 1). The idea behind this was that if the attachment system was imperceptible (both visually and kinesthetically through the sense of touch) and protected by the birds' feathers, it would be subject neither to external conditions nor to the attention of the wearer. In addition, Silastic®'s variable elasticity should be able to accommodate seasonal mass changes in outfitted birds. Our work has proceeded carefully; with trials ranging from days to months, we examined potential behavioural anomalies and possible plumage and skin changes on example species of passerines, gulls, ducks, and corvids, with no deleterious effects observed (Table 1). Fourteen adult jackdaws (*Coloeus monedula*) wore VHF and PTT tags for a maximum of 5 months in captivity before being successfully released in the wild.

Other researchers are also experimenting with a similar approach. Two teams have recently reported recovering tags attached with elastic harnesses from northern wheatears (*Oenanthe oenanthe*; Bairlein *et al.* 2012) and hoopoes (*Upupa epops epops*; Bächler *et al.* 2010) after year-long deployments on wild birds migrating across hemispheres and trans-equatorially, respectively. Such long periods and arduous migrations are a severe test for the attachment protocol, and the results appear promising.

Ultimately, the ability to resolve normal bird movements over long time periods depends on both an appropriate attachment mechanism and minimal tag size, while still maintaining tag contact with a satellite. Future success in this approach has been facilitated by the confirmation that a VHF receiver, dedicated to detection of animal-borne VHF transmitters, will be carried in 2014 by the low-orbiting International Space Station, which is supported by the European Space Agency and the German Air and Space Agency (Pennisi 2011). This system relies on modern CDMA (Code Division Multiple Access) communication technology in miniaturized electronic circuits and thus will not only help to shrink animal tag size but also allow for an expansion in onboard nano-sensing technology. Currently, the ICARUS (International Cooperation for Animal Research Using Space) initiative plans to have 5-g Global Positioning System logging tags and 1-g communication-only tags ready for experiments in 2015.

With technological advances in harnesses and solar-powered transmitters, as well as remote access to satellites, wildlife biologists should be able to track individual birds for years, revealing information on, for instance, where birds perish (e.g. Burnham & Newton 2011), addressing both conservation and pure research issues. Empowered with such science, we may see a day when Wordsworth followers will appreciate that there is no more mystery in bird paths, leaving them to lyricize about remarkable avian traveling feats instead.

Acknowledgments

Although, we could not include acknowledgements for this is not compatible with a letter format, I wish, here, to thank people of the Max Planck Institute for Ornithology (Radolfzell, Germany), in particular; Dr Wolfgang Fieldler, Dr Carlos David Santos, Dr Jesko Partecke and others for their invaluable help. Finally, we are grateful to the OWCN (California, Davis) and the RSPCA (West Sussex, UK) for financial support.

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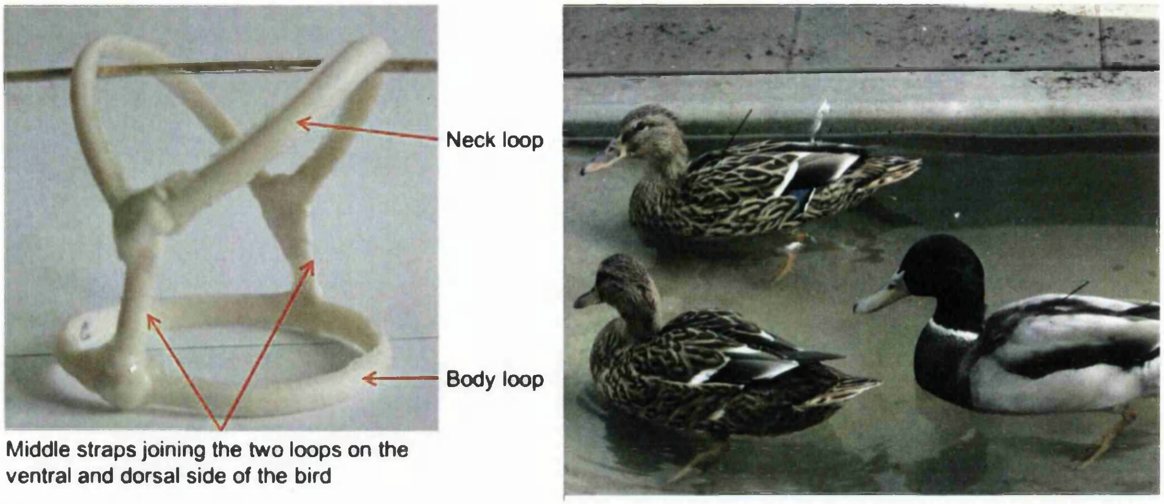

(a) (b)

Figure 1. (a) As with other backpack harnesses, the Silastic® harness is formed of two loops: one neck loop and one body loop joined together by middle straps. The V-shaped neck loop sits on the shoulders, passing under the sternum to avoid disrupting swallowing. The body loop sits around the main body, not too close to the moving limbs (i.e. wings and legs) with the wings going through the open spaces between the two loops. (b) Two mallards (*Anas platyrhynchos*) wearing the harness and carrying mock VHF transmitters (only the antennae are visible). Note that no part of the harness is visible.

Table 1. Summary of the tests performed with the Silastic® harness fitted to different bird species.

Species	**Number of individuals (body mass in grams)**	**Facilities**	**Equipment fitted**	**Deployment duration**
Gulls (*Larus argentatus* and *L fuscus*)	8 (600–850 g)	Outdoor aviaries (WC) and free-living birds	Harness only	3–6 days
Common blackbird (*Turdus merula*)	3 (90–110 g)	Outdoor aviaries (MPI)	Harness only or with a 5-g solar PTT	1 day to 2 months
Mallard duck (*Anas platyrhynchos*)	13 (1100–1300 g)	Outdoor aviaries (MPI)	Harness only or with a 39-g VHF dummy tag	3 weeks to 3.5 months
Jackdaw (*Coloeus monedula*)	14 (175–260 g)	Outdoor aviaries (MPI) and free-living birds	Harness only or with a 13-g VHF/PTT	1 week to >5 months

Keys: MPI = Max Planck Institute, Radolfzell, Germany; WC = RSPCA Wildlife Centre, Mallydams, Hastings, UK

.Chapter 3b: Harnessing a new philosophy for long-term attachment of devices to birds*

Sylvie P. Vandenabeele, Adam Grogan & Rory P. Wilson

Abstract

The use of animal-attached devices has greatly advanced the fields of wild animal biology but devices, including attachment systems, should be minimally deleterious to the bearer. Birds are particularly troublesome in this, being difficult to equip for long periods due to problems with harnesses. This study reasoned that a light, elastic, hypoallergenic harness that could sit on the skin, following body contours, would elicit less reaction from birds than the convention harness type, built to be robust. We tested such a harness made of Silastic® on 8 captive gulls (Laridae) and observed behavioural reactions intensively for 49 hours and compared bird reaction to that of controls before removing the harness and looking for physical damage. Attached harnesses were invisible to observers and although gulls preened more than controls immediately following equipment, levels had returned to normal within 48 hours. Aside from very rare harness pecking, there was no sign of any other detriment so the system, as proposed, would seem promising for further, long-term studies.

Keywords: behaviour, birds, harness, long-term attachment, tagging impact, telemetry

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*The following manuscript was written at an early stage of the study and therefore does not include the latest captive trials performed which, however, are presented in the letter above. The main purpose of the following chapter is to present in further details the method, something that could not be included in the letter.

Introduction

Equipping birds with tracking and recording devices is one of the most illuminating and revealing ways of investigating animal biology in the wild (Ropert-Coudert & Wilson 2005, Rutz & Hays 2009). However, this comes with the responsibility of developing scientifically reliable and ethically acceptable methods of animal tracking (Hawkins 2004, Wilson & McMahon 2006). The attachment of foreign objects to birds began over a hundred years ago with ringing (Stone 1918, Drost 1950) to study migration, populations dynamics or spatial distributions, which progressed through radio-transmitters (Thompson & Ruhberg 1967, Nicholls & Warner 1972, Wanless *et al.* 1988, Johnson *et al.* 1997) and now incorporates electronic devices attached to birds which transmit or record a suite of parameters such as dive depth (e.g. Ropert-Coudert *et al.* 2003), swim speed (e.g. Shepard *et al.* 2008) or behavioural traits through sensing body motion (e.g. Yoda *et al.* 1999). The potential value of such electronic tags is thus unquestionable (e.g. Ropert-Coudert & Wilson 2005) but the reliability of the information collected using these devices depends critically on the fact that animals behave normally despite being fitted with sometimes cumbersome units (Wilson & McMahon 2006).

Bird-attached technology has undergone considerable progress since its origin, especially in terms of weight and size of the instruments (Kooyman 2004, Naito 2004). But the issue is much more complex than weight or size and a critical aspect is the appropriate attachment of units. Ideally, attachment systems should be both durable (for long-term use) and have a minimal impact on animal welfare. Numerous attachment systems have been used to equip birds with external devices, ranging from feather clamps (Kooyman *et al.* 1982, Lishman & Croxall 1983) to harnesses (Kenward *et al.* 2001, Mallory & Gilbert 2008). Attaching instruments to the feathers, using adhesives such as glue (e.g. Raim 1978, Johnson *et al.* 1991) or tape (Wilson & Wilson 1989a, Wilson *et al.* 1997), is probably the least invasive, and thus the most popular method of attachment currently used. A main disadvantage of feather attachment systems, however, is the limited deployment duration, being constrained by feather loss during moulting (Wilson *et al.* 1997). The only suitable long-term, external attachment system for birds, therefore, relies on harnesses. Their use is, however, rather controversial, due to their potential deleterious effects, particularly physical injuries (e.g. Greenwood & Sargeant 1973, Buehler *et al.* 1995).

As a consequence, harness tend to be avoided in many bird studies, such as those involving seabirds, with workers simply using feather attachment systems (see above), with all the time-limitations that these engender. Over recent years, a few studies have reported the use of long-term attachment techniques including different types of harnesses (e.g. the leg-loop harness (Rappole & Tipton 1991, Mallory *et al.* 2008, Kesler 2011) and the two-loop harness (Buehler *et al.* 1995, Steenhof *et al.* 2006) and leg ring attachment system (Carey *et al.* 2009, Ropert Coudert *et al.* 2009), subcutaneous anchor methods with one of the most challenging problems being the inter-specific variation in reaction to any attachment method.

In this work we present a new approach to equipping birds with harnesses. Typically, harnesses used on birds are made of material robust enough to withstand all the physical stresses encountered by the birds in their environment as well as the bird's attempts to remove them. Ironically, the more robust the harness material, the more likely it is to be deleterious to the birds by e.g. interacting with the skin (Marion & Shamis 1977) and disrupting the feathers, and by simply irritating the wearer more. This paper documents an attempt at a new philosophy to bird harnesses and presents preliminary results from trials where captive birds were fitted with harness made of soft, elastic, hypoallergenic material designed to sit under the contour feathers on the down feathers or skin. The reasoning was that, placed under the protection of the feathers, the harness would not be exposed to the normal environment and, if soft enough, would not irritate the bird.

Methods

Following consultation with the literature, a harness design was selected which was tried as a prototype on captive gulls (Laridae) before a final, modified version was tested on other captive birds and their reaction to it documented in detail.

Harness design

We selected a harness that could accommodate a backpack because this placement puts attached devices close to the centre of gravity (Kenward & Kenward

1987, Chiaradia *et al.* 2005). Of the two main models of harness commonly used on birds, the two-loop harness (backpack harness with a neck loop and a body loop; e.g. Quinlan & Hughes 1992, Steenhof *et al.* 2006) and the leg-loop harness (Rappole & Tipton 1991, Mallory & Gilbert 2008), the two loop-loop harness was selected, again, for centre of gravity reasons. The first design (Figure 1) had a neck loop over shoulders not too close to the wings, to avoid disrupting the movement of the bird, and incorporated a V-form in the neck section which allowed the harness to sit just on the sternum in order not to impede swallowing (cf. Wilson & Bain 1984). The second loop, the body loop, sat behind the wings, but not so close to the thighs as to prevent movement of the legs. The neck- and body-loops were connected by a single strap on the dorsal side and two straps on the ventral side. All the straps had a semi-circular cross-section with the curved surface directed outwards and the flat side located under the feathers in contact with the skin, thereby fitting the contours of the bird appropriately.

Fabrication and test of the first prototype

The harness made of a hypoallergenic, soft and elastic material used by the medical industry called Silastic® (Silastic® P1 Base and Curing Agent, Thomson Bros Newcastle Ltd) which can be poured into appropriate moulds before setting. We made semi-circular straps with a width of 10 mm, which seemed appropriate for our first test subjects, herring gulls (*Larus argentatus*), by pouring the Silastic® into semi-circular canals of appropriate dimension. The elasticity of the straps was modulated by mixing the uncured Silastic® with 10% (by volume) silicone oil (Dow Corning® 200 Fluid 50CS, Thomson Bros., Newcastle Ltd). The different straps of the harness were joined using Silastic® although staples were also sometimes used to consolidate existing Silastic® joints.

This first harness model was tested on 2 captive herring gulls at the RSPCA facilities (Royal Society for the Prevention of Cruelty to Animals) at the Mallydams Wildlife centre in Hastings (UK) in April 2009. The birds were housed in an outdoor aviary with a freshwater pool (7 m long x 5 m wide x 40 cm deep) and access to land (a ledge 1.3 m x 5 m and platform 3.50 m x 2 m). The aviary was equipped with a video system composed of 4 cameras placed in each corner to record bird behaviour.

The harness was deployed for a maximum of three days during which visual observations and video recordings of the birds' behaviour were carried out. No statistical analyses were performed on these data given the low sample size. These trials nonetheless played an important role in improving the design of the harness and showed that, for these two individuals at least, the presence of the harness did not cause any immediate or obvious abnormal behaviour or physical damage (such as broken feathers or inflamed skin). Following recapture of the birds and assessment of the harness positioning and fit, we modified the system to produce a final model (see below).

Enhancement of the harness

The two straps linking the neck-loop to the body-loop on the ventral side of the harness (Figure 1) were replaced by a single strap (Figures 3 and 5). We also examined the elasticity of the harness material which could be modulated by the Silastic®-silicone mix. In this, two major elements were considered; (i) whether appropriate elasticity could cope with inter-individual variation in body size and (ii) whether the intra-individual body changes that occur both diurnally and seasonally in many species of birds (Haftorn 1989, Wendeln & Becker 1996, Koenig *et al.* 2005) could be adequately incorporated within the chosen elasticity of the harness.

In order to define the elasticity of the harness, tests were performed on Silastic® straps made with different percentages of silicone oil. Semi-cylindrical strips of 10 mm wide Silastic® measuring 200 mm long and incorporating 0, 10, 20, 30 or 40% of silicone (i.e. amount of silicone oil added relative to the total weight of liquid) were constructed and were stretched using a 600 g Pesola® spring balance to determine the force required to extend each band, held horizontally, by defined lengths (Figure 2). Given that a loose harness may disturb the bird by moving with respect to its body and that a tight harness could cause injury (Buehler *et al.* 1995), we decided to equip birds with a harness whose size corresponded to the minimal body circumference observed (i.e. 26 cm in this study) when unstretched, but with enough elasticity to be appropriate when the body circumference exceeded this minimum. The body circumference was measured using a piece of string placed around the main body in the space between the wings and the thighs and as close as possible to the skin as not to account for the plumage layer.

In order to establish an accurate and efficient method of bonding the straps correctly, we built casts of featherless herring gull bodies using Plaster of Paris (Crystacast plaster; Sepal-Maragon, Herts, UK). These casts were then used as a model on which the different straps of the harness could be assembled with appropriate dimensions and correctly angled straps (Figure 3).

After construction of suitable harnesses, a procedure for fitting the harnesses to the birds was established to minimize handling time and stress (Figure 4). For this, a minimum of two persons was required, one restraining the bird and the other one fitting the harness. Since the surface of Silastic®, is somewhat sticky, harnesses were dusted lightly with hypoallergenic talcum powder before being fitted to the birds.

Further trials on captive birds

The enhanced version of the Silastic® harness (Figure 5a) was tested in July 2009 on 6 captive birds consisting of 5 herring gulls (3 adults and 2 juveniles) and a lesser black-backed gull *(Larus fuscus)* adult at the RSPCA centre in Hastings (Figure 5b). The dimensions of the harness loops ranged from 24 to 26 cm for the body loop while the neck loop measured about 28 to 32 cm (14 to 16 cm on each side of the middle strap; Figure 5a). The birds were kept in the same housing and care conditions as previously detailed. As was the case for the first trials, we initially deployed a harness on one bird, the lesser black backed gull, to test for major anomalies before fitting all the birds. The observations made on this bird, after equipping it with a harness made of 40% silicone oil, chosen based on the results of the elasticity test, showed no obvious deleterious effects resulting from the harness. Subsequently, all the adults were fitted with harnesses made of Silastic® mixed with 40% silicone oil while the 2 juveniles were fitted with harnesses made of Silastic® mixed with 30% silicone oil. Individuals were identified by previously-fitted individual bird rings or plumage details.

Once equipped, all birds were observed for the following 50 h. Observations were based on the scan sampling method which consisted of noting the instantaneous behaviour of each individual, sequentially, once per minute for 1 h immediately after the birds were released and then for 15 min for every subsequent hour. Different types of behaviours ranging from cleaning to social behaviours were noted (Table 1). When information was missed during the visual observations, the video recordings were used to complete the data. Video recording were also used to document bird behaviour prior to being equipped. Video observations were conducted using the same protocol as used in the direct visual observations.

Data processing and statistical analysis

As individual birds could not be identified in video recordings, all statistics were performed on the groups, namely the treatment group (with harness) and the control group (before equipment). In order to remove the time dependence of when birds were equipped, all data were analysed with respect to the time since release following harness attachment.

For each type of behaviour, the mean frequency of occurrence was calculated as a percentage. More precisely, the number of times each behaviour occurred was calculated as a percentage relative to the total number of behaviours recorded for the period considered. For the different behaviours displayed by the birds, a comparison of the frequency between the different sessions of observations made on the treatment group was performed using a Friedman test, the non-parametric version of a two-way ANOVA.

Subsequent analysis was only performed on the major behaviours displayed by the birds (preening and resting) and those expected to be altered by the presence of the harness (flying, walking, swimming). A Wilcoxon test for paired samples with Bonferroni's correction was used to compare behaviour frequencies between treatment and control group.

The mean percent of birds observed performing each of these specific behaviours per minute was calculated and compared between the different periods of observations completed on the treatment group and, then, between the treatment group and the control group using the same tests as used previously for the behaviour frequencies.

A linear regression was performed on the arcsine transformed frequencies of preening and resting as a function of time for 2 different periods of time: from 20 min to 7 h and from 22 to 31 h after release.

All calculations were performed using Excel 2010 (Microsoft inc., USA). SPSS (SPSS® 13.0, SPSS Inc.) was used to perform the statistical analysis. The significance was set at $P < 0.05$ except in the case of the Wilcoxon test for which the Bonferroni's correction was applied.

Results

Harness elasticity

The addition of silicone oil to the Silastic® affected the force required to stretch it profoundly, with greater quantities of silicone oil resulting in greater elasticity. For example, a 50% stretch required forces of 5.25, 3.80, 3.29, 2.53 and 1.96 N for 0%, 10%, 20%, 30% and 40% silicone oil mixes, respectively (Figure 6). Thus, a mix with 40% silicone oil in a stretched body-loop would exert, on average, three times less pressure on the bird as a strap with no silicone oil.

Harness fitting

Unpublished RSPCA data indicate that maximum intra-specific change in the body circumference of adult gulls would cause a maximum necessary extension of 7% of the harness. This corresponds to a force applied to the bird by a harness made of 30 or 40% silicone oil of less than 0.35 N (Figure 6), or the equivalent of a weight of about 35 g acting over the whole surface area exerted by the body-loop. This translates to a pressure of 1.35 g/cm^2 exerted on the bird skin by the strap measuring 26 cm by 1 cm. Inter-individual variation in the body circumference of herring gulls (measurements taken at the time of the study ranged from 26 to 30.5 cm being on avereage 28.7 cm) is much greater than intra-individual variation (about 13% in this study) to the point that the elasticity within the harness may produce unacceptable pressure if a harness appropriate for the smallest gull was then used on the largest individual. For example, if a large bird of 30.5 cm thoracic circumference was fitted with a harness of 40% of silicone but with a body loop of 26.5 cm in circumference (which causes about 15% stretch), it would experience a force of 0.69 N (Figure 6), which translates to a pressure of 2.69 g/cm^2. There are no guidelines in the literature about what pressures might be acceptable in such cases but, for the sake of minimizing risks, we decided to build harnesses of 2 different sizes (small and medium), corresponding to thoracic circumferences of 26 cm and 28 cm, respectively, which would lead to maximum pressure of 1.4 g/cm^2 if used on the largest individuals in the next size category up.

It took between 7 and 11 min (mean = 8.5 min) to equip the birds during the second trial and was markedly easier than during the first trials. In particular, the formalization of the precise manner in which the bird was held and how the harness was placed over it as well as the use of talcum powder facilitated the procedure. The equipment was removed after approximately 2 and a half days for the first tested bird and after 6 days for the other birds, with no apparent physical damage caused by the harness, either to the feathers or to the skin (due to breakage or abrasion, for example). No water was observed to have penetrated the feathers as a result of the harness even though the birds spent appreciable amounts of time swimming.

Behavioural observations

From the trials performed in July 2009, 171 min of indirect observations were made from the video recordings before the birds were equipped (control group) and 345 min of direct observations were completed during the deployment of the harness (treatment group). The observations completed on the treatment group were subdivided in different time categories based on the time the birds were released after being equipped; after 20 min, 30 min, 40 min, 50 min, 2 to 7 h, 22 to 31h and 46 to 49 h. Some time periods are separated by several hours due to the night during which no observations were possible.

The main behaviours displayed during all observations periods were preening and resting (Figure 7). For up to 50 min after birds were released, preening comprised the main behaviour (>50%) while resting was the main activity thereafter. All the other behaviours constituted at most between 2% and 6.3% each.

Preening behaviour.— The frequency with which birds preened in the treatment group was significantly different between the different time categories (Friedman test, $P = 0.002$; Figure 7), but not significantly different from the control (Wilcoxon test, $P > 0.05$ in all cases), primarily due to the high variance in the control group. Due to the weak power of *post-hoc* testing for Friedman tests, it was not possible to determine which sessions of observations were significantly different. There was, nonetheless, a substantial incidence of preening over the first 20 min after being equipped, which decreased over time to 50 h until it was even lower in the harnessed birds than the control group (Figure 7 and 8a).

The mean percentage of birds preening per minute in the treatment group was significantly different between the time categories (Friedman test, $P < 0.001$, Fig 8a); and significant differences were apparent between the control group and the following sessions of observations: 20 min, 2 to 7 h, 22 to 31 h and 46 to 49 h (Wilcoxon test, $P < 0.001$; $P < 0.001$; $P < 0.001$; $P < 0.002$, respectively).

There was a statistically significant effect of time on the frequency of occurrence of preening, with a decrease from 20 min to 7 h after release ($r^2 = 0.50$, F = 3.19, df = 4, $P < 0.02$) while there was no effect of time from 22 to 31 h after release ($r^2 = 0.02$, F = 0.16, df = 2, $P < 0.70$).

Consideration of flapping behaviour as a possible indicator of the discomfort of the bird resulting from the presence of the harness, there was no significant difference in flapping frequency between the different sessions of observations (Friedman test, $P = 0.09$) nor was there a significant difference between harnessed and control group for any of the time categories defined (Wilcoxon test, $P > 0.05$ in all cases).

Resting behaviour.— As with the preening, a significant difference was revealed in the resting frequency for the treatment group between the time categories (Friedman test, $P = 0.001$, Figure 7) although there was no difference to the control, probably due again to high variance in the control group (Wilcoxon test, $P > 0.05$ in all cases). It proved again impossible to determine which sessions were significantly different due to the weak power of the *post-hoc* tests. Low levels of resting during the 20 min-session were, however, observed followed by a progressive increase to levels similar to those of the control group (Figure 7 and 8b). The mean percentage of birds resting per minute was significantly different between the time categories (Friedman test, P <0.001, Figure 8b), and a significant difference was revealed between the 20 min-session and the control group (Wilcoxon test, $P < 0.001$).

No significant effect of time on resting frequency was found for any time categories analysed ($r^2 = 0.34$, $P = 0.08$; $r^2 = 0.03$, $P = 0.64$ respectively).

Harnessed-directed behaviours.— The birds were not observed pulling or pecking the harness for up to 2 h. However, these behaviours were noticed between 2 and 46 h after being equipped, but represented less than 1.1% of the observations. No significant difference was found in the frequency of these behaviours between the different sessions of observations (Friedman test, $P = 0.07$).

Motion behaviours.— Assessment for potential disturbance caused by the harness to motion showed a significant difference was found in the frequency of flying, walking and swimming between the different time categories of the treatment group (Friedman test, $p < 0.005$; $P < 0.01$; $P < 0.002$ for flying, walking swimming respectively) but no difference between these and the control group (Wilcoxon test; $P > 0.05$ in all cases). Few or no occurrences of any motion behaviours were noticed up to 50 min after birds were equipped, followed by an apparent progressive increase to a level close to, or greater than, that of the control group.

Discussion

While it is clear that animal-attached technology is changing the way we understand the biology of free-living animals (Cooke *et al.* 2004, Ropert-Coudert & Wilson 2005), it is becoming increasingly clear that, by obliging them to carry such devices, we can radically change the way they behave (e.g. Murray & Fuller 2000, Hawkins 2004). There is thus an urgent moral and ethical need for quantification of the effects of attached technology, which should include the attachment system for such devices to animals. This is necessary to put acquired data into perspective, but also so that animal-attached systems can be constructed to impact their wearers minimally. Critically, the potential for detriment to animals is a function of the wearing time, with longer studies being likely to be more harmful (Wilson & McMahon 2006, Saraux *et al.* 2011). Currently, there is even no appropriate method for attaching external devices to seabirds (excepting those that use ring-attached systems for minute devices (e.g. Stutchbury *et al.* 2009, Bairlein *et al.* 2012) so as to monitor them over long periods. Existing methods which attach devices to feathers fail, at latest, during the moulting period (Bray & Corner 1972, Kenward & Kenward 1987, Mong & Sandercock 2007) while harnesses, which are conventionally built to be long-lasting and robust, are often deleterious to the wearer (see Withey *et al.* 2001). Thus, there is need for a long-term attachment system for seabirds so as to allow them to be tracked over significant periods of their life cycle without compromising them. This study has sought to create such a system, the Silastic® harness, for deployment on birds that can be used as a basis for the attachment of devices with a view to long-term deployments (months to years). Any system that is intended to be used for long periods should first be assessed intensively for deleterious effects over short periods before, if successful, testing can be extended, and that was the purpose of this study.

An immediate and obvious effect of the Silastic® harness on birds was the temporary and short-term increase in preening which appeared to occur to the detriment of resting. Since no birds were just handled without being fitted with a harness (due to limited bird availability at the RSPCA study site), it was not possible to determine whether this change in the time allocation was caused by handling or by the harness or both. A problem which was dealt with in later studies by making sure that we would have, in addition to naive birds, a group of birds being handled the same way as equipped birds (i.e. birds handled and fitted with the harness before removing it and releasing the birds back in the aviary). Such procedure would allow us to assess potential differences between the treatments ultimetaly showing that the increase in preening was mainly due to the handling and only behaviours directly directed towards the harness (e.g. pulling and peckinh the straps) could therefore be attributed to the presence of the equipment. Excessive preening has previously been documented for birds equipped with externally attached-devices (e.g. Wilson & Wilson 1989b; Hooge 1991). As in our results, such increases in preening have been reported to be only transitory, with the 'normal' state returning once the birds habituate to the presence of the equipment (e.g. Simeone *et al.* 2002; Tremblay *et al.* 2003). In fact, preening constitutes part of normal cleaning for all species of birds (van Rhijn 1977) and represents a significant proportion of bird's time budget (Delius 1988). Preening may occur at any time of the day and is normally not influenced by the environment (Galusha & Amlaner 1978) but can be elicited by specific stimuli such as irritation of the integument by parasites, or following visual stimuli such might occur during the moulting period when feathers become askew (Delius 1988). It has been observed, however, that preening, and other comfort behaviours such as flapping or bathing, may increase in stressful situations (e.g. Gilmer *et al.* 1974; Hill 1983; Williams 1984), being ranked as displacement activities since they constitute out-of-context actions displayed by organisms facing a stressful event (Armstrong 1950; Duncan & Wood-Gush 1972; Delius 1988). It is therefore likely that the presence, and/or fitting, of the harness elicited the observed increase in preening although the displacement of feathers due to the handling may also be relevant here.

The obvious increase in preening occurred at the expense of resting but changes might also have occurred in other behaviours which, while representing less than 7% of the observations, could have been equally important in any assessment of the effects of the procedure on the birds. In fact, behaviours involving motion, such as flying, walking or swimming, did appear affected by the handling or harness since they were absent or rarely displayed by the birds for up to 50 min after being equipped (Figure 11). The fact that these apparent differences were not significantly different from control augurs, however, that the level of these behaviours after being equipped stayed within the natural variation. In this respect, it has been reported that activities of gulls exhibit certain temporal and tidal patterns, with, for example, birds being most likely to sleep at mid-day (Delius 1970; Galusha & Amlaner 1978). Given that the period when the study birds appeared to be least mobile also corresponded to periods around midday, the activity patterns observed could have been modulated by this.

In comparison to the other severe effects that could have been caused by equipping birds with a harness, this behavioural response may be considered tolerable. Indeed, other studies reported that equipping birds with external devices can induce serious effects through the disruption or the impairment of motion (e.g Gales *et al.* 1990, Culik & Wilson 1991, Hooge 1991), the emergence of aberrant behaviours (e.g. Perry 1981, Wilson *et al.* 1990) and/or physical injuries (e.g. Greenwood & Sargeant 1973, Buehler *et al.* 1995, King *et al.* 2000). The apparent absence of physical disabilities and injuries in addition to the virtual absence of behaviours directed against the harness are the most important outcomes of this study. We consider that this is due primarily to the elastic and soft properties of the Silastic® harness, which contrasts starkly to other systems of attachment used on birds (e.g. Falk & Møller 1995, Woolnough *et al.* 2004, Steenhof *et al.* 2006), built to be robust so as to withstand all the stresses of the environment (Kenward 2001, Bögel 2005), but which might irritate accordingly (Hooge 1991, Pietz *et al.* 1993).

Although the results seem promising, only a limited number of birds could be tested and for a duration of only a few days. A greater sample size would have allowed a better understanding of inter-individual variability in birds' response to instrumentation (e.g. only 4 of the 7 birds pecked or pulled the harness on rare occasions in this study) as well as possible gender differences (e.g. Hull 1997, Paredes *et al.* 2005, Ropert-Coudert *et al.* 2007). Both the limited sample size and short study time must temper hasty conclusions given that the system was intended for use on birds over periods of months. Further clarification is also needed on other issues such as the possible emergence of harness-directed behaviours (e.g. pecking at the harness) over time. Some authors have reported that the incidence of such behaviours is generally high immediately following instrumentation but then decreases with time as birds habituate (e.g Gilmer *et al.* 1974, Simeone *et al.* 2002, Chipman *et al.* 2007). Others, however, report no evidence of habituation (e.g. Wilson & Wilson 1989b, Wilson *et al.* 1990, Garrettson *et al.* 2000). To our knowledge, there are no published studies of such behaviours getting worse over time but this does not mean that it does not happen.

It is thus clear that these outcomes represent only the first steps in the development of the Silastic® harness as a less invasive long-term attachment system for seabirds. Further work is needed to determine that physical injury does not occur or that movement is not impaired when the Silastic® harness is worn for weeks or months. Part of this work needs to consider how both these might be related to the tightness of fit of the harness. Quantification of the force and pressure exerted by harnesses of different elasticities on birds in relation to the stretch expected by fitting birds of different sizes with different harnesses should enable workers to propose appropriate multi-size harness according to morphology. These are, however, simple physical measures which, to be useful, need to be translated into the actual effect that they might invoke on the birds. Behavioural and physical examination of birds wearing harnesses of different tightness should clarify this issue so that proper protocols can be proposed rather than having to resort to vague recommendations such as the 3% or 5% rule it has been proposed for the mass-bearing capacity of birds (Croll *et al.* 1992, Kenward 2001, Phillips *et al.* 2003) without any obvious experimentation.

Proper testing of the Silastic® harness must take the study into the field and compare the behaviour of equipped wild birds with those of unequipped conspecifics, preferably over extended periods. This could be done by simple observations but also by examining features which relate to performance such as breeding success since deleterious effects are more likely to be manifest when birds are having to work harder (cf. Saraux *et al.* 2011). Ultimately, wild animals encumbered with external devices are expected to fare worse than unequipped conspecifics. Indeed, it is easy to understand how, by adding extra weight or drag, the attachment of external devices to seabirds might affect their diving or flying performance and thus their foraging efficiency (e.g. Wilson *et al.* 1986, Gales *et al.* 1990, Taylor *et al.* 2001). Among the aberrant behaviours observed in seabirds following their being equipped with devices are, for example, nest desertion (e.g. Watanuki *et al.* 1992, Falk & Møller 1995) and low adult return rates to colonies after foraging trips (e.g. Froget *et al.* 1998, Jackson & Wilson 2002, Paredes *et al.* 2005). An important aspect of this method of attachment is that the Silastic® harness is intended to be deployable on a wide array of seabird species. Unfortunately, and for practical reasons, the first trials of the Silastic® harness could only be conducted on gulls. Although a gull-appropriate harness shape should be suitable for all Larids (e.g. kittiwakes *Rissa sp.*) and most Procellariifomes (e.g. northern fulmars *Fulmaris glacialis*), the body shape of some taxa, such as auks (Alcidae) may differ appreciably, requiring modification to the basic design. Given that the harness is intended to sit beneath the contour feathers, it probably does not need to be particularly robust with respect to environmental conditions. However, some seabirds such as puffins (*Fratercula sp.*) have powerful beaks and may be able to bite through the straps. In that case, modification may be needed to prevent the harness being cut. Although the Silastic® harness disappeared beneath the herring gull plumage to the point where it was invisible, this does not mean that it does not compromise the waterproofing of the plumage in diving birds. Auks, for example, may dive to depths in excess of 100 m (Burger & Simpson 1986, Jury 1986, Jones *et al.* 2002), thus exposing the plumage (and the insulating air contained within it) to 11 atmospheres of pressure. Careful trials will have to be undertaken to ensure that Silastic® harnesses do not compromise plumage properties, especially in diving seabirds.

Thus, between the concept that it might be possible to create a new long-term attachment system for seabirds and its realisation, there is a huge divide. This project still has a long way to go but the first steps have been taken with promising results. In particular, this study has demonstrated that a new approach based on the use of skin-friendly, soft, elastic material (Silastic®) could potentially lead to the construction an attachment system that can stay in place for months while impacting the wearer minimally. Success in this venture would provide an invaluable methodology for many people and its use would substantially enhance our knowledge about seabirds, ultimately improving the management and conservation measures established to protect them.

Acknowledgements

We thank the RSPCA which made this study possible by providing financial support and allowing access to their facilities at Mallydams Wildlife Centre in Hastings, UK to carry out the first trials of the Silastic® harness on captive birds. We are also sincerely grateful to all people (RSPCA staff and members of SMART) who have, by one way or another, contributed to this study. This study was supported in part by the California Department of Fish and Game's Oil Spill Response Trust Fund through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis, USA.

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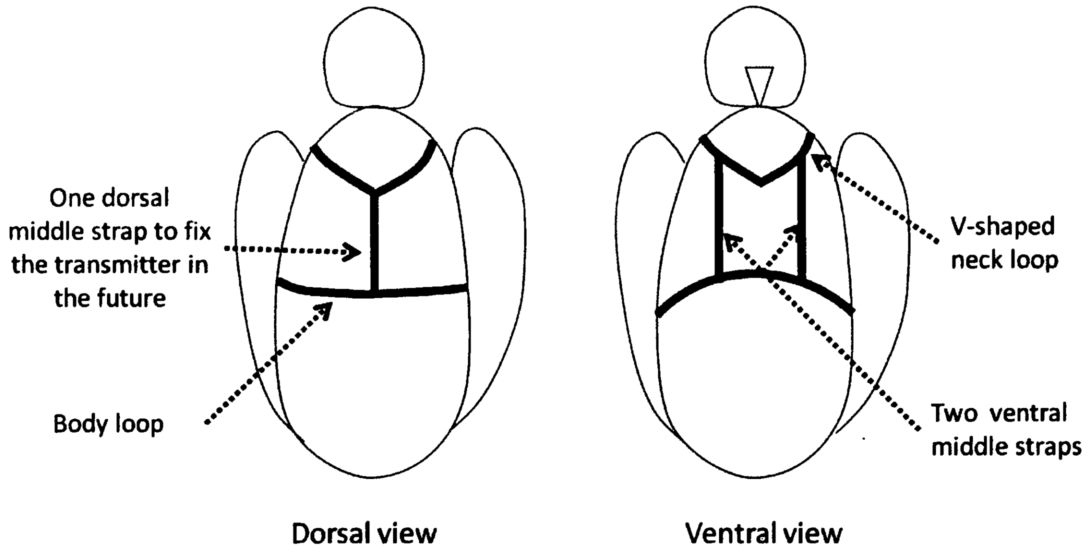

Figure 1. Design selected for the first prototype Silastic® harness.

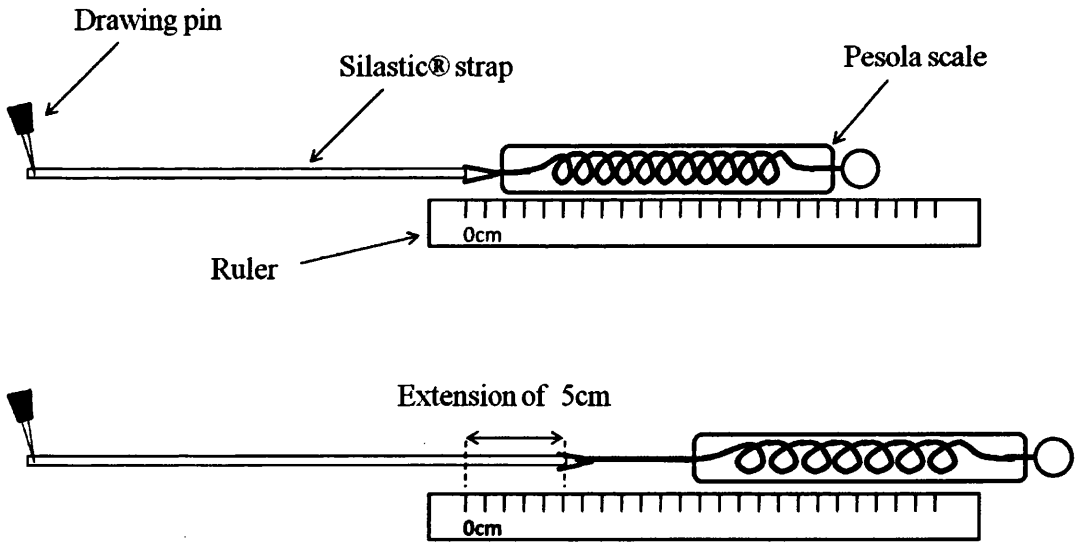

Figure 2. Experimental design to test the elasticity of Silastic® straps incorporating different amounts of silicone oil.

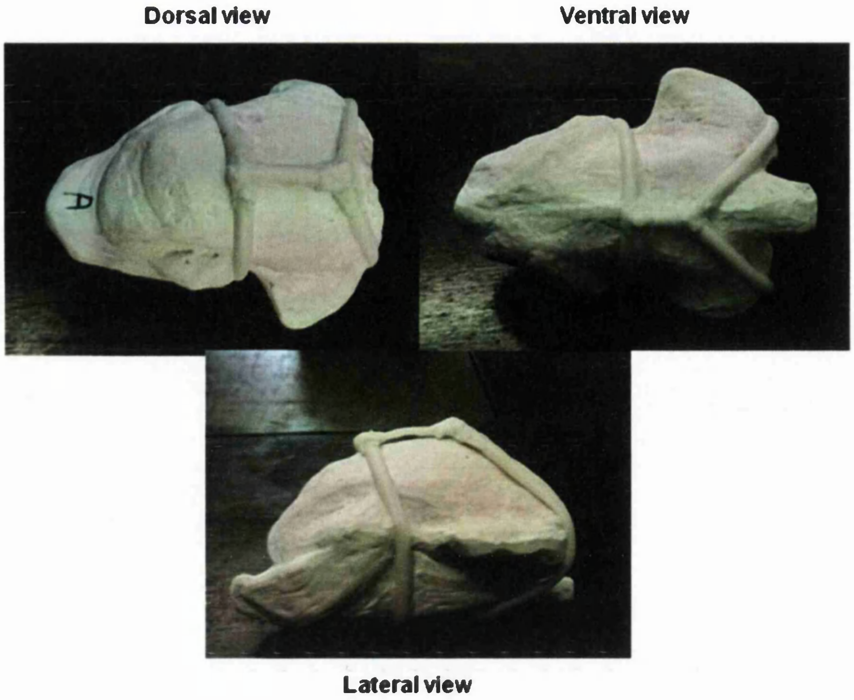

Figure 3. Pictures of the harness in place on a plaster cast of a herring gull body.

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1) Extension of the harness with both hands

2) Harness passed over the bird's head

3) Shoulder straps placed on the shoulders

4) Wings pulled through the lateral spaces between the two loops

5) Body loop sat behind the wings

6) Feathers rearranged using a dissection kit seeker to flick them from underneath the straps

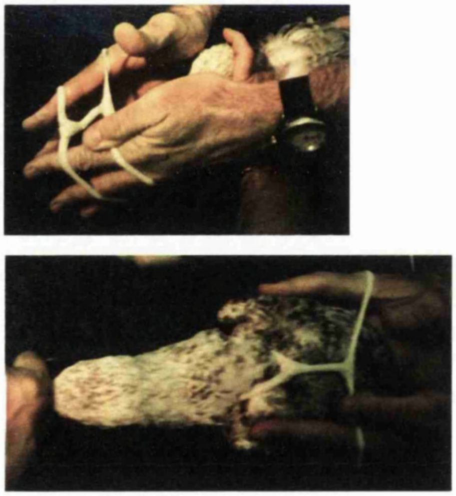

Figure 4. Diagram describing the fitting procedure of the Silastic® harness to a bird. The pictures show a herring gull (*Larus argentatus*) being fitted. Note the orientation of the fingers and hands in relation to the harness and the bird, which ensures that the harness is placed quickly and cleanly with minimal feather disruption.

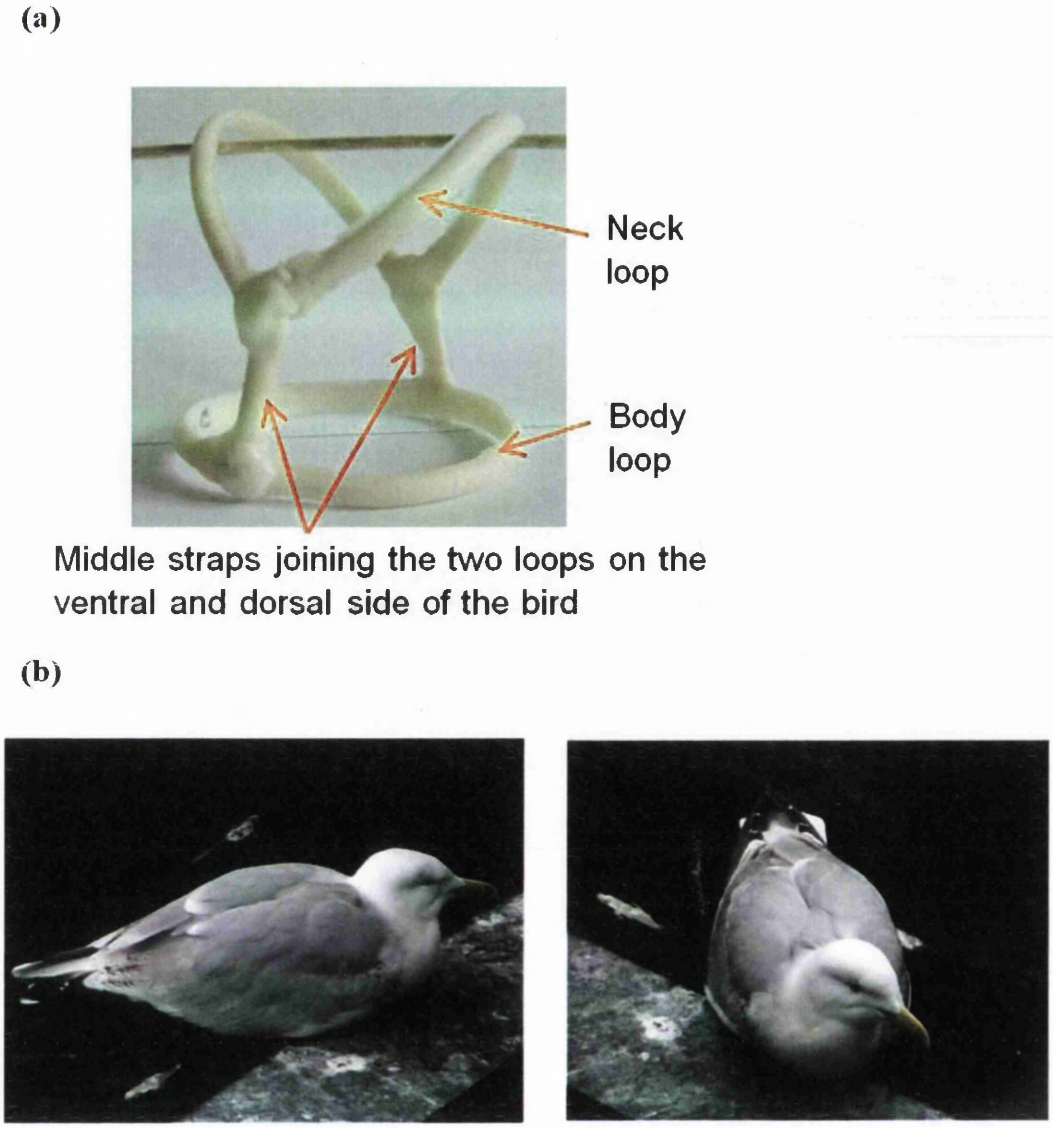

Figure 5. Pictures showing (a) the design of the second (enhanced) Silastic® harness as modified after the first trials undertaken on herring gulls and (b) a gull in captivity wearing this harness. Note that the harness itself is not visible and neither is there any external evidence of it being present via displaced feathers.
NB: Compared to the first version, there is no distinction between the ventral and dorsal sides with just one middle strap of same length on each side. The dimensions of the harness were 28 cm in circumference for the neck loop, 3.5 cm for each middle strap and 26 cm in circumference for the body loop.

Table 1. Description of the main behaviours noted during the observations and the corresponding abbreviations.

Behaviours	**Preening**	**Resting**	**Harness- directed behaviours**	**Walking**	**Flying**	**Swimming**
Description	Bird using its beak or head to preen feathers	Bird motionless, standing or lying on the ground	Bird pulling or pecking the harness with its beak	Bird on the ledge or the platform walking	Bird in the air flying around in the aviary	Bird on the water, surface paddling
Abbreviations	P	R	H	W	FL	SW
Behaviours	**Eating**	**Beak in the water**	**Flapping**	**Shaking**	**Plunging**	**Beak point**
Description	Bird ingesting food	Bird putting its beak in the water	Bird flapping its wings but not engaging substantially in flight	Bird shaking its body	Bird at the water surface plunging into the water	Bird using its beak to aggress another individual
Abbreviations	E	BWA	F	SH	PLU	BI

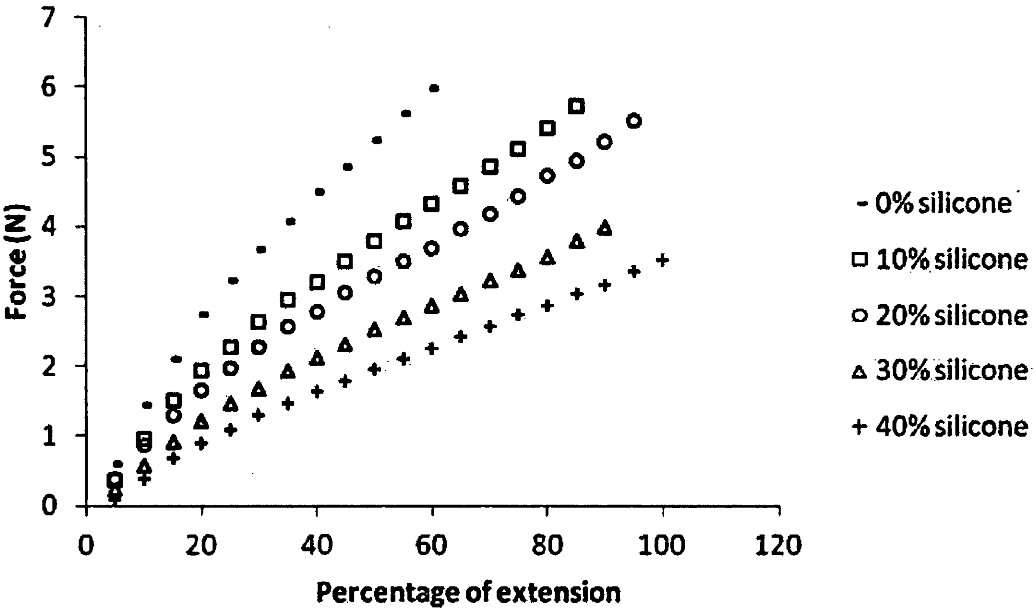

Figure 6. The force required to extend 10 mm wide, semicircular in cross-section, 200 mm-long Silastic® straps made of different percentages of silicone oil. The percentage of extension calculated (X-axis) is the length by which the strap was extended relative to its initial length.

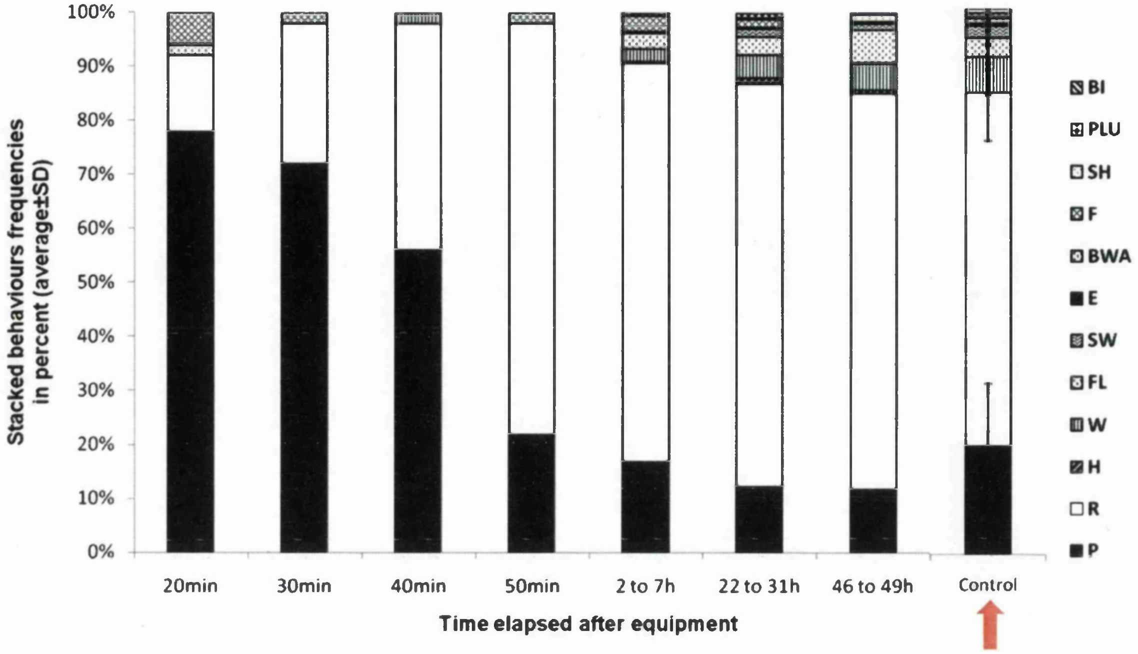

Figure 7. Frequency of occurence of preening and other behaviours in captive, Silastic® harness-fitted gulls (N = 6) as a function of time since being equipped, and compared to observations made on the same unfitted birds (control – indicated by arrow– which also shows standard deviations on arcsine transformed data). Standard deviations for the time categories of the treatment group are not shown for the purpose of clarity.

Keys: P preening, R resting, H harness-directed behaviours, W walking, Fl flying, SW swimming, E eating, BWA beak into the water, F flapping, SH shaking, PLU plunging and BI beak point.

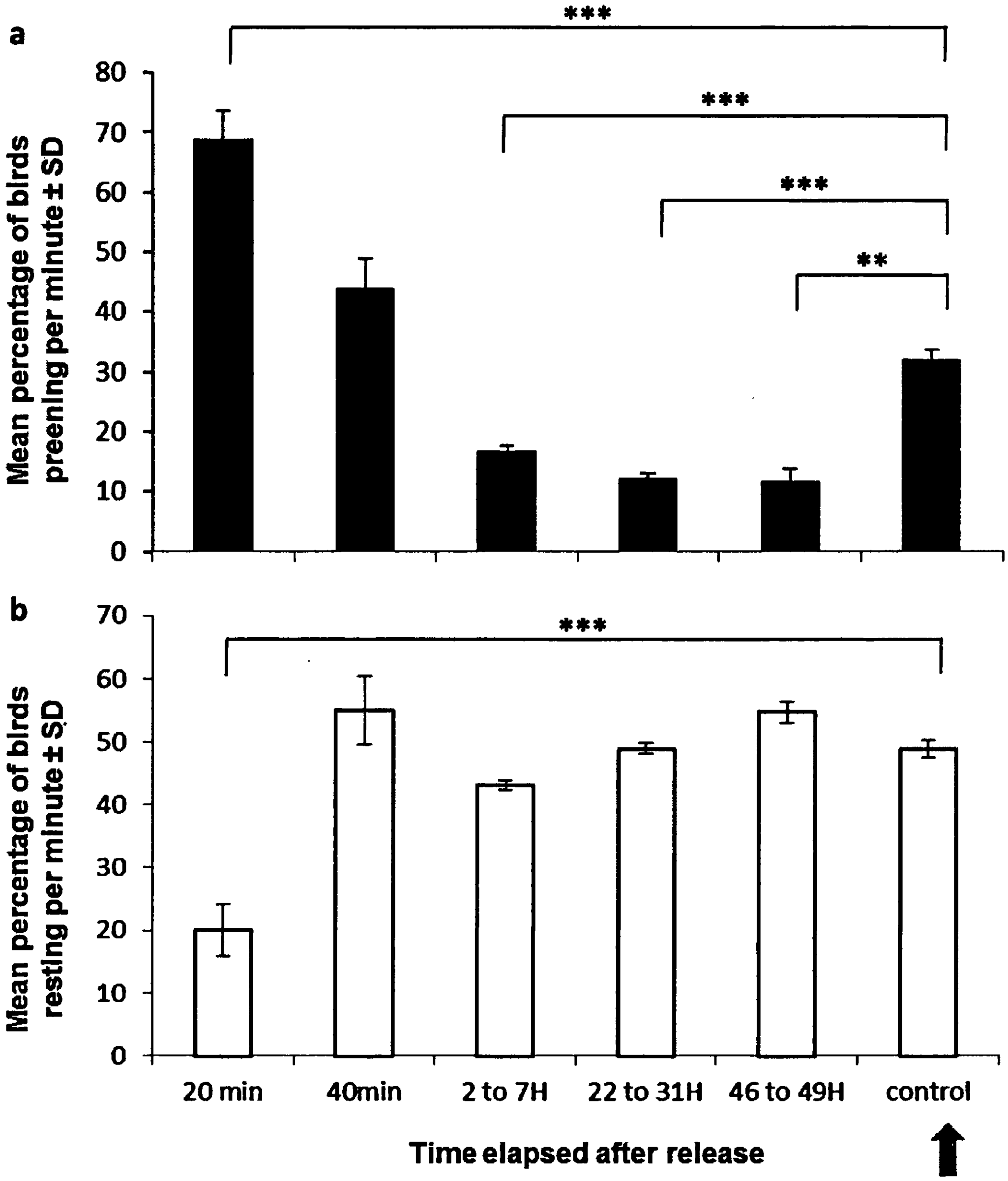

Figure 8. Mean proportion of birds observed (a) preening and (b) resting per minute in captive, Silastic® harness-fitted gulls (N = 6) as a function of time since being equipped, and compared to observations made on the same unfitted birds (control – indicated by arrow). The standard errors were calculated on arcsine transformed data. Stars indicated a significant difference between the treatment group and the control group (Wilcoxon test, *** $P \leq 0.001$, ** $P \leq 0.01$, * $P \leq 0.05$).

Chapter 4:

When three percent may not be three percent; device-equipped seabirds experience variable flight constraints

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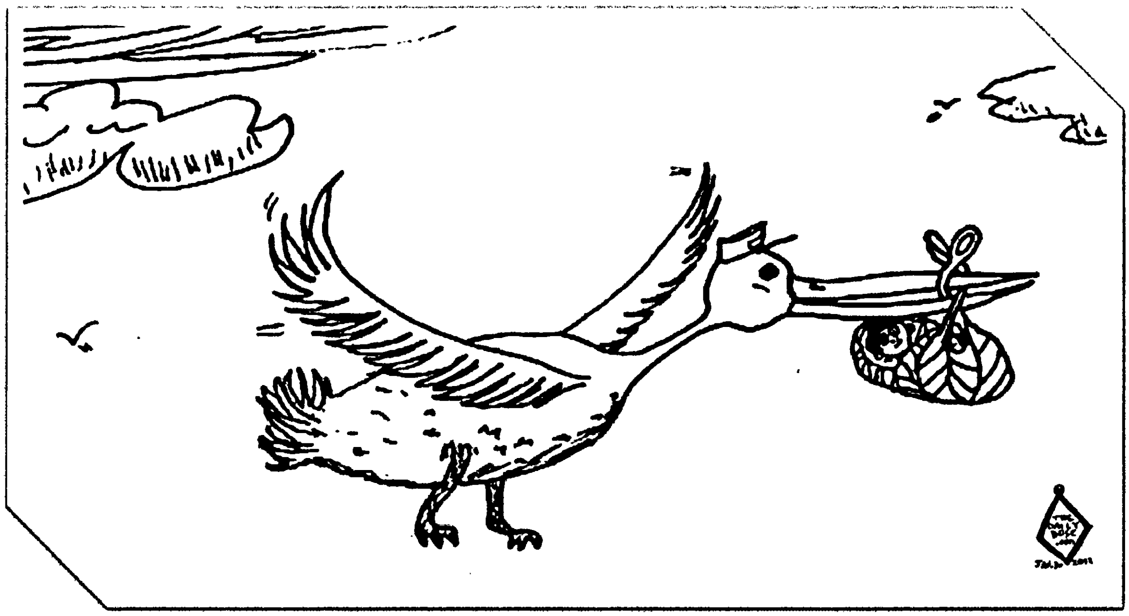

SPV performed the flight modelling calculations and interpreted the results with support from Prof. C. Pennycuick. SPV wrote the manuscript with contributions from RPW, ELCS and AG
Marine Biology (2012) 159, 1-14

Abstract

Current guidelines for instrumenting birds state that external devices should not exceed 3-5% of the birds' body mass, however, the energetic consequences of carrying any given device mass are likely to vary according to the morphology and ecology of the species concerned. We used a freeware program to estimate the mechanical power requirements of flight at the minimum power speed for 80 species of flying seabird from 8 major groups with payloads of increasing mass. Devices representing 3% of the bird's body mass resulted in an increase in energy expenditure for flight ranging from 4.67% to 5.71% without accounting for the increase in body drag coefficient associated with external devices. This effect differed within and between seabird lineages with members of the Alcidae and Phalacrocoracidae experiencing the highest energetic costs of any increase in device mass. We propose that device effects on seabirds could be further reduced through consideration of species-specific effects of added payload and drag.

Keywords: biotelemetry, payload, bird mass, flight cost, energetics

Introduction

Animal-attached devices have immensely enhanced our knowledge about free-living animals (e.g. Gillespie 2001, Wikelski *et al.* 2007, Rutz & Hays 2009) and especially in marine animals, which, though often conspicuous, are difficult to observe continuously (Gauthier-Clerc & Le Maho 2001, Burger & Shaffer 2008). Not only do such devices provide essential information on the biology and ecology of marine species and their role in the oceans (Croxall 1987), but they may also provide quantitative data on a range of physical parameters (Furness & Camphuysen 1997, Fedak 2004, Piatt *et al.* 2007), leading to a better understanding of what governs animal distribution within marine ecosystems (e.g. Fraser & Trivelpiece 1996, Huettmann & Diamond 2001, Yen *et al.* 2004). In an age where technological advances are enabling the instrumentation of an increasing number and diversity of animals (e.g. Ropert-Coudert & Wilson 2005), the need to prevent such devices from deleteriously affecting the bearers is particularly pertinent. This is particularly challenging for seabirds that generally move in two different media, air and water, so that devices may compromise both aerodynamic and hydrodynamic performance. In fact, although attempts have been made to quantify some of the deleterious effects of attached tags on animals swimming underwater (e.g. Bannasch *et al.* 1994, Culik *et al.* 1994, Watson & Granger 1998, Hazekamp *et al.* 2010), there is little systematic attempt to quantify how attached devices may affect flying birds (but see Obrecht *et al.* 1988). Indeed, not having a theoretical basis for understanding the effects of devices has made the question of what exactly constitutes 'deleterious' to remain controversial. For example, whereas an equipped bird experiencing mass loss of 2-3% over 24 h was considered to constitute a serious negative impact on Thick-billed murres (*Uria lomvia)* for Benvenuti *et al.* (1998), Paredes *et al.* (2005) considered that a body mass loss of 2-5% over 24 to 48 h was not drastic. Device impacts can be manifest in different ways; behavioural (e.g. Pietz *et al.* 1993, Paredes *et al.* 2005, Ropert-Coudert *et al.* 2007), energetic (e.g. Culik & Wilson 1991, Schmid *et al.* 1995) and via changes in time constraints (see Culik & Wilson 1992) in addition to physical injuries (e.g. Greenwood & Sargeant 1973, Buehler *et al.* 1995, Wilson & McMahon 2006). Some behavioural abnormalities can be fairly readily assessed (Wilson & Wilson 1989, Blanc & Brelurut 1997, Bowman & Aborn 2001), as can physical injury (Perry 1981, Tuyttens *et al.* 2002, Zschille *et al.* 2008), but determining how attached devices impact the energetics of their carriers is more problematic.

The energetics of birds may be directly affected by externally attached devices in two primary ways. Birds must either expend extra energy countering both the additional mass (e.g. Gessaman & Nagy 1988, Croll *et al.* 1992) and the increased drag (Culik & Wilson 1991, Croll *et al.* 1992, Culik & Wilson 1992, Culik *et al.* 1994) or decrease some aspects of their performance, such as speed (e.g. Wilson *et al.* 1986, Ropert-Coudert *et al.* 2007). Over long deployments such behavioural and energetic changes may affect the individual's fitness, survival and/ or reproductive success (e.g. Paquette *et al.* 1997, Naef-Daenzer *et al.* 2001, Reynolds *et al.* 2004, Saraux *et al.* 2011.

In recognition of the generic disturbance caused by the attachment of external devices, scientists usually comply with two generally accepted recommendation that the weight of the devices should not exceed 3% of a bird's body mass (Kenward 2001) and their cross-sectional area which should be more than 1% of the bird cross-sectional area (Ballard *et al.* 2001). The "3% rule", which is of particular importance when working with flying birds, is however based on scattered observations of various deleterious effects of external devices although consideration of the effect on energetics is conspicuously absent. This stems primarily from the difficulty of measuring the energy expenditure of free-living birds (cf. Butler *et al.* 2004), particularly as it relates to activity-specific metabolic rate.

In this study, we address the paucity of literature on the effects of attached devices on the energetics of flying birds by using a web-based program (Flight 1.22 software – Pennycuick 2008) on a particular bird group (seabirds) to model the energy expended by birds flying with and without extra payloads. We also aim to highlight one of the main potential weaknesses of the current "3% rule", that is to be solely concerned with device mass, by incorporating the effect of drag resulting from externally mounted devices. Specifically, the software allowed us to differentiate drag caused by an increase in the frontal cross-sectional area from the drag caused by the disruption air-flow around a bird's body.

Methods

'Flight' freeware

The Flight program (version 1.22) was developed by Colin Pennycuick (Pennycuick 2008) (latest version of this freeware available online at *http://www.bristol.ac.uk/biology/people/colin-j-pennycuick/index.html*) has been used in one form or another by various authors (e.g. Kvist *et al.* 2001, Norberg & Winter 2006, Tieleman *et al.* 2008, Xirouchakis & Andreou 2009) and was used to simulate the flight costs of different species of seabirds. This software uses aerodynamics theory to estimate the flight parameters of any bird. The user inputs morphological parameters (including body mass, wing span and wing area) and environmental parameters (i.e. air density). Morphometric data are available in the program for a range of species (referred as 'preset birds' on the setup screen) but it is also possible to enter morphometric data for additional species. These data are used to generate a curve of power against speed.

Device mass effect

The aim of this study was to determine the energetic cost of flight in terms of mechanical power by birds carrying different payload masses. This is made possible because the software allows the users to specify a payload mass, separate to the bird body mass. Where the data were available, calculations were performed using the seabird species in 'preset birds'. Morphometric data for additional species were also used, hereafter referred to as 'user birds' in order to enhance the sample size. Note that the term 'bird' refers to a representative individual of a particular bird species and for which the morphometric parameters are mean values calculated from data collected on adults of both sex. A total sample of 80 species, 10 species from each of 8 major lineages of flying seabirds (Alcidae, Diomedeidae, Hydrobatidae, Laridae, Phalacrocoracidae, Procellariidae, Sternidae and Sulidae) was examined (Table 1). For each group of seabirds, we attempted to choose a wide body mass spectrum since body mass affects the energetics of flight substantially (Klaassen 1996, Jenni & Jenni-Eiermann 1998, Hambly *et al.* 2004b). The morphological parameters of the 'user birds' were taken from Del Hoyo *et al.* (1992, 1996), Snow *et al.* (1998), Harrison (1983) and *http://www.bto.org/birdfacts/index.htm*. All calculations used an air density of 1.22 kg m^{-3}.

In order to reach a sample size of 10 birds per group examined, 'user birds' were added that were not available originally available in the program. To be able to enter new species into the program, information on wing area or aspect ratio (see Pennycuick 2008 for definitions) is required. Measurements of wing area and aspect ratio are rare in the literature whereas measurements of span are more readily available. Therefore, we calculated an index that would allow us to derive the wing area from the wing span systematically for morphologically similar species. This index was the wing span divided by the wing area (units: per metre) using data of wing area to wing span available in the program (i.e. data from 'preset birds'). This index was taken from a mean calculated for a minimum of 3 'preset bird' for each of the 8 major groups of seabirds examined for each of the 8 groups of birds. Then it was used to determine the wing area of the additional 'user birds' which meant for each 'user bird' dividing the wing span found in the literature by the index calculated for the group to which it belonged (Table 1). Of the total of 80 birds examined, 29 were 'preset birds' and 51 were 'user birds'.

In this study, we examined the mechanical power required for birds to fly at their calculated minimum power speed (V_{mp}) which is the air speed at which the least power is required from the flight muscles (Pennycuick 2008). This variable was selected as it was considered to be one of the variables most broadly applicable to the range of seabird species examined. All further references to power are to estimates of the mechanical rather than chemical power. The flight mechanical power was calculated for a given flight speed which corresponds to the speed of the bird relative to the air (which may or may not be moving relative to geographic coordinates, as in wind, for example) and therefore does not correspond to groundspeed (except where wind speed = 0). In addition, the mechanical power appeared not to be affected by the flight style of the birds since by definition, for the calculation of flight power, the program only considers continuous flapping flight (rather than bounding flight for example). The power at V_{mp} was computed for 6 different scenarios of payload mass: (1) birds with no payload; (2) birds with a payload that represented 1%; (3) 2%; (4) 3%; (5) 4% or (6) 5% of the bird's body mass.

The increase in power at V_{mp} was also calculated per kilo of body mass in order to enable comparisons of payload effect across species of variable body mass. The mean of the mass-specific power at V_{mp} was determined for each seabird family and its variation was assessed with respect to the load added to the birds. We calculated the gradients and the intercepts from regressions of the mass-specific power at V_{mp} and the size of the load, and these were examined as a function of the body mass using Spearman's correlation (r_s). We considered this at the family level (using the 10 species per family) as well as over the whole dataset or over the following different groups of families: the group including Hydrobatidae, Procellariidae, Sternidae, Sulidae, Laridae and Diomedeidae and the group formed by Alcidae and Phalacrocoracidae.

Device drag effect

All calculations were initially made considering that the birds were equipped with a perfectly streamlined device, with the extra drag resulting only from an increase in the frontal cross-sectional area of the bird. This was obtained by using the default value of 1 set by the program for the payload drag factor which means that the bird's body drag coefficient remained unchanged. To get a more realistic view, however, we also calculated for one species of each family (i.e. 8 species in total) the mechanical power to fly at V_{mp} for a non-streamlined device which would increase the bird body drag coefficient by a factor of 1.5 (the factor is derived from unpublished data of drag measurements we collected in a wind tunnel on a bird model wearing different-sized squares). The calculations were performed for a non-streamlined payload weighing 3% of the bird's body mass. The percentage of increase in the flight cost between the non-streamlined scenario and the unequipped scenario was determined and compared to the percentage increase in flight cost observed between a streamlined scenario (for a payload weighing 3% of the bird's body mass) and the unequipped scenario.

All the tests were performed using Minitab (MINITAB® Release 14.1 version 2003) and a significance threshold of $P < 0.05$.

Results

The calculated power for flying at V_{mp} in unequipped birds varied between 0.12 W (for the least storm-petrel *Halocyptena microsoma* smallest) and 49.8 W (for the grey-headed albatross *Diomedea chrysostoma*). Addition of payloads increased the level of power required to fly as a function of payload mass. Specifically, the additional mechanical power expended by a bird carrying a device (expressed as a percentage of the unequipped mechanical power at V_{mp}) increased linearly with device mass (also expressed as a percentage of body mass), with values for devices weighing 1% of bird body mass inducing increases between 1.3% (great black-backed gull *Larus marinus*) and 2.0% (antartic prion *Pachyptila desolata*); and devices weighing 5% of body mass inducing increases between 8% (European storm-petrel *Hydrobates pelagicus*) and 9.2% (antarctic prion *Pachyptila desolata*) (cf. Figure 1). With respect to devices weighing 3% of bird body mass, an increase in flight cost ranging from 4.67% for the light mantled albatross (*Phoebetria palbebrata*) and 5.71% for the blue footed booby (*Sula nebouxii*) was observed.

Combination of mass-specific power at V_{mp} from all species into mean mass-specific values for families showed that mass-specific power at V_{mp} increased with payload mass at the family level but that slopes and intercepts varied between families (Figure 2 and Table 2). Auks and cormorants had the highest mass-specific power at V_{mp} of the families considered and also the steepest gradients in response to payload. Terns had the lowest values in mass-specific power at V_{mp} and the shallowest gradients. Body mass appeared to affect both gradient and intercept in some instances (Figure 3) with a significant relationship found between intercept and body mass for the Procellariidae and the Laridae (Spearman rank correlation, N = 10, $r_s = 0.72$, $P = 0.02$ and N = 10, $r_s = 0.70$, $P = 0.03$ respectively; Figure 3b plain lines). In the analysis involving all birds from 8 families (i.e. 80 species as one group), there was a significant positive correlation between both gradient and intercept and body mass (Spearman rank correlation, N = 80, $r_s = 0.41$, $P < 0.001$; N = 80, $r_s = 0.42$, $P < 0.001$ for the gradient and intercept, respectively). Consideration of just auks and cormorants together yielded no correlation in either gradient or intercept (Spearman rank correlation, N = 20, $r_s = - 0.43$, $P = 0.06$; N = 20, $r_s = - 0.44$, $P = 0.05$ for the gradient and intercept, respectively) although both were significant when all six other families were grouped (Spearman rank correlation, N = 60, $r_s = 0.58$, $P < 0.001$; N = 60, $r_s = 0.59$, $P < 0.001$ for the gradient and intercept, respectively, Figures 3a and 3b dashed lines).

The mean difference in flight mechanical power at V_{mp} found between the streamlined and the non-streamlined scenarios was X ± SE = 11.5 ± 0.6%, N = 8 and ranged from X ± SE = 10.4 ± 0.2%, N = 10 for the black-browed albatross *(Diomedea melanophris)* to X ± SE = 16.9 ± 3.2%, N = 10 for the common guillemot *(Uria aalge)* (Table 3).

Discussion

Over the past 20 years devices have been deployed on an increasing number and diversity of free-living animals (Ropert Coudert *et al.* 2009, Barron *et al.* 2010), necessitating a broader understanding of the deleterious effects of such devices, and how they may be minimised (Murray & Fuller 2000, Godfrey & Bryant 2003, Barron *et al.* 2010). Among the different features of external devices that can affect birds are the mass (cf. Phillips *et al.* 2003), the shape (cf. Culik *et al.* 1994), the position (cf. Chiaradia *et al.* 2005) and even the colour of the equipment (Wilson *et al.* 1990). This study concentrates on the effects of mass in an added payload, although devices are also likely to result in an increase in the body drag coefficient of the bird (cf. Obrecht *et al.* 1988, Bannasch *et al.* 1994) caused by the disruption of the air flow around the body (Pennycuick 2008). Even when the payload is assumed to be well-streamlined, the software does incorporate the increase in cross-sectional area of the subject animal due to the device.

Mass is critical for flying birds because it changes bird energetics (e.g. Cairns *et al.* 1987, Gessaman & Nagy 1988, Massey *et al.* 1988, Hooge 1991, Passos *et al.* 2010). This is highlighted in migratory birds which limit the amount of fuel they store because increases in body mass lead to a concomitant increase in the cost of transport (Pennycuick 1989). Although scientists may attempt to minimize device mass problems, and particularly behavioural aberrations, by complying with the recommended limit of 3% of the bird's body mass as suggested by Kenward in 2001, there is little information on how device mass affects bird energetics. Cairns *et al.*

(1987) report an increase of 6.1% in the flight costs of common guillemots fitted with units representing about 2.5% of the bird's body mass and this is similar to estimates from our study where, for the 80 species examined, a payload of 3% of the bird's body mass increased energetic cost of flight by approximately 5%. In fact, a 3% in increase in payload does not translate into a simple 3% increase in energetic flight costs. Conversely, no energetic effect of payload was found by Nudds & Bryant (2002) working on zebra finches (*Taeniopygia guttata*) carrying an extraordinary 27% additional mass. Errors in the doubly labelled water methodology (for review see Nagy 1980, Butler *et al.* 2004) used in this study, which can lead to high variance in estimates (e.g. Schultner *et al.* 2010, Shaffer 2010), may be responsible for this. The zebra finch study also only incorporated routine short flights performed between two perches in an aviary and much of the variance presumably stemmed from the way birds partitioned other activities.

Based on Flight's model calculations (Pennycuick 2008), we also assessed the potential effect of extra mass on the energetic expenditure of flying birds by looking at the gradient of the regression between amount of load and energy expenditure. Highest gradients correspond to the greatest effect of extra payload mass. This is in addition to the difference in the amount of power required to fly unencumbered between species, as shown by the variation in intercept (corresponding to no payload) (Figure 2 and Table 2) and which presumably results from morphological differences as well as from variation in wing kinematics and flight styles (e.g. Dial *et al.* 1997, Rayner 1999, Tobalske *et al.* 2003). Here, our analysis indicates that bird energetic response to payload during flight seems to depend critically on species and group (Figures 2 and 3), probably due to differences in morphology, behaviour and ecology (cf. Pennycuick 1987). Flapping flight is one of the most energetically expensive modes of locomotion for vertebrates (Norberg 1990, Hedenström 1993, Rayner 1993), which explains why continuously flapping birds generally have higher energy expenditure than gliding or partially gliding (glide-flappers or flap-gliders) birds (e.g. Birt-Friesen *et al.* 1989, Klaassen 1996). Our results are consistent with this since auks and cormorants, which are continuous flappers (Pennycuick 1987, Spear & Ainley 1997), appeared to have the most energetically expensive flight at V_{mp} (cf. differences in the intercept; Table 2). These two sets of species also appeared to be the most impacted by the payload mass (cf. differences in the gradient; Table 2). However, we noticed that other flapping species such as gulls and terns showed an energetic flight cost at V_{mp} similar to the species using partial gliding such as storm petrels, procellarids and gannets/boobies (Pennycuick 1987, Spear & Ainley 1997). Thus, flight mode is unlikely to be the only parameter to affect payload-based flight energetics.

Various foraging strategies have been documented for different seabird species, ranging from surface feeders to pursuit divers (Cramp & Simmons 1983, Harper *et al.* 1985). Efficient diving is at odds with efficient flight (Wilson *et al.* 1992). Morphological adaptations for diving such as an increase in muscle mass and blood volume (Lovvorn & Jones 1994) and wettable plumage (Mahoney 1984, Ribak *et al.* 2005, Ortega-Jiménez *et al.* 2010) generally result in higher body masses which, associated with the reduced size of the wings (Storer 1960, Rayner 1988, Lovvorn & Jones 1994) lead to an increase in wing loading and therefore higher flight energy expenditure (Pennycuick 1987, 1989, Norberg 1990). The substantial adaptations to diving displayed by auks and cormorants (Pennycuick 1987, Hodum *et al.* 1998, Watanabe *et al.* 2011) in part explain their high power costs for flight as well as their apparent sensitivity to payloads. In fact, there is a significant positive correlation between wing loading and the gradient of the mass-specific mechanical power for flight *versus* payload mass for the four families of flapping species examined in this study (Figure 4, Spearman rank correlation, $r_s = 0.87$, $N = 40$, $P < 0.001$). More precisely, auks and cormorants, which had the highest wing loadings (mean wing loadings of $X \pm SE = 131.6 \pm 0.3$ N m^{-2}, $N = 10$ and $X \pm SE = 89.0 \pm 0.2$ N m^{-2}, $N = 10$, respectively), also had steeper gradients than gulls or terns (mean wing loadings of $X \pm SE = 38.2 \pm 0.1$ N m^{-2}, $N = 10$ and $X \pm SE = 23.5 \pm 0.07$ N m^{-2}, $N = 10$), strongly suggesting that wing morphology and body mass are key factors in modulating the impact of payloads on the flight energetic of seabirds.

The issue of how bird mass affects the energetics of flight in device-equipped birds in general has been previously discussed by Tucker (1977) and Caccamise & Heidin (1985), who noted that device mass impacts larger birds more because heavier birds have less 'power surplus'. In a similar manner, large migratory birds using flapping flight face greater energetic costs than small birds (Pennycuick 1972, Klaassen 1996). Our work on flap-gliders also points to larger birds being absolutely more affected by devices, although significant intra-family differences were only apparent in gulls and procellarids, perhaps because individuals from these groups had the broadest range of body mass (from 0.16 to 4.50 kg and from 0.23 to 3.15 kg, respectively) but also because it is likely to be a multifactorial problem. Similarly, Birt-Friesen *et al.* (1989) noted significant differences in intercepts of regressions of metabolism and body mass in various bird groups, including albatrosses, alcids, diving petrels, gannets, gulls, penguins, procellarids and storm-petrels.

Beyond mass, although the drag associated with tags has been relatively well studied on swimming birds (e.g. Wilson *et al.* 2004, Ropert-Coudert *et al.* 2007, Saraux *et al.* 2011), little is known about the negative impacts of tracking devices attached to flying birds. Despite the lower density of air compared to water, our results indicate that flying birds equipped with non-streamlined devices may have power costs some 17.1±2.3% (mean calculated for the 8 species presented in Table 3) higher than unequipped birds. This is about 3 times higher than the 5.1±0.2% average increase observed between birds equipped with streamlined devices and unequipped birds (mean calculated for the 8 species presented in Table 3). Clearly, consideration of both mass and drag are important in proper formulation of a "3% rule" especially since the devices currently used on birds are unlikely to be perfectly streamlined.

Limitations of the study

Calculations of energy expenditure based on aerodynamic models usually overestimate the measured energetic cost of flight of birds carrying extra load (Kvist *et al.* 2001, Hambly *et al.* 2004a, Schmidt-Wellenburg *et al.* 2007, 2008). One explanation for this is that birds may adjust their behaviour and/or body condition or physiology so that energy expenditure can remain approximately at the same level in equipped and unequipped birds. This occurs at the expense of other flight parameters, however. Among the main behavioural responses recorded are a decrease in flight speed (e.g. Videler *et al.* 1988, Hambly *et al.* 2004a), a decrease in take-off velocity (e.g. Nudds & Bryant 2002) and/or a change in the time spent flying (e.g. Gessaman *et al.* 1991, Hooge 1991). Although such responses ostensibly reduce the energetic cost of flight, they have associated costs, such as reduced foraging efficiency (Gales *et al.* 1990, Weimerskirch *et al.* 2000, Navarro *et al.* 2008) or a decrease their capacity to escape predators (Burns *&* Ydenberg 2002). Importantly, device effects may vary in relation to deployment duration and the environmental conditions (Wilson & McMahon 2006, Saraux *et al.* 2011).

Our study examines one flight metric (power) whereas many, if not all, of the flight characteristics of a bird carrying extra mass can be affected, some that are also detailed by the Flight program. For example, a great cormorant (*Phalacrocorax carbo*) carrying a payload of 5% of its body mass would have its maximum rate of climb reduced from 0.43 to 0.41 m s^{-1} (a drop of 4.7%), show an increase in its minimum power speed from 16.5 to 16.8 m s^{-1} (an increase of 1.8%), incur an increase in the speed at which it has the maximum effective lift:drag ratio from 26.4 to 26.8 m s^{-1} (an increase of 1.5%) while the lift to drag ratio would decrease from 13.8 to 13.7 (0.7%) and the wing-beat frequency at V_{mp} would increase from 5.09 to 5.18 Hz (1.7%), (Table 4). The ecological significance of these changes presumably varies according to the species concerned so a case by case analysis would seem appropriate.

Our method also assumes that all birds examined can be effectively modelled by the Flight program (Flight 1.22) without taking into account the differences inherent in the way species live. For example, albatrosses and petrels rely heavily on dynamic soaring for efficient flight (Pennycuick 2002) and have energy expenditures for flight that are correlated with wind speed (Calvo *&* Furness 1992, Furness *&* Bryant 1996, Bowlin *&* Wikelski 2008) so the impact of attached devices will presumably vary according to meteorological conditions. Similarly, many gulls use thermal soaring to move (Brown 1963, Croxall 1987) and some seabirds such as shearwaters (Rosén *&* Hedenström 2001) and cormorants (De la Cueva *&* Blake 1993) may even use the ground effect. All these behaviours may cause estimated energetic flight costs to vary from those calculated and may even help mitigate the effects of device mass.

Free-living birds routinely have to carry payloads when flying with food in their digestive system or in their beaks or gular pouches (cf. Vermeer 1981, Mehlum *&* Gabrielsen 1993, Sydeman *et al.* 1997), either for provisioning their chicks or for self-provisioning. In this respect, our calculations are conservative since we have assumed all birds to be flying empty. The amount of weight carried as food by seabirds generally varies between approximately 2% for sooty terns (*Sterna fuscata*, Ricklefs & White 1981) to about 15-20% (ignoring non-volant species) for albatrosses although they have been recorded flying with payloads of about 30% of their body mass (Weimerskirch *et al.* 1997, 2000). We note that incorporation of device mass on top of mass carried as food could prove pivotal for power requirements during flight. For instance, a great cormorant transporting an average food load mass of 330 g (Grémillet *et al.* 1996) would have to provide 18% more power to fly at V_{mp} than an empty conspecific, and if additionally equipped with a 3% payload, this figure would increase to 22%. Likewise, the amount of time spent in flight per day can vary considerably inter-specifically (e.g. Pelletier *et al.* 2008, Ryan *et al.* 2010, Thaxter *et al.* 2010) so birds that spend little time flying, such as thick-billed murres, which spend on average 7.1% of their time flying (1.7 hours per day, Falk *et al.* 2000), will presumably use relatively less energy per day compensating for device mass than, for example, an albatross such as the grey-headed albatross, which spends up to 74% (up to 13-20 hours per day) of its time aloft (Prince & Francis 1984, Afanasyev & Prince 1993). Intra-specific variation in flight duration (e.g. Hull *et al.* 2001, Ryan *et al.* 2010) will be affected similarly.

Overall, although the Flight program clearly has its limitations, it does at least give a first assessment of the expected costs of flight for seabirds carrying payloads, which we would argue is markedly more informative than simple adherence to the 3% rule (Kenward 2001). As early as 1985, Caccamise & Hedin (1985) argued that, given the range of variation in load weight based on a fixed percentage of body mass between large birds and small birds, it is inappropriate to apply the same tagging method to all birds. In addition, variation in the amount of time that particular species spend flying, coupled with putative payloads due to food could, and should, be built into assessments of the effect of devices on birds by researchers who can access the Flight program as freeware. Such an approach would allow workers to determine whether their proposed research is likely to compromise the study animal's welfare unacceptably or, at the very least, allow them to consider how, and to what extent, bird ecology, behaviour and welfare might be impacted.

It is unlikely that we will ever be able to put an external device on a free-flying bird without impeding it somewhat (cf. Calvo & Furness 1992), despite the huge advances that are being made in the miniaturization of electronics (Ropert-Coudert & Wilson 2005) but careful consideration of how birds are likely to react to devices can be theoretically assessed via models such as that used in the Flight program. We note that a quantitative treatment of the relationship between device shape, size, placement on the body and the consequences of this for an animal's energy expenditure may require more detailed consideration. Nonetheless, the type of approach taken in this study should bolster visual observations (e.g. Fraser *et al.* 2002, Garthe *et al.* 2007, Watanuki *et al.* 2008) and other quantitative examinations of behaviour (Wilson *et al.* 1986, Ropert-Coudert *et al.* 2007), to inform us of the strengths and weaknesses of device systems that we may aspire to use and ultimately give us clues as to their biological utility.

Acknowledgments

We are grateful to Colin Pennycuick for his help at various stages from the use of his Flight program to his constructive comments on the manuscript. We also thank Adrian Gleiss for helpful discussions. Finally, this study would have not been carried out without financial support from the California Department of Fish and Game's Oil Spill Response Trust Fund (through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis) and the Royal Society for Prevention of Cruelty to Animals (RSPCA, Wilberforce Way, Southwater, Horsham, West Sussex, RH13 9RS, United Kingdom).

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Table 1. List of the species of seabirds examined in the study sorted by family and presenting the body mass used for the analysis and the average (X ± SE) ratio between wing span and wing area (units: per metre) used to derive the wing area from the wing span when required. In black are the names of the 'preset birds' and in blue the names of the 'user birds'.

Family	**Species name**	**Body mass (kg)**	**Mean ratio wing span to wing area**
Hydrobatidae	European Storm-petrel *(Hydrobates pelagicus)*	0.03	X ± SE = 18.55 ± 1.29 m^{-1}, N = 5
	Grey-backed Storm-petrel (*Garrodia nereis)*	0.03	
	Wilson's Storm-petrel (*Oceanites oceanicus)*	0.03	
	Black-bellied Storm-petrel (*Fregatta tropica)*	0.07	
	Least Storm-petrel (*Halocyptena microsoma)*	0.02	
	Leach's Storm-petrel (*Oceanodrona leucorhoa)*	0.04	
	White-faced Storm-petrel (*Pelagodroma marina)*	0.05	
	Fork-tailed Storm-petrel (*Oceanodroma furcata)*	0.06	
	White-bellied Storm-petrel (*Fregatta grallaria)*	0.06	
	Tristram's Storm-petrel (*Oceanodroma tristrami)*	0.08	
Procellariidae	Antartic prion *(Pachyptila desolata)*	0.16	X ± SE = 10.98 ± 0.65 m^{-1}, N = 7
	Cape petrel *(Daption capensis)*	0.42	
	Northern fulmar *(Fulmaris glacialis)*	0.85	
	White-chinned petrel *(Procellaria aequinioctialis)*	1.23	
	Northern giant petrel *(Macronectes halli)*	3.80	
	Grey petrel *(Procellaria cinerea)*	1.00	
	Antarctic petrel *(Thalassoica antarctica)*	0.68	
	Soft-plumaged petrel *(Pterodroma mollis)*	0.31	
	Flesh-footed shearwater (*Puffinus carneipes)*	0.57	
	Southern giant petrel (*Macronectes giganteus)*	4.50	
Sternidae	Brown noddy (*Anous stolidus)*	0.17	X ± SE = 11.37 ± 0.62 m^{-1}, N = 3
	Sooty tern (*Sterna fuscata)*	0.20	
	Little tern (*Sterna albifrons)*	0.06	
	Royal tern (*Thalasseus maximus)*	0.45	
	Artic tern (*Sterna paridisea)*	0.10	
	Caspian tern *(Sterna caspia)*	0.65	
	White-winged black tern *(Childonias leucopterus)*	0.06	
	Black tern *(Childonias niger)*	0.07	
	Forster's tern *(Sterna forsteri)*	0.16	
	Bridled tern *(Sterna anaethetus)*	0.14	
Alcidae	Razorbill *(Alca torda)*	0.66	X ± SE = 14.52 ± 0.50 m^{-1}, N = 4
	Common guillemot (*Uria aalge)*	0.86	
	Atlantic puffin *(Fratercula artica)*	0.40	
	Black guillemot *(Cephus grylle)*	0.45	
	Little auk (*Alle alle*)	0.15	
	Pigeon guillemot (*Cepphus columba*)	0.51	

	Tufted puffin (*Fratercula cirrhata*)	0.78	
	Thick-billed murre (*Uria lomvia*)	1.12	
	Horned puffin (*Fratercula corniculata*)	0.61	
	Least auklet (*Aethia pusilla*)	0.09	
Phalacrocoracidae	Great cormorant (*Phalacrocorax carbo*)	2.53	X ± SE = 6.29 ± 0.12 m^{-1}, N = 4
	Common shag (*Phalacrocorax aristotelis*)	1.75	
	Double-crested cormorant (*Phalacrocorax auritus*)	1.51	
	Imperial shag (*Phalacrocorax atricep)*	2.23	
	Bank cormorant (*Phalacorocrax neglectus*)	1.80	
	Long-tailed cormorant (*Phalacorocrax africanus*)	0.68	
	Spotted shag (*Phalacrocorax punctatus*)	0.96	
	Japanese cormorant (*Phalacrocorax capillatus*)	2.80	
	Red-faced cormorant (*Phalacrocorax urile*)	2.10	
	Little black cormorant (*Phalacrocorax sulcirostris*)	0.87	
Sulidae	Red-footed booby (*Sula sula*)	1.05	X ± SE = 7.46 ± 0.23 m^{-1}, N = 3
	Brown booby (*Sula leucogaster*)	1.15	
	Northern gannet (*Morus bassana*)	2.11	
	Cape gannet (*Morus capensis*)	2.60	
	Blue-footed booby (*Sula nebouxii*)	1.55	
	Australasian Gannet (*Morus serrator)*	2.00	
	Masked booby (*Sula dactylatra*)	1.79	
	Nazca booby (*Sula granti*)	1.30	
	Abbott's booby (*Sula abbotti*)	1.46	
	Peruvian booby (*Sula variegata*)	1.41	
Laridae	Black-legged kittiwake (*Rissa tridactyla*)	0.39	X ± SE = 7.65 ± 0.59 m^{-1}, N = 7
	Black-headed gull (*Larus ridibundus)*	0.29	
	Lesser black-backed gull (*Larus fuscus*)	0.80	
	Herring gull (*Larus argentatus*)	0.86	
	Great blac- backed gull (*Larus marinus*)	1.52	
	Kelp gull (*Larus dominicanus*)	1.11	
	Black-billed gull (*Larus bulleri*)	0.23	
	Heermann's gull (*Larus heermannii)*	0.51	
	Ivory gull (*Pagophila eburnea)*	0.61	
	Common gull (*Larus canus)*	0.43	
Diomedeidae	Black-browed albatross (*Diomedea melanophris)*	3.15	X ± SE = 5.79 ± 0.41 m^{-1}, N = 3
	Grey-headed albatross (*Diomedea chrysostoma)*	3.60	
	Sooty Albatross (*Phoebetria fusca)*	2.50	
	Light-mantled albatross (*Phoebetria palbebrata)*	3.00	
	Black-footed albatross (*Phoebastria nigripes)*	3.10	
	Laysan albatross (*Phoebastria immutabilis)*	2.85	
	Shy albatross (*Thalassarche cauda)*	3.90	
	Atlantic yellow-nosed albatross (*Thalassarche chlororhynchus)*	2.20	
	Waved albatross (*Phoebastria irrorata)*	3.40	
	Salvin's albatross (*Thalassarche salvini)*	3.59	

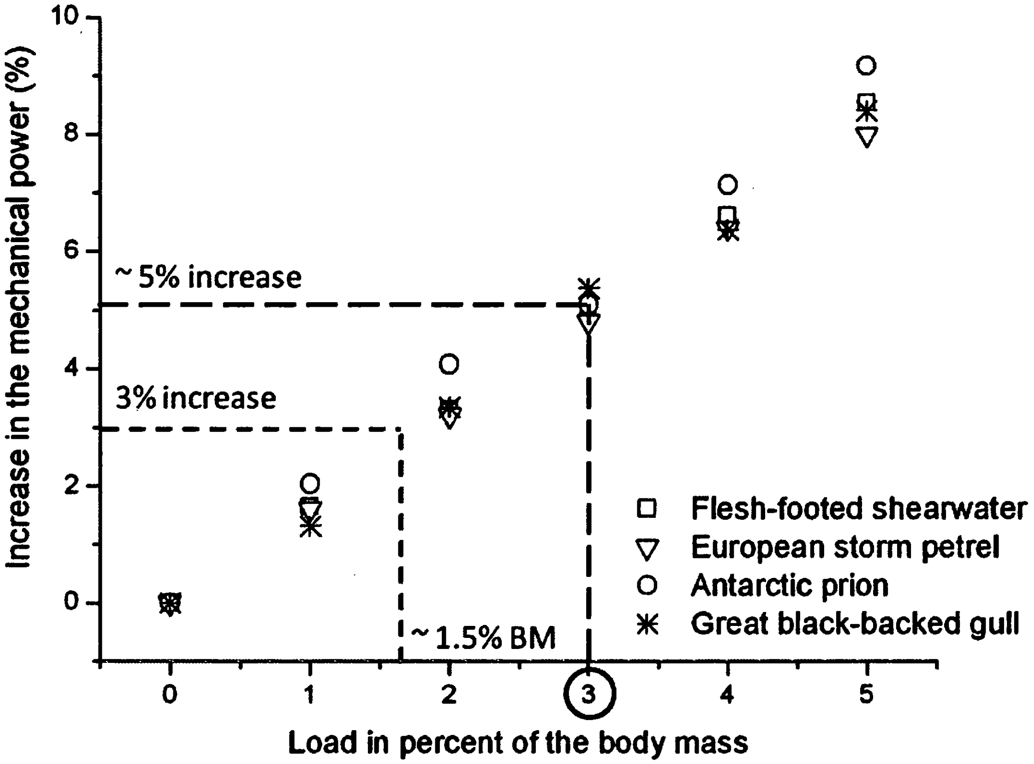


Figure 1. Examples of the mechanical power at V_{mp} used by different seabird species during flight (expressed as a percentage of the power power required for unequipped flight at V_{mp}) as a function of the extra mass carried. The dashed lines show how loads amounting to *ca.* 1.5% and 3% of bird body mass equate to *ca.* 3% and 5% increases in mechanical power, respectively.

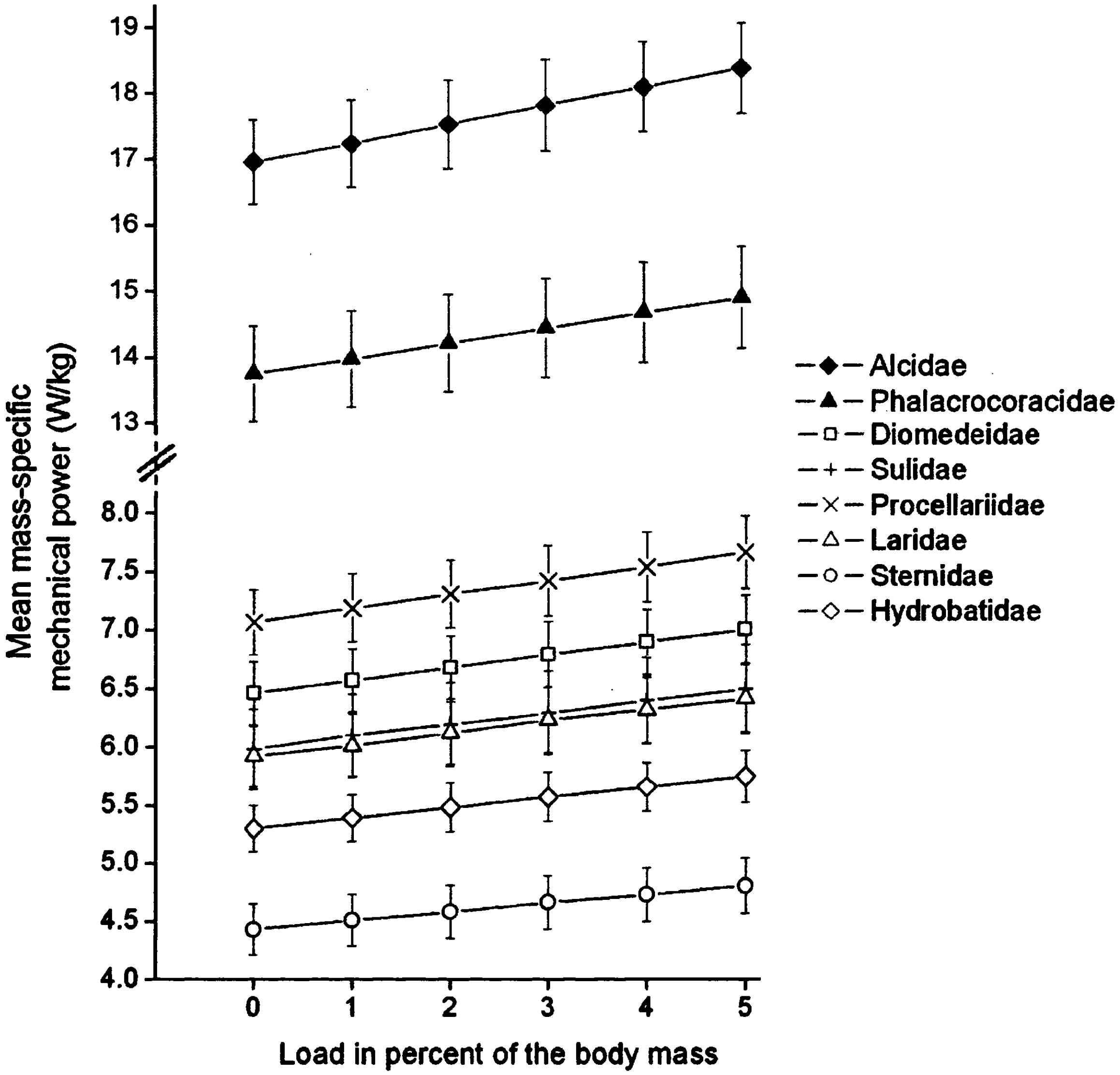


Figure 2. The mean mass-specific mechanical power at V_{mp} calculated for 10 species from 8 major groups of seabird as a function of the payload mass (expressed as a percentage of the body mass). Bars show standard error. Gradients and intercepts of the regression are shown in Table 2.

Table 2. Mean gradient and intercept obtained from the regressions between the mass-specific mechanical flight power at V_{mp} and the payload mass calculated for each of the 8 groups of seabird included in this study (see Figure 2). The species are sorted in ascending order in terms of energetic impact of the payload. This table provides an easy way for researchers to estimate the mass-specific power at V_{mp} for any seabird species belonging to one of the illustrated families during flight when equipped with a given payload.

Familly	**Gradient**	**Intercept**
Sternidae	X ± SD = 0.07 ± 0.0113, N = 10	X ± SD = 4.43 ± 0.6942, N = 10
Hydrobatidae	X ± SD = 0.09 ± 0.0111, N = 10	X ± SD = 5.30 ± 0.6289, N = 10
Laridae	X ± SD = 0.10 ± 0.0151, N = 10	X ± SD = 5.92 ± 0.8299, N = 10
Sulidae	X ± SD = 0.10 ± 0.0178, N = 10	X ± SD = 5.99 ± 0.9858, N = 10
Diomedeidae	X ± SD = 0.11 ± 0.0140, N = 10	X ± SD = 0.50 ± 0.8279, N = 10
Procellariidae	X ± SD = 0.12 ± 0.0147, N = 10	X ± SD = 6.99 ± 0.9052, N = 10
Phalacrocoracidae	X ± SD = 0.23 ± 0.0371, N = 10	X ± SD = 13.74 ± 2.2635, N = 10
Alcidae	X ± SD = 0.29 ± 0.0293, N = 10	X ± SD = 16.95 ± 2.0533, N = 10

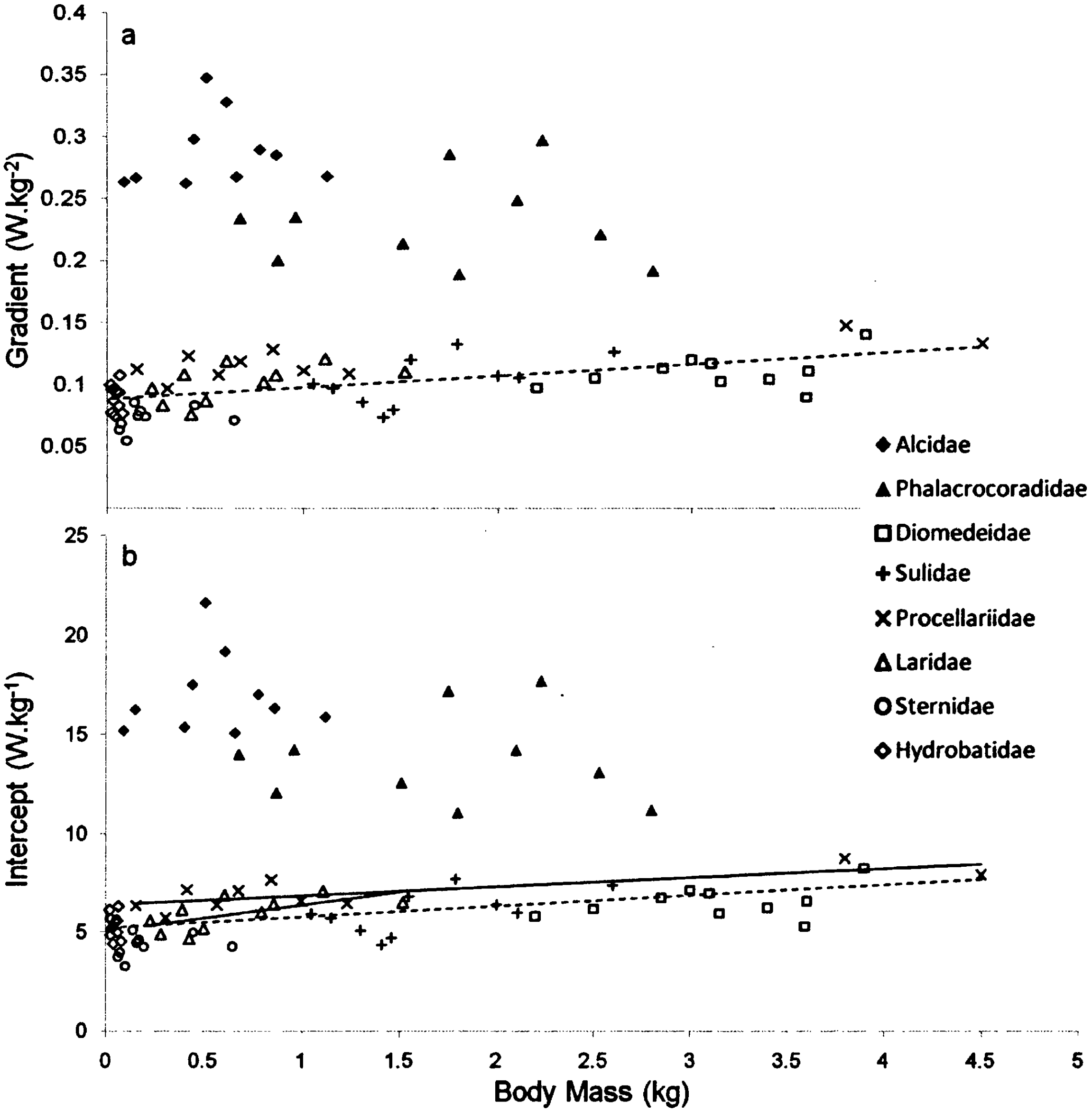


Figure 3. The gradient (a) and the intercept (b) obtained from the regression between the mass-specific mechanical power for flight at V_{mp} and the extra mass added to a bird (see Figure 2 and Table 2) for each of the 10 species from the 8 major groups of seabirds considered in this study as a function of body mass. Each point represents a species from a particular seabird family denoted by the symbol. Only the significant Spearman rank correlations between the body mass (X axis) and either the slope (Y axis in Figure 3a) or the intercept (Y axis in Figure 3b) are shown. The linear regression equations are: $y = 0.0046x + 0.1341$ (group including Hydrobatidae, Procellariidae, Sternidae, Sulidae, Laridae and Diomedeidae; dashed line Figure 3a), $y = 1.3301x + 5.0207$ (Laridae; short plain line Figure 3b), $y = 0.4589x + 6.3727$ (Procellariidae; long plain line Figure 3b), $y = 0.2646x + 7.9208$ (group including Hydrobatidae, Procellariidae, Sternidae, Sulidae, Laridae and Diomedeidae; dashed line Figure 3b).

Table 3. Mechanical power to fly at V_{mp} for unequipped birds, birds equipped with a streamlined payload (i.e. the bird drag coefficient remains unchanged) and birds with a non-streamlined payload (i.e. the bird drag coefficient is increased by a factor of 1.5– see text). For the device scenarios, the flight mechanical power costs were calculated for payloads weighing 3% of the bird's body mass. The results are given for just one species from each of the 8 seabird families examined in this study.

Species	**Scenario**	**Mass-specific flight mechanical power cost (W/kg)**	**Increase in flight mechanical power cost compared to unequipped scenario (%)**
Black-browed albatross *(Diomedea melanophris)*	Unequipped bird	5.94	-
	Streamlined device	6.03	5.35
	Non-streamlined device	6.16	16.04
Sooty tern *(Sterna fuscata)*	Unequipped bird	4.27	-
	Streamlined device	4.34	5.02
	Non-streamlined device	4.41	16.15
Black-legged kittiwake *(Rissa tridactyla)*	Unequipped bird	6.12	-
	Streamlined device	6.22	5.39
	Non-streamlined device	6.32	16.60
Wilson's storm petrel *(Oceanites oceanicus)*	Unequipped bird	5.19	-
	Streamlined device	5.28	5.03
	Non-streamlined device	5.36	16.20
Northern fulmar *(Fulmarus glacialis)*	Unequipped bird	7.65	-
	Streamlined device	7.77	4.95
	Non-streamlined device	7.90	16.23
Brown booby *(Sula leucogaster)*	Unequipped bird	5.70	-
	Streamlined device	5.79	5.04
	Non-streamlined device	5.89	16.34
Great cormorant *(Phalacrocorax carbo)*	Unequipped bird	13.12	-
	Streamlined device	13.32	4.82
	Non-streamlined device	13.56	16.27
Common guillemot *(Uria aalge)*	Unequipped bird	7.22	-
	Streamlined device	7.33	4.98
	Non-streamlined device	7.46	22.83

Table 4. Examples of flight characteristics other than the flight mechanical power at V_{mp}, computed using the Flight program for a great cormorant (*Phalacrocorax carbo*), that are predicted to be modified as a consequence of extra mass. Minimum power speed V_{mp} is the speed for minimum mechanical power in level flight; Maximum range speed V_{mr} is the speed at which the effective lift:drag radio is at a maximum; Maximum rate of climb is the rate of climb when flying at V_{mp} and exerting maximum power; Maximum effective L/D is the value of the effective lift:drag ratio when flying level at the maximum range speed V_{mr}; Wingbeat frequency is the wingbeat frequency expected in level flight at V_{mp}.

	Unequipped bird	**Bird with a payload of 5% its body mass**	**Difference in %**
Minimum power speed V_{mp} (m s^{-1})	16.5	16.8	1.8 (+)
Maximum range speed V_{mr} (m s^{-1})	26.4	26.8	1.5 (+)
Maximum rate of climb (m s^{-1})	0.432	0.411	4.7 (–)
Maximum effective L/D	13.8	13.7	0.7 (–)
Wingbeat frequency (Hz)	5.09	5.18	1.7 (+)

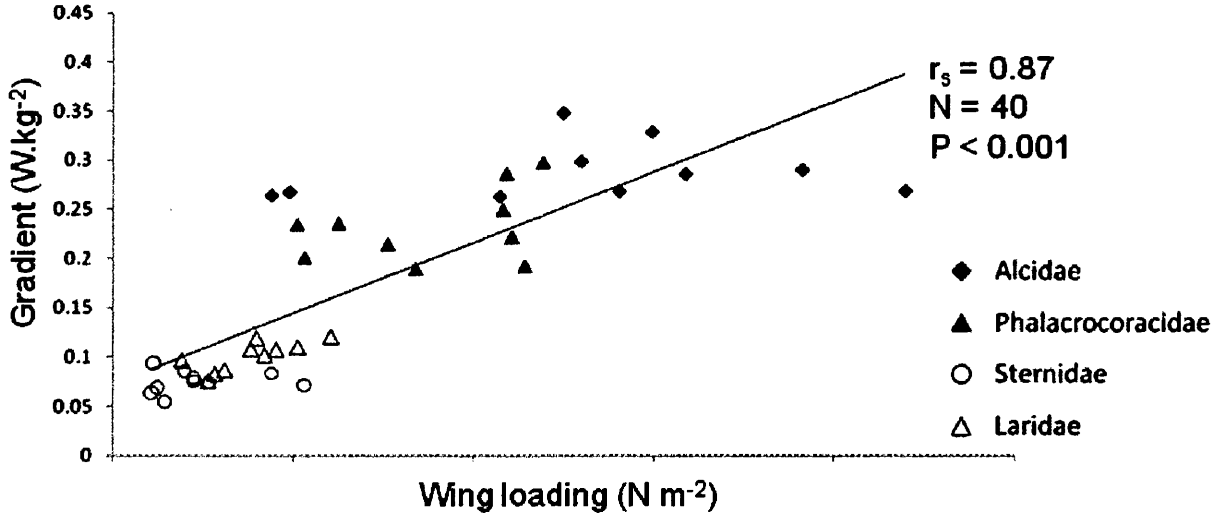
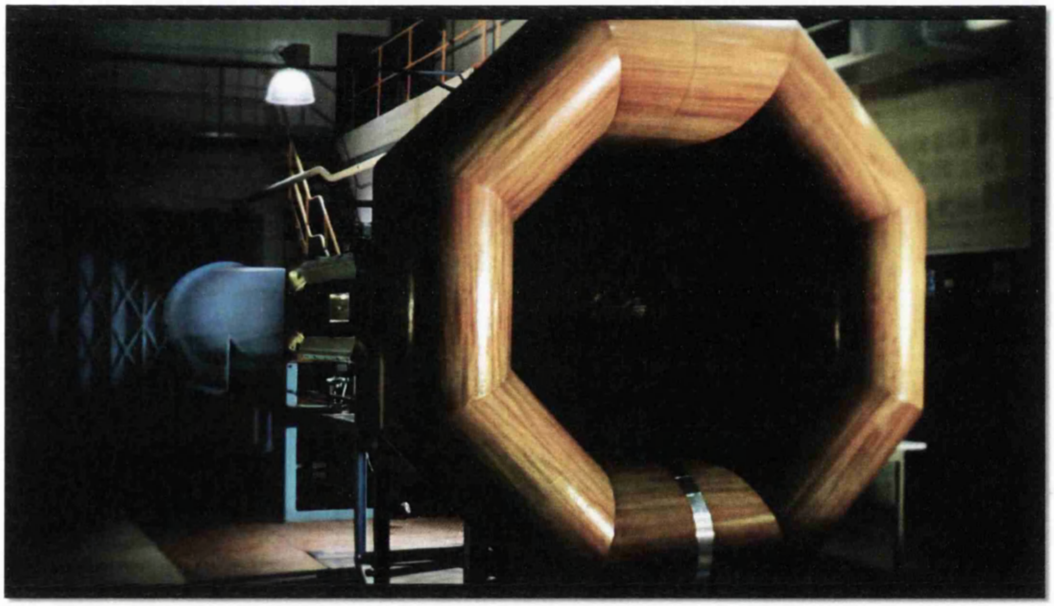


Figure 4. The gradient obtained from the regression between the mass-specific flight mechanical power at V_{mp} and the extra mass added to a bird (see Figure 2 and Table 2) for each of the 4 families of flappers (Pennycuick 1987, Spear & Ainley 1997) considered in this study as a function of their wing loading. Each point represents a species from a particular seabird family denoted by the symbol. The line indicates a significant correlation between wing loading and gradient.

Chapter 5:

Best practice for attaching external tags to birds; minimizing drag by modulating device shape and placement

Sylvie P. Vandenabeele & Rory P. Wilson



Wind tunnel facility at Swansea University

SPV, advised by RPW, conducted the wind tunnel tests with assistance from colleagues. SPV analysed the data and wrote the manuscript (short paper following an oral presentation) with inputs from RPW.

Proceedings of the 11th International Effects of Oil on Wildlife Conference (2012) New Orleans, Louisiana, USA

Abstract

Determination of the fate and movements of rehabilitated oiled seabirds is one of the most pressing issues facing oiled wildlife care organizations*. Although satellite tracking technology would make this technically possible, potential device-induced deleterious effects make this approach equivocal. Very few attempts have been made in order to assess the negative effects of such devices on the subject animals. This project aspires to determine how external packages potentially affect the aero-/hydro-dynamism of seabirds and seeks to formalize a package that can be used in post-release tracking studies on rehabilitated seabirds with defined, and acceptable, effects. Based on wind tunnel measurements could be quantified device-induced-drag on a cormorant model according to device size, shape and placement. The outcomes from this work will not only empower scientists with informed guidelines on how best to construct and attach tags to seabirds to minimize deleterious effects but, as a concrete application, will enable monitoring the fate of rehabilitated oiled seabirds using minimal impact tags.

*The present version of this work was written as a short paper summarising results presented at the 11th International Effects of Oil on Wildlife Conference and therefore was purposely accentuated on the benefits it could bring to wildlife rehabilitation programs. However, and given the presumed broad applicability of such findings, it is planned to make this work more largely accessible to the scientific community, perhaps through publication in a peer-review journal such as Animal Biotelemetry.

Keywords: bird, telemetry, external tag, drag, aero/hydrodynamics

Introduction

Determining the movements and fate of birds has been a challenge for scientists for many years, starting with ringing studies and now using tracking technology (e.g. Combreau *et al.* 2001, Kjellén *et al.* 2001, Fiedler 2009). The outcomes of such studies relate to a very broad range of fields, from fundamental biology to animal conservation and management (Wikelski *et al.* 2007, Bridge *et al.* 2011). Although, the benefits of many tracking studies are unquestionable, the potential deleterious effects of tracking devices on their wearers are a perennial cause for concern (McMahon *et al.* 2011, Vandenabeele *et al.* 2011a). Device effects are particularly relevant in the study of rehabilitated birds where the fate of treated individuals is important in informing best practice for welfare programs and where animal fitness may, in any case, be compromised.

Potential device effects on birds are myriad, ranging from aberrant behaviors to physical injuries (Wilson & McMahon 2006, Ropert-Coudert *et al.* 2007b), but one particularly intractable aspect relates to the increased drag to which flying birds are subject due to device-induced disruption of air-flow over the body (Bannasch *et al.* 1994, Culik *et al.* 1994). Wind tunnel experiments are a manner with which such problems can be addressed (Pennycuick 2008, Bowlin *et al.* 2010, Hazekamp *et al.* 2010) although such facilities are rare, so results derived from them are correspondingly limited. Indeed, only one, Obrecht *et al.* (1988), has studied how the form and size of external devices affects the drag of flying birds (using large waterfowl and raptors) with models in a wind tunnel, although a similar approach was adopted by Watson & Granger (1998) to assess the impact of external devices on swimming turtles.

We used the study by Obrecht *et al.* (1988) as a starting point and further investigated the effect of tag size, shape, and placement on a model seabird placed in a wind tunnel and simulated both flying and swimming conditions. The outcomes of this study should provide informed guidelines on how best to construct and attach tags to seabirds to minimize deleterious effects. A specific aim of this study was intended to relate to rehabilitated oiled seabirds so that their fate could be followed using optimally constructed and correctly placed satellite tags resulting in minimal, and partially defined, impact.

Methods

The wind tunnel experiments were conducted in the engineering department at Swansea University (UK) in a unit which provides laminar air flow for speeds up to 28 m/s (see Orme *et al.* 2001 for details). A wooden model was crafted of a great cormorant (*Phalacrocorax carbo*) in the underwater swimming position based on attitudes of diving birds taken from photos and videos and dimensions provided by a frozen adult great cormorant carcass. This was also considered to simulate rather well the flying position of the bird apart from the absent wings which, in any case for a bird model of this size, could not fit inside the test section of the wind tunnel. The wooden model was placed in the wind tunnel test section using three supporting struts (Figure 1) connected to a balance system that measured the forces (lift, drag, and pitch) experienced by the model resulting from the air flow. The drag force was measured over a range of model body angles to define the angle at which the drag was minimized before setting the model in this position for further trials. The balance was calibrated using standard masses and all readings for drag transformed into force (N).

Tag size effect

Initially, the model, without any externally attached device, was exposed to a range of air speeds emulating swimming speeds displayed by the species in the wild (from ~0.2 to ~1.8 m/s (Ropert-Coudert *et al.* 2006) and the drag determined. This was achieved by using air speeds in the wind tunnel that corresponded with the Reynolds number equivalent to that of the required swimming speeds (thus compensating for the different viscosities of air and water [Beal 1946]). Following drag measurements of the cormorant body without any external device, we re-ran the measurements after fitting the model with four different device sizes. Devices were constructed of polyurethane foam, and shape was cuboid with equivalent relative dimensions in the height and width dimensions (height/width ratio of 0.56) and sizes corresponding to cross-sectional areas of between 7.88 and 11.25 cm^2 (Table 1). For this series of tests, the units were attached to the lower back of the bird model as recommended by Bannasch *et al.* (1994). The air flow around the model was also examined using the smoke visualization technique (or smoke-wire technique, Batill & Mueller 1981).

Tag position effect

The largest device was used for additional tests, which aimed to assess the influence of tag position on the drag experienced by the bird model. This device was therefore fixed at four different places on the back of the bird model (Figure 2) ranging from anteriorly, through a position close to the center of gravity, assumed to be ideal for flying birds carrying extra mass (Culik *et al.* 1994, Healy *et al.* 2004), to the caudal position described as that constituting minimal drag by Bannasch *et al.* (1994) for swimming penguins. For this series of tests, the model was placed in the swimming scenario with the same range of swim speeds as used in previous tests. Although the bird model was wingless (a bird the size of a great cormorant with spread wings would not fit in the test section anyway), we also simulated the flying conditions with a flight speed of 24 m/s as observed in the wild (i.e., 70 km/h, Van Dobben 1952).

Tag shape effect

After identifying the two device positions where minimum drag values were obtained, we kept the largest device in these positions to perform a last series of tests. Here, we changed the shape of the device by adding molded pieces of plasticine (Plasticine 500 g grey from Maragon Arts & Crafts online website) to either the front or front and back of the device, while maintaining a constant maximum cross-sectional area, to examine how shape modulates drag. Based on the device shape tested by Obrecht *et al.* (1988), we tested four different shapes of noses and tails (Figure 3). At each position, the device was first tested with just the different noses. Once the nose shape with minimum drag was identified, the different tails were applied to the model and the drag measured once more.

The tests were conducted in an indoor facility over three consecutive days to minimize variation in the atmospheric conditions. Since we used a closed-wall wind tunnel, and because of the relatively large size of the bird model, we applied a correction to the measurements to account for the wall-blockage effects. For each test scenario, we performed between three and five runs to measure the drag. All drag measurements were averaged, and the increase in drag between the situation when the bird model was fitted with devices and the unequipped situation was determined. This increase in drag was finally represented as a function of tag cross-sectional area, tag position, and tag shape.

Results

The drag measured with just the bird model placed in the test section and exposed to a swim speed of 1.6 m/s had a mean of 1.4 N. The drag measured when the bird model was fitted with the different sized devices ranged from 1.8 to 2.1 N, corresponding to an increase in drag of between 28.5 and 46.3% for the smallest to the largest device respectively (Figure 4). By using the smoke visualisation technique, a clear disruption of the air flow could be observed with vortices being generated above and at the rear of the device (Figure 5).

Placement of the device in different positions had a marked effect on drag, which increased in a non-linear manner between 35% above the norm, for the most caudal position, to 49% for the position on the lower back (Figure 6). This applied to both swimming and flying scenarios. However, strict comparison between swimming and flying conditions showed a relatively constant difference in drag between the two, with flight drag being on average 2% lower than the swim drag, whatever the position of the unit.

In all cases, the addition of a nose to make the unit more streamlined reduced the drag by at least 16% compared to when the model is fitted with the original cuboid. In general, the greatest decrease in drag was obtained by adding a long nose, rather than a short one, both in flying and swimming conditions (giving about 20% decrease in drag for position 3 and 30% for position 4 for the long nose terminating on the body, Figure 7). Although the addition of a tail to the tag always resulted in a decrease in drag regardless of its shape (with the best nose kept in place), with decreases being roughly constant, for the tag placed in position 3, the long nose and tail decreased the drag by about 40% (instead of 20% as in the other cases [Figure

7]). The pattern of variation in drag was similar in both flying and swimming scenarios with, as before, flight drag being approximately 2% lower than swim drag. Finally, even though the drag measured was higher when the largest, untapered unit was placed in position 4 compared to position 3 (see above), the mean drag observed when this device was fitted with different shapes of noses and tails was about the same between these two positions (1.7 ± 0.20 N and 1.6 ± 0.14 N for position 3 and 4, respectively).

Discussion

Tracking devices have shed light on many aspects of animals' lives by providing particular information about animal activity where they cannot be seen (Ropert-Coudert & Wilson 2005). Indeed, the rapid development in this technology is allowing ever greater insights into smaller and more intractable species (Wikelski *et al.* 2007). Nonetheless, it is imperative that this apparent boon be tempered by appropriate consideration of the potential negative impact of devices on their bearers. There is now appreciable documentation of the ways in which various tags affect animals (Murray & Fuller 2000, Hawkins 2004), although precisely why some tags cause behavioral changes is often poorly understood.

In studying how tags change the physical properties of animal carriers, we have at least a solid basis with which to attempt to understand how this might relate to behavioral changes. Drag is part of this domain, and its reduction in a general sense is considered important in modulating bird morphology (Bannasch *et al.* 1994). Our results derived for both swimming and flying scenarios for great cormorants have revealed the complexity of the drag issue and confirmed some, but not all, of the outcomes of previous studies. As expected, the size of the device plays a role in modulating the drag, although, surprisingly, the difference in drag between the smallest and largest unit was relatively low, with even the smallest units producing substantial drag. This is consistent with the wind tunnel study made by Pennycuick *et al.* (2011) who showed fitting even a harness to starlings (*Sturnus roseus*) increased the drag coefficient (a dimensionless parameter used to quantify the resistance of an object in a fluid environment and found in the equation determining the drag force [Hedenström & Liechti 2001]) of the birds by 50%, whereas the addition of devices did not lead to further increase. Thus, it would appear that disruption of the air flow around the bird's body can occur with even the smallest object. Notably, the Pennycuick *et al.* (2011) study was conducted with the units placed on the lower back of the bird, the position commonly adopted when fitting devices to diving birds since it is assumed to minimize drag (Bannasch *et al.* 1994). Our results confirmed this, because we obtained least drag with the unit at the most caudal position, however, with devices as large as the one we tested, such a position may not be realistic since half of the device would be placed over the tail. Interestingly, the other posterior position tested (position 4), which might be considered suitable for attachment because it concurs largely with the recommendations made by Bannash *et al.* (1994), seemed a poor option (Figure 6).

Although a similar pattern in drag variation in relation to device placement was observed between flying and swimming scenarios, what appears as the best place in one case may not be in the other. Indeed, the lifestyle of the studied species plays a critical role in this. An important consideration for flying birds is the position of the device with respect to the center of gravity (Culik *et al.* 1994, Healy *et al.* 2004). Devices attached to birds in air will exert a force that will be more deleterious the farther away it is from the center of the bird's gravity due to the effect of the moment arm, although quite how flying birds respond to such forces in unclear.

Based on the results of this study, it would seem that tags on flying birds should be best placed at a spot slightly posterior to the middle back but before the rump (position 3). Here, the device would not be far from the center of gravity while the drag, even though not reduced maximally, would still be lower than at all other positions bar 5. Where seabirds spend appreciable time traveling in both air and water, consideration of the proportions spent in each medium should help to decide how far down the back the unit should be placed.

Tag size and position aside, our work also demonstrated the importance of tag shape, something that was made obvious by the Obrecht *et al.* (1988) study. The addition of a simple nose reduced drag substantially with, in a manner similar to that observed by Obrecht *et al.* (1988), an elongated shape being preferable to a short one. But the situation is complex. Whereas in position 3, only the long and downward-pointing tail improved the situation significantly (almost 40% after fitting the nose), the shape of the tail in position 4 changed things little, reducing the drag by about 34% in all cases. Interestingly, the mean drag measured with the unit fitted with nose and tail appeared to be of the same magnitude for both positions 3 and 4. Thus, with streamlined devices and these two positions available as the best options for minimum drag, tag placement can simply depend on the lifestyle of the bird (see above), with position 3 being favored for species spending significantly more time in the air and position 4 (or lower if the size of the tag allows it) being preferable for species spending most time diving (see also Ropert-Coudert *et al.* 2007a).

This study emphasizes previous findings about tag effects and also brings new insights by examining device-induced drag for birds in both swimming and flying scenarios. There are, however, numerous caveats. First, wooden models may be poor substitutes for real birds because it is unknown the extent to which feathers may act as compliant surfaces and reduce drag anyway. Based on studies that looked at the effect of feathers on drag (Tucker 1990, Lovvorn *et al.* 2001), we suspect that our measurements actually overestimate the actual drag experienced by a real bird without a device. Secondly, only one species was tested, and, although a useful pointer, a more rigorous analysis would include a number of different species and morphologies. Nonetheless, for other species tested in a similar manner, we expect drag measurements to differ in absolute value but for the main conclusions to be comparable.

We appreciate too, that the units that we tested here are oversized compared to the size and shape of many devices currently used (e.g. Afanasyev 2004, Naef-Daenzer *et al.* 2005), so we probably constitute a worst-case scenario perspective. However, some researchers do use such bulky devices (e.g. Moll *et al.* 2007), and, as pointed out by the Pennycuick *et al.* (2011) study, and partially reiterated here, smaller devices seem to produce a disproportional amount of drag, even if it is lower than the larger units.

Finally, the documentation of drag for tags to be attached to birds is an important step in reducing deleterious effects of the tags but simple adherence to the recommendations made here should not preclude researchers from being watchful for signs of detriment stemming from other causes such as device coloration (Wilson *et* *al.* 1990), method of attachment (Dixon 2011, Peniche *et al.* 2011), and mass (Passos *et al.* 2010, Vandenabeele *et al.* 2012).

Acknowledgements

We are grateful to Clive Francis, the 'Q' of Swansea University, for having conceived handsome George, the model cormorant. A special thank you to Dr Emily Shepard, Lama Qasem, Adrian Jenkins and Dr Onur Bilgen for their assistance with the wind tunnel, an ingenious machine which though requires more than two hands to be mastered. We would like to acknowledge the people from Tri-State Bird Rescue & Research, who gave Sylvie the chance to present this work at the 11th International Effects of Oil on Wildlife Conference (without forgetting Adam Grogan who initiated all this). The study was carried out as part of a doctoral project funded by the California Department of Fish and Game's Oil Spill Response Trust Fund (through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis) and the Royal Society for Prevention of Cruelty to Animals (RSPCA, Wilberforce Way, Southwater, Horsham, West Sussex, RH13 9RS, United Kingdom).

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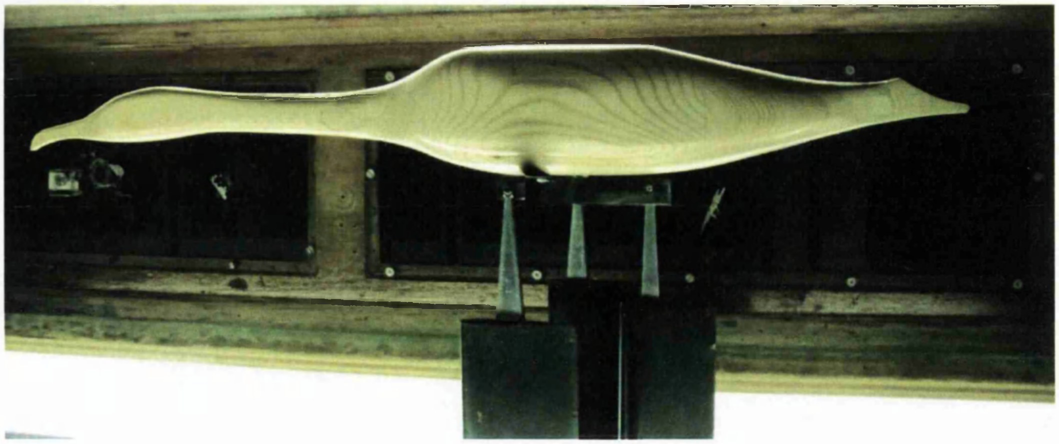
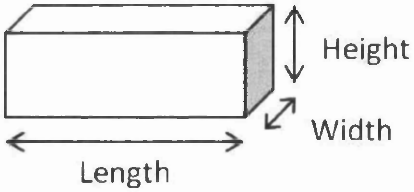


Figure 1. Wooden model of a swimming great cormorant mounted on three struts in the test section of a wind tunnel (Swansea University facility, UK). The struts were connected to balances that allow measurement of the drag experienced by the model when exposed to various air speeds (emulating the swim and/or flight speeds of the species).

Table 1. Dimensions and frontal cross sectional area of the different sized devices used in wind tunnel tests. The ratio between width and height was constant and equal to 0.56.



Device size	**Length (cm)**	**Width (cm)**	**Height (cm)**	**Cross sectional area (cm^2)**
1	8.30	3.75	2.10	7.88
2	8.30	3.90	2.20	8.58
3	8.30	4.30	2.40	10.32
4	8.30	4.50	2.50	11.25

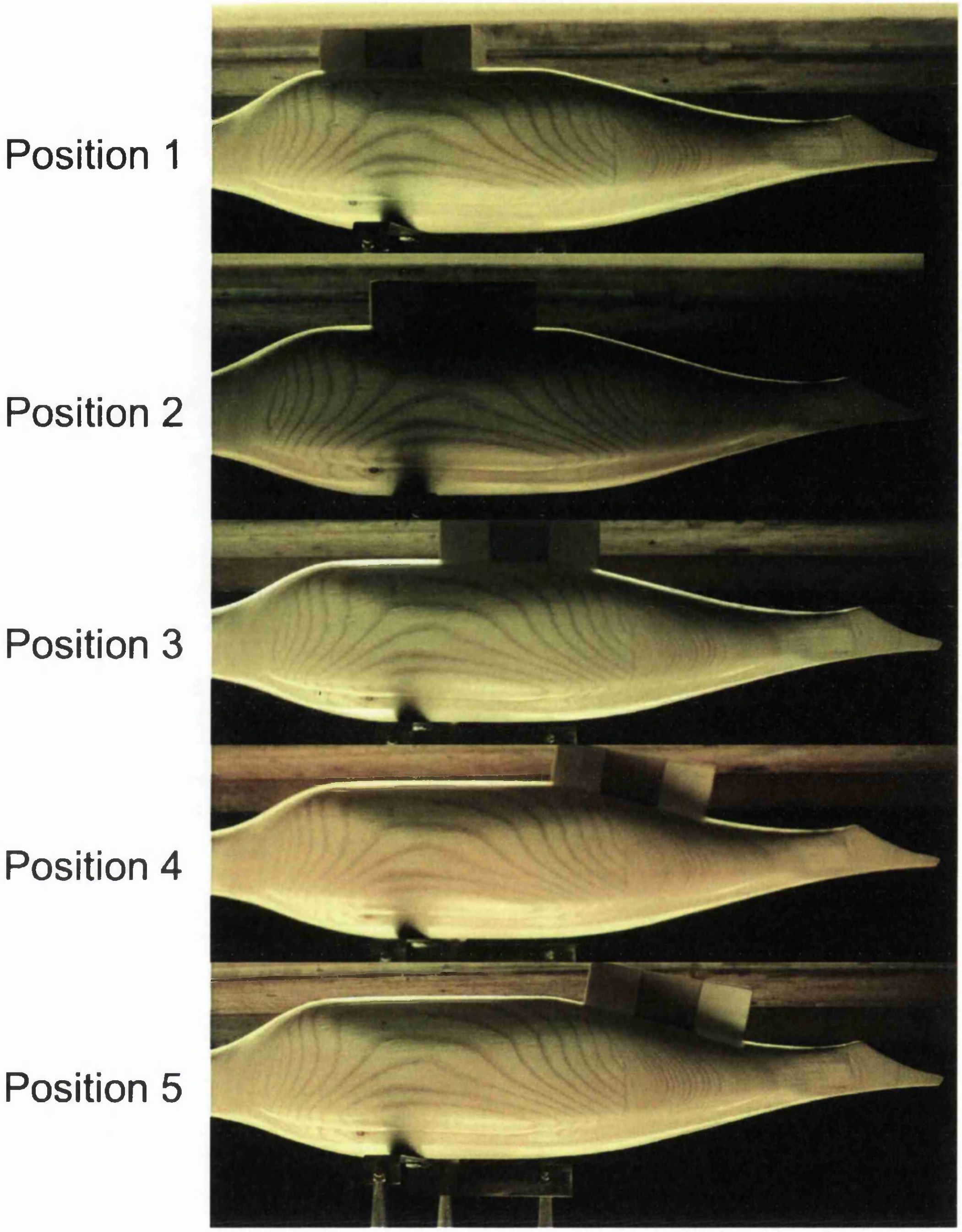
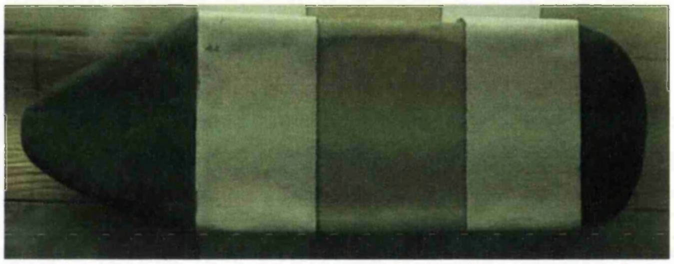


Figure 2. The lateral view of the cormorant model placed in the test section of the wind tunnel with the largest cube fixed at the defined, different positions on its back.

Lateral view



Top view

Figure 3. The side view of the four different shapes of nose and tail and a top view of the cube fitted with nose and tail of different shapes in order to assess the effect of shape on the drag associated with the tag placed on the back of the bird model.

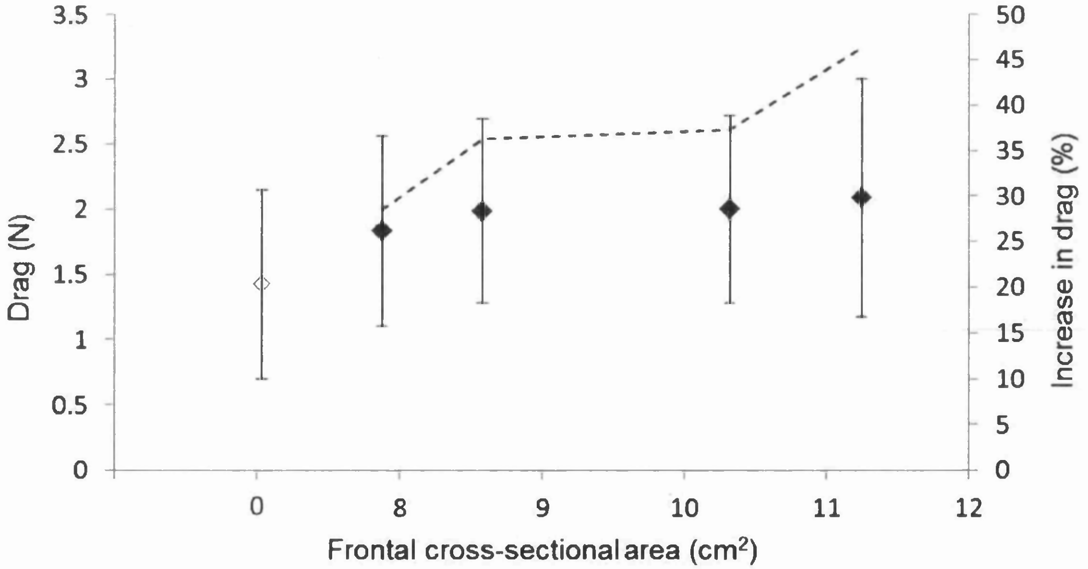


Figure 4. Mean drag measured in a wind tunnel on a cormorant model swimming at 1.6 m/s as a function of the frontal cross-sectional area of the cube fitted to its lower back. The error bars show standard deviations. The dashed line represents the increase in drag expressed as a percentage of the drag experienced by the unequipped bird model.

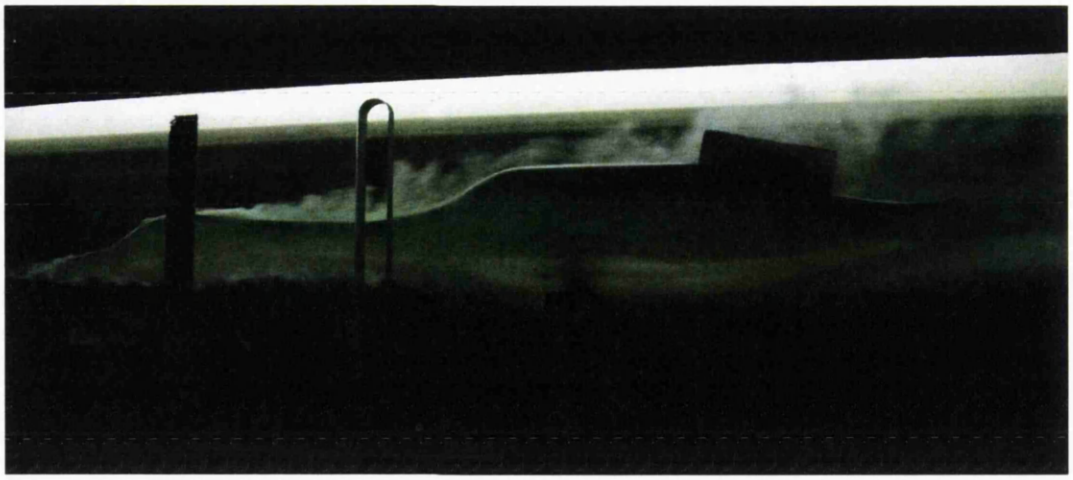


Figure 5. The model cormorant in the wind tunnel using smoke visualization to show how air-flow separation occurs largely at the site of the tag, which accounts for the increases in drag.

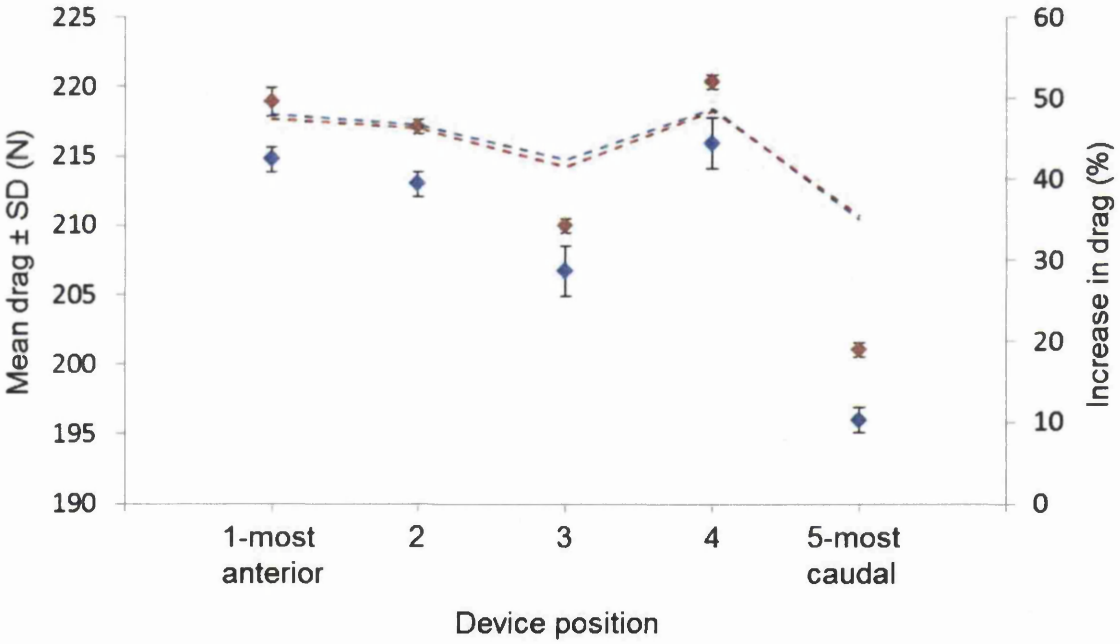


Figure 6. Wind tunnel experiment data collected from a model cormorant flying at 24 m/s (in blue) or swimming at 1.6 m/s (in red) while wearing a cube with cross-sectional area of 11.3 cm^2 to show the relationship between tag position and the drag experienced by the model. Error bars show standard deviation. The increase in drag expressed as a percentage of the drag experienced by the unequipped bird model is represented by the dashed lines with appropriate color coding.

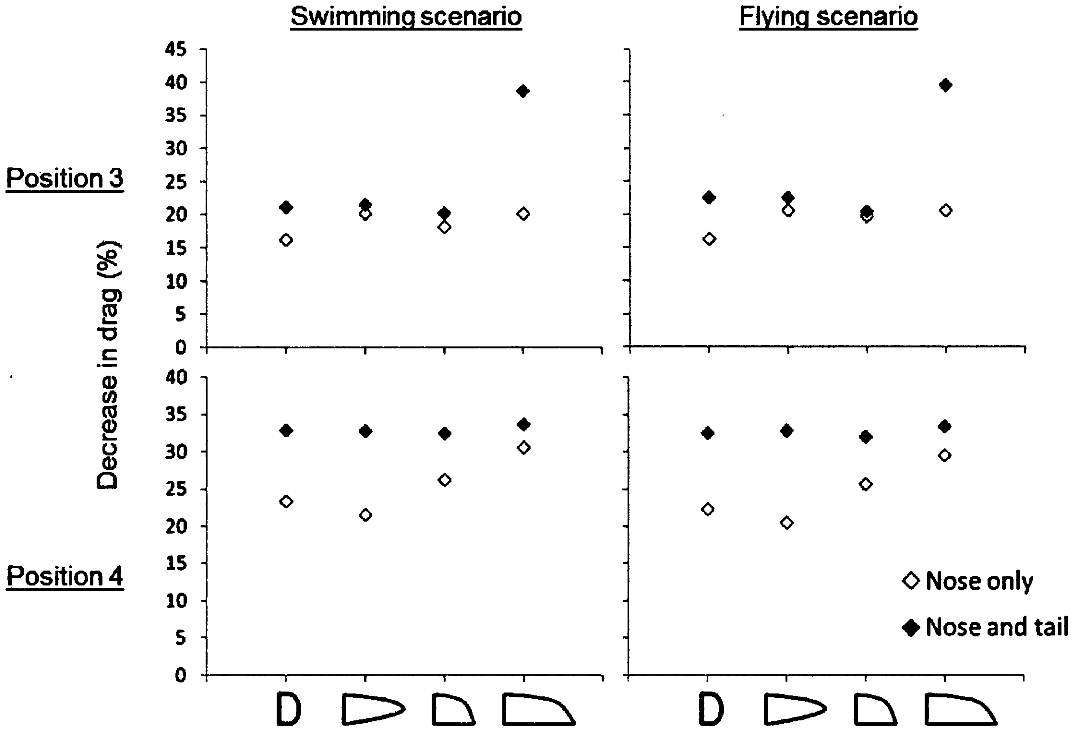


Figure 7. Wind tunnel experiment data collected from a model cormorant flying at 24 m/s (right panel) or swimming at 1.6 m/s (left panel) wearing a tag with cross-sectional area of 11.3 cm^2 to show the effect of shape (modified by the addition of different noses and tails to the original cuboid unit) on the measured drag. The percentage of decrease in drag is calculated in relation to when the bird model is fitted with the original cube.

Chapter 6:

Are bio-telemetric devices always a drag? Behavioural and energetic consequences of external tags on great cormorants *Phalacrocorax carbo*

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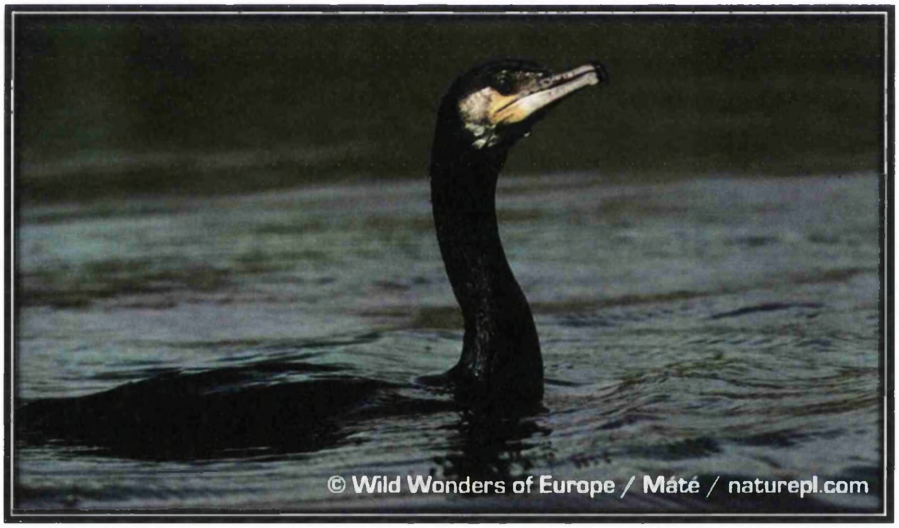
Graham Martin & Rory P. Wilson



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SPV and ELCS conducted the trials on captive birds with the help of PJB and GM. DG provided the data on free-living birds. SPV and RPW performed the analysis and wrote the manuscript with contributions from ELCS and PJB

In preparation for Functional Ecology

Abstract

The attachment of external devices to diving animals can affect foraging performance, notably by increasing the overall drag. We determined the drag of a model great cormorant *Phalacrocorax carbo* in a wind tunnel, including how it changed with attached devices, and derived a formulation to predict how drag changes as a function of swim speed and device cross-sectional area. Similar devices containing tri-axial accelerometers were used on 6 captive great cormorants and showed that overall dynamic body acceleration (ODBA), as a proxy for the metabolic costs of locomotion, increased with increasing drag but that this metric was a poor predictor under the constrained laboratory conditions. Wind tunnel-derived drag metrics were combined with literature data to construct a model to predict energy expenditure of diving cormorants according to device size. The model was then used on data on the diving behaviour of 6 free-living great cormorants implanted (and therefore subject to no increased drag) with time-depth recorders, to predict that devices constituting about 6% of the birds cross-sectional area would cause a 4% increase in power consumption to swim at normal swim speeds. However, if birds maintain constant power underwater by decreasing foraging speed with increasing drag, this device would result in a 13% reduction in distance travelled during the bottom (active hunting) phase. The study highlights the criticality of both the drag coefficient and the swim speeds of device-equipped diving animals noting that high-speed, low drag animals are most likely to suffer detrimental effects from externally attached tags.

Keywords: biotelemetry, swimming bird, drag, energetics, foraging

Introduction

A recent study conducted over 10 years examining the effect of flipper bands on penguins found that the simple addition of small, seemingly inoffensive, bands to help identify birds can affect population processes. Saraux *et al.* (2010) determined that flipper-banded king penguins (*Aptenodytes patagonicus*) had 39% lower breeding success and 16% lower survival rate than unequipped conspecifics over the decade study period. The exact cause for this profound effect is unknown but indirect calorimetry work on Adélie penguins (*Pygoscelis adeliae)* in a swim canal indicates that the cause might be energy-based because the addition of a flipper band to these birds caused metabolic power requirements for normal underwater swimming to increase by 24% (Culik *et al.* 1993). An explanation for how such small external objects may impact the carriers so profoundly might be provided by the extremely low drag coefficient of penguins which, at 0.003 (Clarke & Bemis 1979), is the lowest determined for any bird. Thus, although small external bodies may appear minimal, the increase in turbulence and corresponding drag stemming from the water flow may be relatively substantial, particularly on bodies that have such low drag coefficients anyway (Culik & Wilson 1991, Bannasch 1995).

The drag caused by external bodies attached to animals has been measured by a relatively limited number of authors. Obrecht *et al.* (1988) studied how the form and size of external devices affected the drag of large waterfowl and raptors using models in a wind tunnel and Pennycuick (2012) reported a dramatic increase in drag for starlings *Sternus vulgaris* wearing a small harness and flying under similar conditions. A similar approach, albeit using water instead of air, was adopted by Watson *et al.* (1998) to assess the impact of external devices on swimming turtles while Wilson *et al.* (2004) used model penguins moving up a swim channel to determine the drag of external antennae in relation to that of penguins. Ideally, however, such studies need to expand their findings to free-living animals so as to put findings into a behavioural and ecological context.

In an attempt to do this, we determined the drag of various devices on a model great cormorant (*Phalacrocorax carbo*) in a wind tunnel before using these same devices on cormorants trained to swim underwater in a defined experimental set-up. Bird performance was determined by video cameras and further defined by miniature loggers housed within the external devices. Measurements of swim speed determined using the video system could be combined with the logger-recorded depth and triaxial acceleration so that, using Overall Dynamic Body Acceleration (ODBA) as a proxy for metabolic rate associated with movement (Wilson *et al.* 2006, Halsey *et al.* 2009, Green *et al.*2009, Gleiss *et al.* 2010, Elliott *et al.* 2012), bird energetic response and performance could be assessed in relation to drag.

In this work, we attempt to quantify links between drag, performance and energy expenditure of diving great cormorants and consider how external devices of defined drag might impact the behavioural ecology of foraging wild birds using data derived from great cormorants implanted with depth gauges (see Grémillet *et al.* 2005 for details). Implanted birds are presumed to suffer none of the drag constraints incurred by birds with externally attached devices (e.g. Green *et al.* 2004, Ritchie *et al.* 2010). This work should help the move towards an approach that puts experimentally determined results into a wider ecological context with a view to serving as an example of good practice for other studies (Wilson & MacMahon 2006).

Methods

Wind tunnel measurements

We conducted wind tunnel experiments in the Swansea University engineering facility which houses a unit that provides laminar air flow for speeds up to 28 m/s. A wooden model of a great cormorant was crafted in the underwater swimming position based on attitudes of diving birds taken from photos and video and dimensions provided by a frozen adult great cormorant carcass. The model was secured in the wind tunnel test section using three supporting struts (Figure 1) connected to a balance system that measured the forces (drag, lift and pitch) experienced by the model. The drag force was first measured over a range of model body angles to define the angle where this was minimum before setting the model in this position for further trials. The balance was calibrated using standard masses and all readings for drag were transformed into force (N).

Initially, the model, without any externally attached device, was exposed to a range of air speeds emulating swimming speeds displayed by the species in the wild (from ~0.2 to ~1.8 m/s (Ropert-Coudert *et al.* 2006; see Table 2) and the drag determined. This was achieved using air speeds that correspond to the Reynolds number (*Re*) equivalent to that of the required swimming speeds (thus compensating for the different viscosities of air and water). Measurements were also made from the model fitted with 4 different device sizes (the same as used in the experimental set-up with live birds, see below). Devices were constructed from polyurethane foam with a cuboid shape with equivalent height to width ratios (ratio of 0.56), and cross-sectional areas of 7.88 - 11.25 cm^2 (Table 1). Devices were attached to the lower back of the model bird as recommended by Bannasch *et al.* (1994) and this same position was used for the captive cormorant trials (see below).

Captive bird trials

Six adult great cormorants weighing between 1.77 and 2.79 kg were used in this study. They were housed communally in a 130 m^2 outdoor aviary at the Edgbaston campus at Birmingham University. Details of bird care are given in White *et al.* (2007). The cormorants had been previously trained to swim through an underwater channel 2.8 m long fashioned from stainless steel grating and sunk in a 1 m deep 8 x 4 m tank that was continuously replenished with fresh water.

Cormorants were equipped with the same polyurethane foam units as used in the wind tunnel (see above – Table 1), attaching them to the lower back (in the same position as the drag tests – see above) using Tesa tape (Wilson & Wilson 1989). However, the polyurethane blocks were hollow in order to house small multiple-channel loggers (5.6 x 2.4 x 1.5 cm; total mass in air 19.7 g). These loggers were set to record tri-axial acceleration (in the dorso–ventral, anterior–posterior and lateral axes; hereafter referred to as heave, surge and sway, respectively) and depth at 12 Hz, with absolute accuracies > 0.05 *g* and 0.02 m, respectively. The combined units of a logger plus polyurethane foam were made to be neutrally buoyant in fresh water by adding small lead weights where necessary. During trials, the time taken for a bird to swim through the 2.8 m straight section of the channel was determined using a stopwatch, and the procedure was filmed. Birds performed between 0 and 30 runs per day over 6 consecutive days and each of the four sized units were tested on all individual birds.

Speed, rate of change of depth, duration and total ODBA were calculated for all dives, along with the descent and ascent durations (see Halsey *et al.* 2007 for definition). ODBA has been shown to correlate well with energy expenditure (Wilson *et al.* 2006, Halsey *et al.* 2009, Green *et al.* 2009, Gleiss *et al.* 2010, Elliott *et al.* 2012) and was determined by a three stage process; (i) using a running mean over 2 seconds for each of the three orthogonal acceleration channels so as to determine the static acceleration from the signal (Shepard *et al.* 2008), (ii) subtracted these values from the raw acceleration recorded for each channel to derive the dynamic acceleration (Wilson *et al.* 2006) before, (iii) making all dynamic values positive and summing them (Gleiss *et al.* 2010).

Free-living bird data

Dives from six great cormorants breeding on Disko Island, West Greenland (69°30′N, 54°05′W), equipped with implanted loggers (see Grémillet *et al.* 2005 for details), were used to quantify the variation in dive parameters as a function of maximum depth. Dive duration, maximum depth, descent, bottom and ascent duration, and vertical velocity of the descent and ascent phases were calculated for 20 dives from each bird, resulting in a total of 120 dives.

Analyses were performed using MT-dive software (MultiTtrace, Jensen Software Systems, Germany) and Origin (version 8.5.1, OriginLab Corp., USA). All statistical tests were carried out using SPSS (SPSS® Release 16.0.1 version 2007) with a significance threshold of $P < 0.05$.

Results

Wind tunnel measurements

There was a clear and significant increase in drag with swim speed for the model cormorant equipped with variously sized devices (Figure 2). The relationships between swim speed (v, in m/s) and drag (F_D, in N) according to device size were: bird model only, $F_D = 0.0073 + 0.5494\ v^2$; model with device 1, $F_D = 0.0041 + 0.7042\ v^2$; model with device 2, $F_D = 0.0042 + 0.7591\ v^2$; model with device 3, $F_D =$

$0.0039 + 0.7751\ v^2$; model with device 4, $F_D = 0.0042 + 0.7990\ v^2$ (all P-values $<$ 0.001). Larger devices elicited higher drag values for any given swim speed (Figure 2). We found no relationship between device cross-sectional area and the intercepts from the relationship between drag and swim speed (above) ($P > 0.05$), but a very clear, linear relationship between the gradients of these relationships (m) and device cross-sectional area (X_s, cm^2) according to $m = 0.0222\ X_s + 0.5482$ ($r^2 = 0.97$, $P = 0.001$). Thus, the relationship between drag and speed as a function of device cross-sectional area could be given by;

$$F_D = (0.0222\ X_s + 0.5482)\ v^2 \qquad \text{(i)}$$

assuming the intercept to be 0.

Captive bird trials

A total of 233 dives was conducted by six captive cormorants, with individuals executing between 5 and 88 dives. Mean swim speed for individual birds varied between 1.02 and 1.28 m/s and there was no apparent relationship between device cross-sectional area and ODBA ($P > 0.05$). For the descent and ascent phases, the increase in device size appeared to result in a significant decrease in the rate of change of depth (Pearson's correlation test, N = 233, $r^2 = 0.13$, $P < 0.001$; N = 233, $r^2 = 0.08$, $P < 0.001$ respectively).

However, calculation of the overall drag (obtained using the regressions performed between the swim speed and the drag for the different sized squares – see above) showed a significant effect, with increasing (mean) ODBA for the entire dive with drag according to;

$$ODBA_{(dive)} = 0.14\ F_D + 0.46 \qquad \text{(ii)}$$

(N = 233, $r^2 = 0.07$, $P < 0.001$) and of increasing (mean) ODBA with drag during the descent phase of dives according to;

$$ODBA_{(descent)} = 0.24\ F_D + 0.53 \qquad \text{(iii)}$$

($N = 233$, $r^2 = 0.08$, $P < 0.001$) although both relationships had notably little of their variation explained by this. No significant effect was found between drag and ODBA for the ascent phase of the dive.

Combining data from wind tunnel tests with published data

Although there was no significant change in ODBA associated with the presence of the different-sized cubes (see above), an equation relating power consumption to drag can be derived based on the relationship found between drag (F_D) and swim speed (v) for an unequipped bird (see wind tunnel trials);

$$F_D = 0.5494 * v^2 + 0.0073 \qquad (1)$$

and the calculations by Schmid *et al.* (1995) which give the power input of great cormorants swimming in a water canal as a function of swim speed;

$$Pi = 3.6v^3 - 12.2v^2 + 21.5v + Pr \qquad (2)$$

where Pr the power consumption of the bird resting at the water surface which is equal to 14.1 W kg^{-1}.

Graphing out Pi against F_D for different speeds gives a relationship between the two for an unequipped bird of;

$$Pi = 28.72 + 1.31 * F_D^2 \qquad (3)$$

($r^2 = 0.99$, $P < 0.001$)

Using the equation derived previously which relates drag to cross sectional area and swim speed (eqn (i)) according to;

$$F_D = (0.0222 * X_s + 0.5482)\, v^2$$

the equation becomes, after simplification;

$$Pi = 28.72 + [1.31 * (0.0222 * Xs * v^2 + 0.5482 * v^2)]^2 \qquad (4)$$

The estimations for the power consumption of an unequipped bird as a function of speed found with using equation (4) or that of Schmid *et al.* (1995) appeared to be in good agreement (Figure 3). Equation (4) can be used to estimate the power consumption of cormorants wearing different-sized devices based on dimensions of external units commonly used on cormorants (2, 4 and 8 cm^2) and swimming speeds up to 4 m/s (device dimensions and swim speeds found in the literature are shown in Table 2).

Free-living bird data

There were significant relationships between all the primary dive parameters and maximum dive depth for free-living great cormorants (Figure 4) although all showed considerable variability. All dive parameters showed a linear relationship with maximum depth (D, in m) except for the bottom duration (BT, in s), where a second degree polynomial best described the relationship with maximum depth reached during the dive according to;

$$BT = - 0.3882*D^2 + 6.5752*D + 3.1797 \qquad (5)$$

($r^2 = 0.32$, $P < 0.001$, Figure 5).

Discussion

Only few changes in the swimming behaviour of the captive cormorants could be attributed to the presence of external devices, with a marginally slower rate of change of depth during the descent and ascent phases, and fairly small impact in terms of energetics based on the proxy derived from acceleration ODBA (Wilson *et al.* 2006, Halsey *et al.* 2009, Green *et al.* 2009, Gleiss *et al.* 2010, Elliott *et al.* 2012), as evidenced by the low coefficient of determination in regressions of ODBA *versus* drag. This is despite the evidence obtained from wind tunnel measurements of an apparently appreciable increase in drag associated with the rather cumbersome devices used on the birds (Figure 2). Among the factors that could explain this are; (a) the relatively short distance that our experimental laboratory birds had to travel underwater (2.8 m), which will tend to increase 'boundary' errors, such as the amount of spring that birds put into initiating their dive (cf. Wilson *et al.* 1992), which will impact the speed at which they first begin their descent and (b) the marked ability of cormorants to adjust inhaled air volumes for dives (cf. Sato *et al.* 2002), profoundly affecting buoyancy and therefore the energy used to dive (Wilson & Zimmer 2004). Therefore, in contrast to ODBA data derived from wild birds, which concur very closely with predicted energy expenditure scenarios (Wilson *et al.* 2006, Gómez-Laich *et al.* 2011), we conclude that the use of ODBA as a metric for determining the effects of external tags on the energetics of laboratory cormorants shows too much variation to be useful (cf. Enstipp *et al.* 2011).

As an alternative, we combined results from the wind tunnel work on the drag associated with external devices with data from a previous study (Schmid *et al.* 1995) which had looked at power consumption of cormorants swimming in a water canal, so as to theorize how external devices might affect the energetics of swimming cormorants. The result of this exercise was the derivation of an equation which linked power input from diving cormorants with swim speed and device size (equation (4) above). Below, we use this equation together with data from wild great cormorants, diving with drag-free internal devices (Figure 4) to examine the extent to which external devices may affect foraging performance. In this, we concentrate on the bottom phase of the dive, ignoring descent and ascent phases (where buoyancy effects tend to dominate rather than drag – Lovvorn 1999, Watanuki *et al.* 2003, Wilson *et al.* 2011) for simplicity. The bottom phase of the dive is also the period where great cormorants specifically engage in foraging for their benthic prey (Wilson & Wilson 1988, Grémillet *et al.* 1999, Wanless *et al.* 2009).

Three different scenarios are explicitly examined below; (1) the energetic costs and bottom duration constraints when birds maintain a given swim speed while carrying different-sized devices (2) the distance penalty incurred by cormorants maintaining constant power costs by modulating speed while swimming with different-sized devices and (3) the capacity for burst swimming in prey capture for cormorants wearing different-sized devices.

Scenario 1; The consequences of maintaining bottom speed

Great cormorants underwater swim at a variety of speeds (see data summarized in Table 1) but normal values appear to be of the order of 0.8 to 1.4 m/s. We can use equation (4) above, to calculate the power requirements of unequipped birds to swim at these two speeds and compare them to the power requirements of birds swimming at the same speeds wearing differently sized devices (we chose cross-sectional areas of 4 and 8 cm^2 based on the dimensions of devices that have been used on cormorants; see Table 2). Here, power increments to swim at speeds of 0.8 and 1.4 m/s, even while wearing the large (8 cm^2 cross-sectional area) devices, are only predicted to be between 0.4 and 3.8% higher than unequipped birds (29.0 and 31.37 W compared to 28.88 and 30.23 W, respectively). Assuming that wild, unequipped great cormorants have bottom durations that vary with depth according to equation (5), we can work out the energy consecrated to the bottom duration by these birds if they swim at 0.8 and 1.4 m/s by multiplying the bottom duration by the power requirements. Subsequently, assuming that device-equipped birds use the same total amount of energy during the bottom phases, we can work out the length of time that these birds would spend during the bottom phase of their dives to varying depths. Again, this process shows minimal differences between equipped and unequipped cormorants (amounting to a maximum of 3.6%) equating to bottom durations varying by a maximum of about 1 s, even if the equipped birds are wearing largest devices and swimming at the higher speeds (Figure 6).

The increasing and then decreasing form of the bottom duration *versus* depth derived from our free-living great cormorants (Figure 5) is typical among diving endotherms (e.g. McIntyre *et al.* 2010, Zimmer *et al.* 2010, Doniol-Valcroze *et al.* 2011, Cook *et al.* 2012) and is considered to be a result of two processes. One process is that, in order to optimize for foraging time on the seabed, deeper dives, which have longer transit durations (e.g. Shepard *et al.* 2009, Cook *et al.* 2012; see Figure 4), should have increasing bottom durations (e.g. Gómez-Laich *et al.* 2012, Wilson *et al.* 2011). However, as total dive durations increase, animals have to spend disproportionately longer periods at the surface recovering from dives (e.g. Butler & Jones 1997, Wilson & Quintana 2004, Halsey & Butler 2006). Thus, as diving endotherms approach (and exceed) their aerobic dive limit (see Butler 2004 for discussion of this), they have to incur a reduction in bottom duration (e.g. Chappell *et al.* 1993, Kooyman & Kooyman 1995, Bevan *et al.* 1997). Our modelled effect of device-induced changes in the bottom duration does not change this process and nor, indeed, does it appreciably change the length of time that great cormorants would be able to stay on the bottom during dives even if these birds do not change swim speed with device size (cf. Wilson *et al.* 1986).

Scenario 2; Bottom distance penalties associated with maintaining constant power input with device size

One option suggested for device-equipped diving birds is that they might maintain power input at a constant level during swimming by reducing speed with increasing device size (Wilson *et al.* 1986). If great cormorants do this, unequipped birds swimming at 1.4 m/s would have the same power requirements (30.23 W) as birds equipped with devices with cross-sectional areas of 4 and 8 cm^2 swimming at about 1.30 and 1.22 m/s, respectively. The distance that these birds would cover during the bottom phase of their dives (derived by multiplying the swim speed by the bottom duration taken from equation 5) decreases by some 7.1 and 12.9% compared to the unequipped birds, for birds wearing the smaller and larger devices, respectively (Figure 7). If distance swum equates to number of prey encountered or to the probability that prey will be encountered (see Wilson *et al.* 1996), great cormorants reducing speed to maintain power use during diving will incur a significant reduction to their foraging capacity by carrying external devices of the size modelled here.

Scenario 3; Capacity for burst swimming in prey pursuit

Some authors have noted that great cormorants catch prey underwater after a pursuit phase (Ashmole 1971, Cooper 2008), during which time speeds may greatly exceed the mean values used here (Table 2), with some speed estimates being as high as 4 m/s (Wilson & Wilson 1988, Ropert-Coudert *et al.* 2006). Our model of the effect of attached devices allows us to equate the power used by an unequipped bird to swim at any given speed with the speeds that variously equipped birds could swim for that power. This speed equivalence approach (Figure 8) shows increasing disparity between equipped and unequipped birds with increasing speed such that, for example, a great cormorant equipped with a device with a cross-sectional area of 8 cm^2 could not even reach speeds of 3.5 m/s while an unequipped bird could reach

4.0 m/s (but see Ropert-Coudert *et al.* 2006). While, at 14%, the extent of such a reduction is appreciable, the potential for real detriment here lies in the compromised capacity of the bird to catch faster prey. Other things being equal, faster prey tend to be larger, for reasons discussed in Peters (1983), and therefore also represent a greater source of nutrients. In essence, therefore, perhaps the most telling detriment of great cormorant carrying an external tag of the types modelled here, lies in the extent to which the birds pursue large, fast prey. In fact, these birds consume a wide variety of prey, both in terms of species and size (Harris & Wanless 1993, Veldkamp 1995, Grémillet *et al.* 2004) so that, for example, great cormorants found in Normandy (France) mainly feed on small fish like labroids (Grémillet & Argentin 1998), are unlikely to be substantially affected by the burst speed power problem whereas birds in Iceland which can take large sandeels and bull-routs (Lilliendalht *et al.* 2006), are.

Determination of device detriment in cormorants

This exercise highlights a number of important issues in attempts to determine the drag-related detrimental effects of externally attached tags to birds in general and cormorants in particular. A major finding is that it is inappropriate to extrapolate linearly between device dimensions (here represented by cross-sectional area) and device detriment. A device with a cross-sectional area of 8 cm^2 constitutes about 6 % that of a great cormorant at its maximum point of girth (*ca.* 127 cm^2), but this is only predicted to cause a roughly 4% increase in power consumption to swim at normal foraging speeds. However, if birds maintain power use during dives constant, the same device should reduce the distances travelled along the seabed by some 13%, and ultimately make it impossible for birds to catch prey that can swim faster than 3.5 m/s if they can normally achieve burst speeds of 4 m/s. This highlights the dangers of overly simplistic rules used by ethical bodies to judge the detrimental effects of animal-attached tags based on simple metrics. A good example of this is the 3% rule, whereby tags used on birds should not exceed 3% of their body mass (Kenward 2001 but see Vandenabeele *et al.* 2012). The thinking behind creating a 'rule of thumb' is laudable but the effect of detriment needs to be considered carefully according to life-style of the animal in question.

In this regard, two factors are critical in the drag issue. One is the drag imposed by the device itself in relation to the drag coefficient of the animal carrier. Published values for the drag coefficients of cormorants, determined by a variety of methods (cf. Lovvorn *et al.* 2001, Ribak *et al.* 2005) accord roughly with ours estimated to be around 0.02 (for a calculated surface area of 0.12 m^2 and a *Re* = $1*10^{-6}$). Although the effect of compliant surfaces (Bannasch 1995, Choi *et al.* 1997) and precise measurement protocol can lead to appreciable variation in estimates (cf. Lovvorn *et al.* 2001, Ribak *et al.* 2005; see Pennycuick 1989 for discussion) so values, including ours, need to be treated with caution. Nevertheless, values for cormorant drag are nothing like as low as the surface drag coefficients ascribed to penguins, for example, which are reported to be of the order of 0.003 (Clark & Bemis 1979, Bannasch 1995). Clearly, the lower the drag coefficient of the animal carrier, the more critical the effects of an attached device are likely to be. This explains why, for example, the simple attachment of a flipper band to penguins increases the energy expenditure for normal swimming by 24% (Culik *et al.* 1993), with such dramatic consequences for breeding success and long-term survival (Saraux *et al.* 2011). Thus, the higher drag estimates for cormorants would seem to make them less susceptible to the deleterious effects of externally attached tags than penguins, but the extent of any detriment will also be critically dependent on speed, as the accelerating values of drag with increasing speed (Figure 2) attest. In this regard it may be no coincidence that studies conducted to determine the normal (bottom phase) swim speed of great cormorants using externally attached loggers report values that generally do not exceed 1.4 m/s, a point where the effect of such devices appears virtually negligible (Figure 2), whereas other studies on non-equipped birds report swimming speeds of up to 4 m/s (Wilson & Wilson 1988). We need to be aware of the circularity of using device-derived data to inform models and the error that such an approach can engender.

Conclusion

Our work is an attempt to explore how some of the features of cormorant foraging ecology might change as a result of birds having to carry external devices. The exercise highlights the difficulties of determining the drag in itself, but also in quantifying how the ramifications of increased drag might affect wild birds. We tentatively conclude that devices of the size we used are unlikely to have a profound effect on cormorant foraging behaviour but temper this conclusion with the acknowledged, appreciable weaknesses in our methodology. Critically though, our work does show that the animals most likely to be affected by the placement of external loggers are those that habitually swim fast and have low drag coefficients. Based on this, we propose that those wishing to undertake studies on high swim-speed vertebrates estimate the drag coefficients of their subjects as well as the amount of time devoted to high-speed phases in addition to whether high speed manoeuvres are critical for e.g. prey acquisition, so as to better quantify the impact of proposed devices.

Acknowledgements

We are grateful to Clive Francis, the 'Q' of Swansea University, for making the model cormorant, Dr Onur Bilgen for his assistance with the wind tunnel and Dr Norman Day for his assistance with the cormorant trials. This work has been supported by a number of grants received from the Natural Environment Research Council, UK, the French Polar Institute and CNRS, and finally the Oiled Wildlife Care Network and Royal Society for Prevention of Cruelty to Animals.

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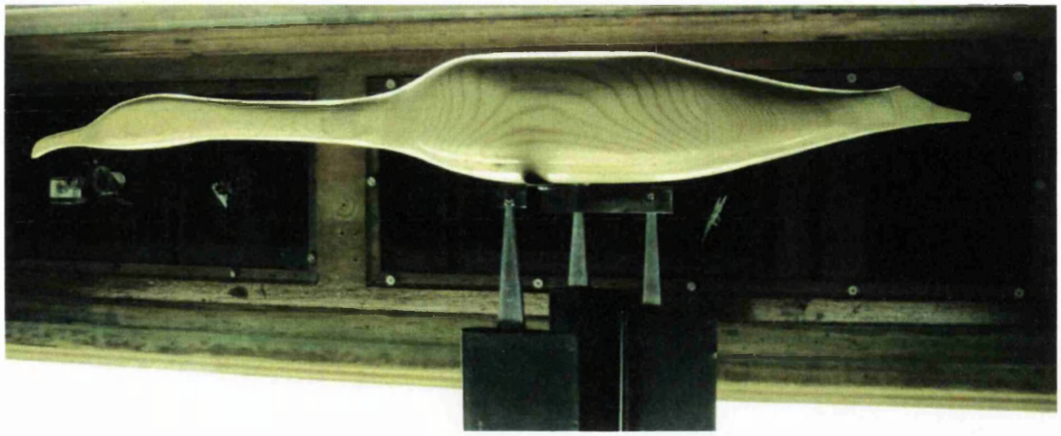
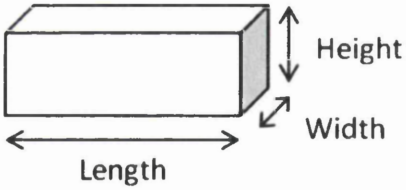


Figure 1. Wooden model of a great cormorant mounted on three struts in the test section of a wind tunnel (Swansea University facility, UK). The struts are connected to balances that allow measurement of the drag experienced by the bird model when exposed to various air speeds (emulating the swim and/or flight speeds of the species).

Table 1. Dimensions and frontal cross sectional area of the different sized devices used in wind tunnel tests and deployed on captive great cormorants.



Device size	Length (cm)	Width (cm)	Height (cm)	Cross sectional area (cm^2)
1	8.30	3.75	2.10	7.88
2	8.30	3.90	2.20	8.58
3	8.30	4.30	2.40	10.32
4	8.30	4.50	2.50	11.25

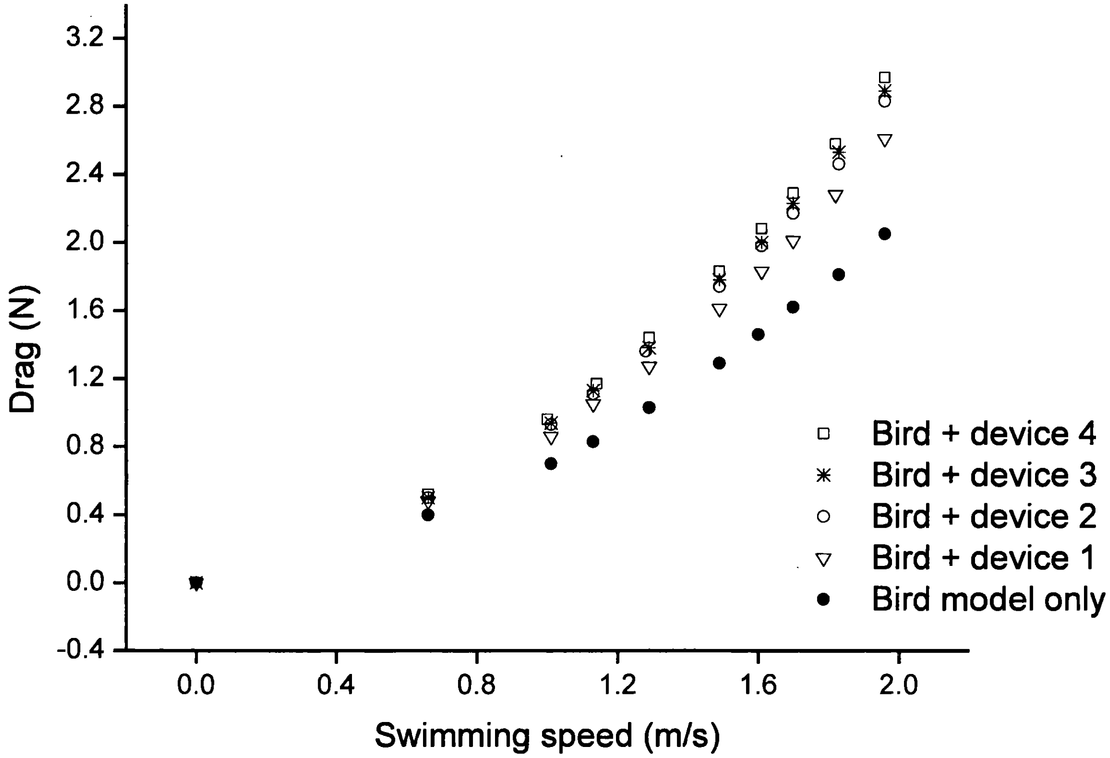


Figure 2. The drag of a great cormorant model as a function of swim speed, with different-sized devices attached (for key to device size see Table 1).

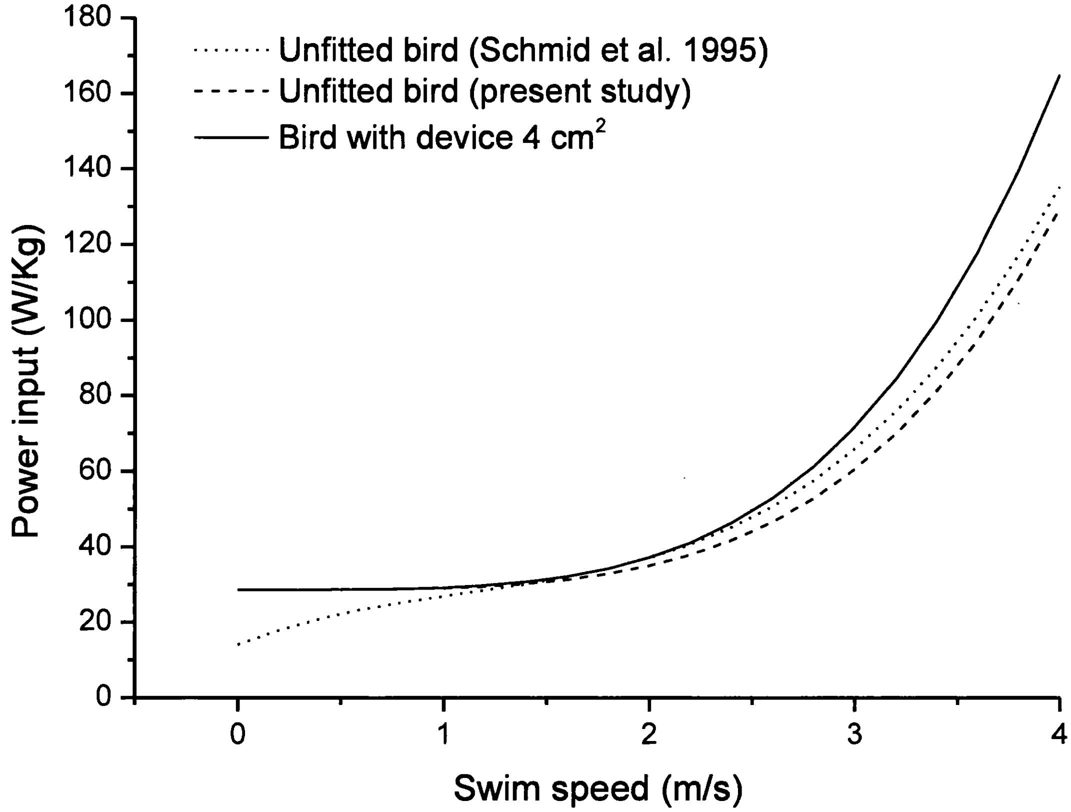


Figure 3. Energy consumption of a cormorant swimming underwater as a function of speed derived from the equation from Schmid *et al.* (1995) in comparison to the values obtained using equation (4) derived in this study. This equation relates power input to speed and cross sectional area of a device and can therefore be used to estimate the energy spent by cormorants wearing any kind device when swimming underwater.

Table 2. Examples of device size (cross-sectional area) fitted on cormorants and swim speeds recorded for great cormorants (*Phalacrocorax carbo*) gathered from the literature.

Study	**Cross sectional area of the devices (cm^2)**	**Swim speed during bottom phase**
Paredes *et al.* (2005)	1.7-1.9	NA
Tremblay *et al.* (2005); Watanuki *et al.* (2006)	2	NA
Watanuki *et al.* (2008)	3.46	NA
Ropert-Coudert *et al.* (2006)	3.14	average of 0.8 m/s (range 0.2-4 m/s)
Grémillet *et al.* (2003)	NA	1.35 m/s
Voslamber & van Eerden (1991)	NA	1.4 m/s
Wilson & Wilson (1988)	NA	depth dependent (range 0.2-4 m/s)
Ross (1976)	NA	maximum of 3 m/s

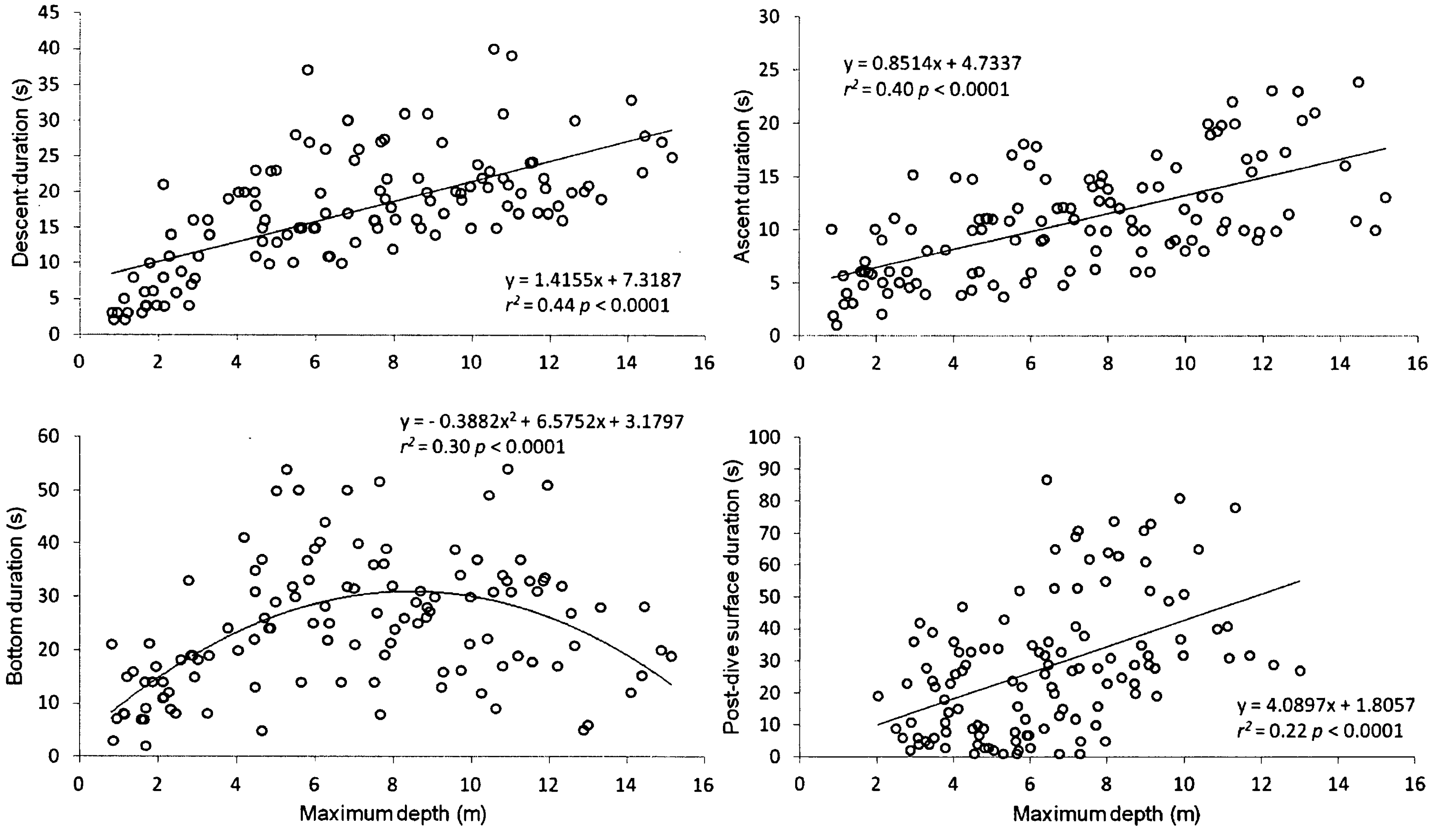


Figure 4. Regressions between the dive parameters and the maximum depth extracted from data collected on 6 wild great cormorants while diving (20 dives per bird giving a total dataset of N = 120 dives).

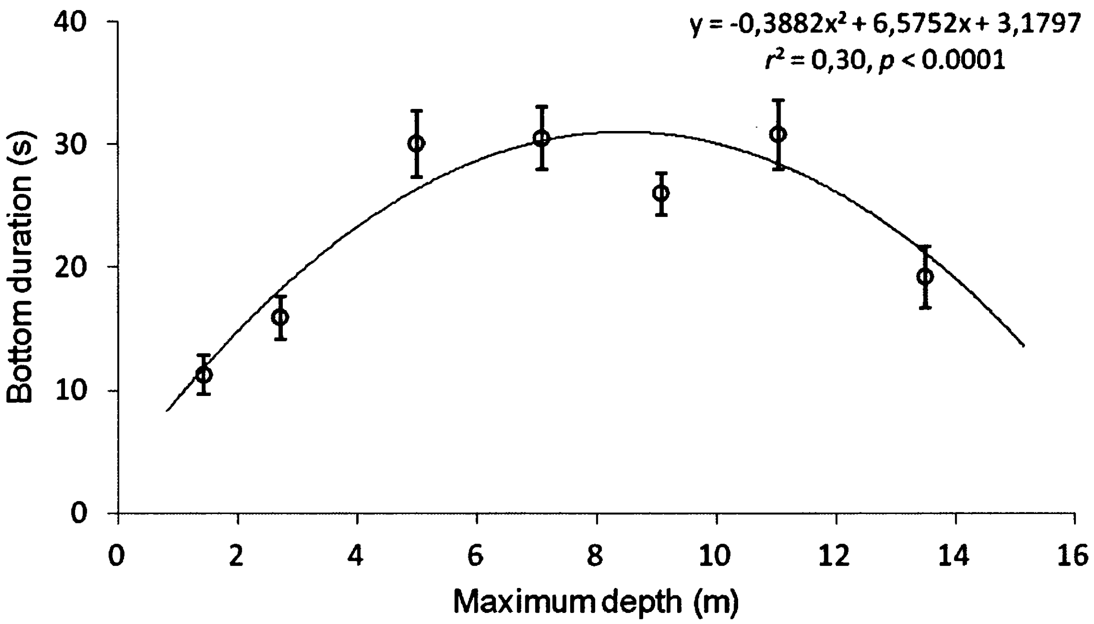


Figure 5. Relationship between time spent at the bottom and the maximum depth reached by free-living great cormorants (*Phalacrocorax carbo*) and grouped by bins with an interval of 2 m depth. Data were collected using internal loggers by Grémillet *et al.* in 2005.

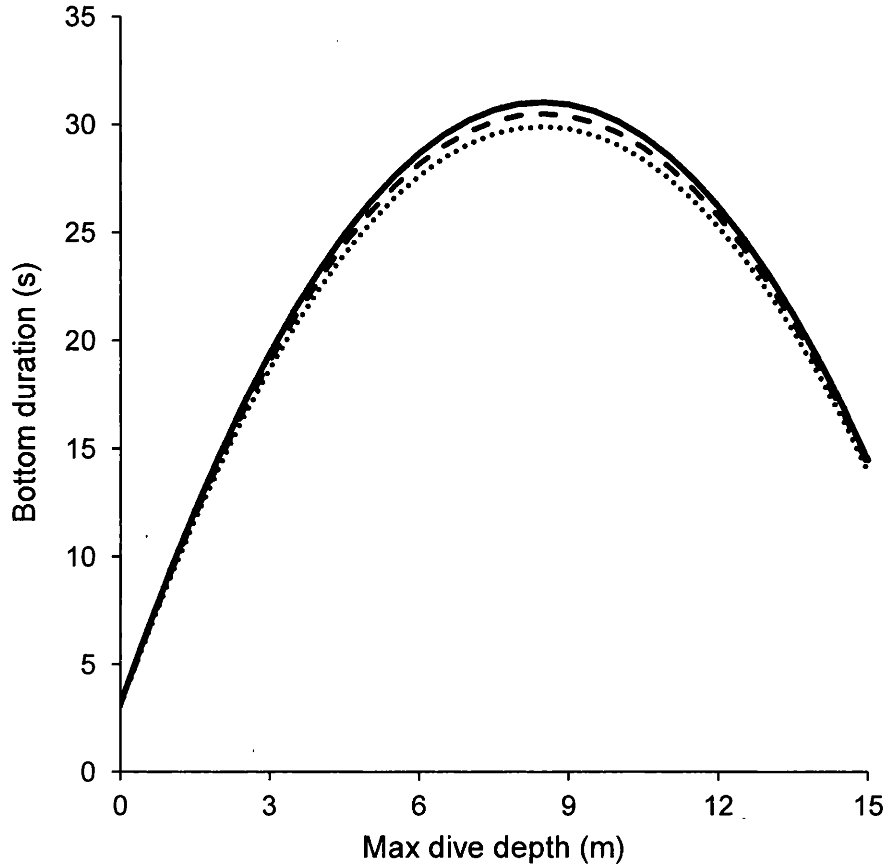


Figure 6. The predicted duration that great cormorants equipped with different-sized devices would spend during the bottom phase assuming they maintain travelling speed irrespective of device size, and thereby vary power requirements (see text). The continuous line shows the predicted bottom duration for an unequipped bird (swimming at 1.4 m/s; see Table 2) while the dashed and dotted lines show predicted durations from birds wearing devices with cross-sectional areas of 4 and 8 cm^2 respectively, swimming at the same speed as the unequipped bird.

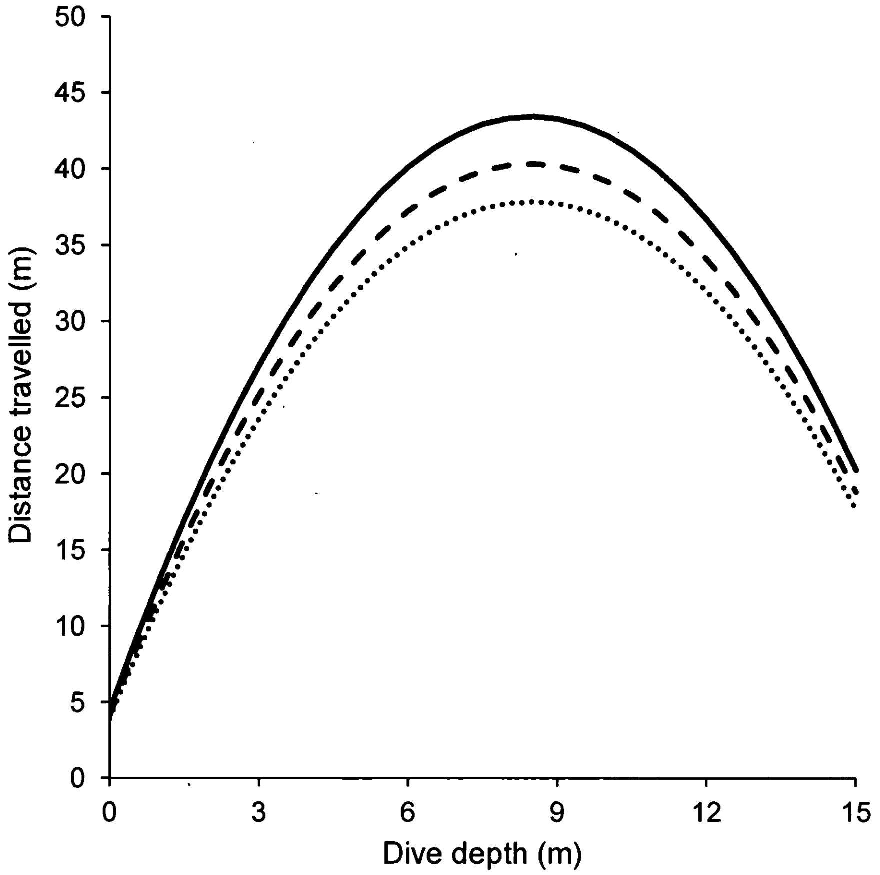


Figure 7. The predicted distance travelled during the bottom phase of dives to different depths made by great cormorants equipped with different-sized devices assuming they change speed so as to maintain power requirements constant. The continuous line shows the predicted distance for an unequipped bird (swimming at 1.4 m/s) while the dashed and dotted lines show predicted distance values from birds wearing devices with cross-sectional areas of 4 and 8 cm^2 and swimming at 1.3 and 1.22 m/s, respectively (see text and Table 2).

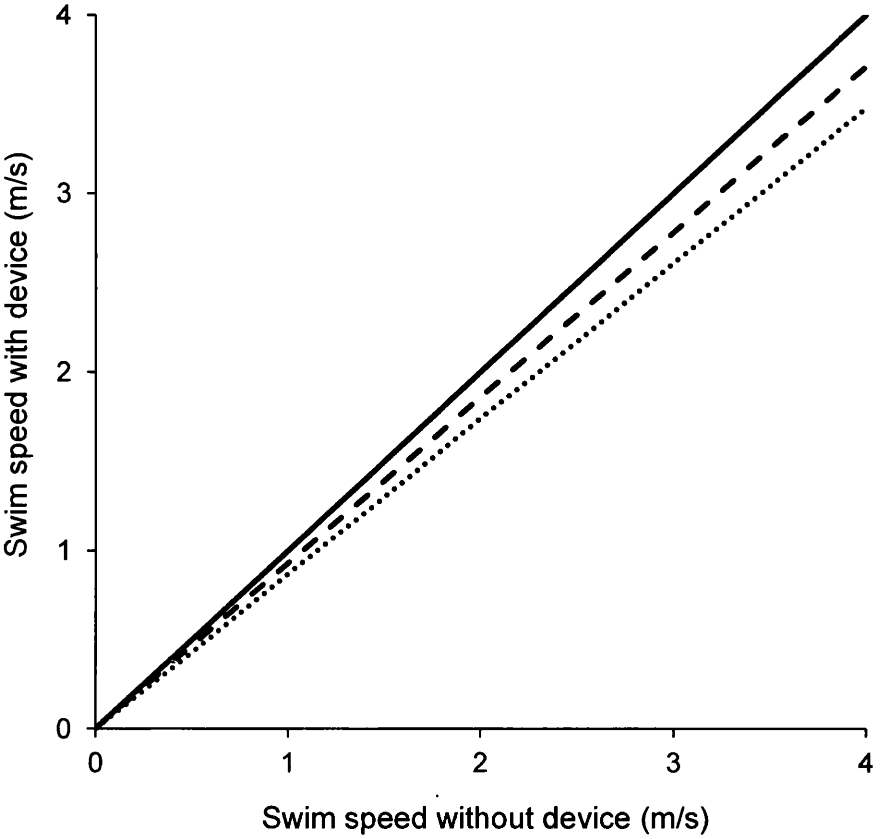


Figure 8. Predicted power equivalence speeds for great cormorants swimming underwater with variously sized devices. The continuous black line shows an unequipped bird which serves to highlight the difference between encumbered and unencumbered birds. The dashed and dotted lines show birds wearing devices with cross-sectional areas amounting to 4 and 8 cm^2 (see text). Note the increasing divergence with increasing speed.

Chapter 7:

Balancing under the high wire; a study into PTT antenna effects on the common guillemot *Uria aalge*

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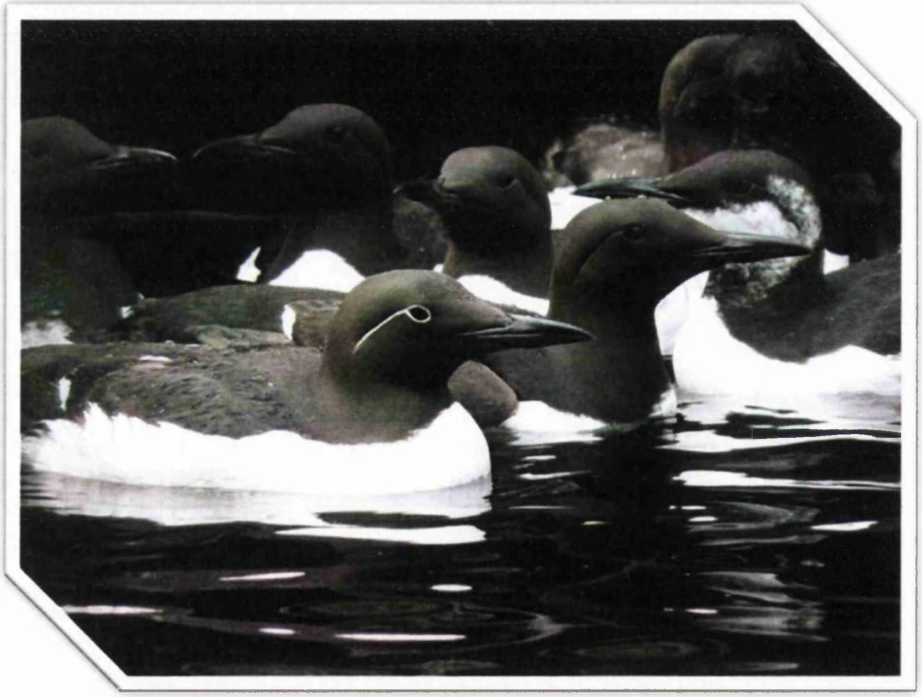

RPW, ELCS, AG, RT & ACG collected the data. SPV performed the analysis and wrote the manuscript with inputs from RPW, ELCS & AG.
Submitted to Bird Study

Abstract

External tags fitted to diving birds can affect them in many ways with the most critical effect being an increase in drag. The effects of transmitters can be even more acute due to the presence of a protruding aerial. The study assesses the impact of PTT antenna on the behaviour and energetics of device-equipped guillemots (*Uria aalge*) in captivity. Birds with antenna-devices appeared to consume about 20% more energy than non-antenna birds during the descent phase of the dive. The stability of the birds while diving or resting on the water also appeared to be compromised by the presence of an antenna. Based on these first results and because transmitters are one of the most common methods used to track animals, it appears critical to determine what impact these devices, and particularly antenna, can have on their bearers and try minimize it.

Keywords: transmitter, aerial, bird, impact, drag

Introduction

Oil pollution at sea is a major factor influencing seabird survival (Heubeck *et al.* 2003, Boulinier & Riffaut 2008) and known to impact local populations around UK (Parr *et al.* 1997, Votier *et al.* 2005). Many animal welfare groups attempt to minimize mortality by rehabilitation programs where affected animals are cleaned and released. However, there has been criticism of this since there is evidence that survival of even rehabilitated birds is unacceptably low (e.g. Sharp 1996, Goldsworthy 2000). Clearly, it is critical to be able to quantify animal well-being and fate following release and this is typically currently only done using ring/recapture procedures. This suffers from sporadic and unpredictable information and typically highlights mortality because recoveries are often birds that have died and been washed ashore, (Walraven 1992, Cooke 1997), a problem is not limited to the study of oiled rehabilitated birds but any study based on band recovery data (Seber 1972, Nelson *et al.* 1980, Lakhani 1983). An effort to refine this would particularly benefit from tracking studies since the speed and range of movement in tandem with the success of birds returning to normal foraging or breeding areas could be verified. The only system currently available that allows wide-ranging seabirds to be tracked and have their position relayed back to researchers uses Argos technology and PTTs (Platform Transmitter Terminals; Howey 1992, Kenward 2001). Indeed, this approach has been used widely to elucidate space use by non-rehabilitated seabirds, particularly the larger ones such as albatrosses (e.g. Weimerskirch & Robertson 1994, Fernández *et al.* 2001). However, devices attached externally to birds can affect them appreciably, for example in changing their behaviour (e.g. Wilson *et al.* 1986, Ropert-Coudert *et al.* 2007a), energetics (e.g. Culik & Wilson 1991, Godfrey *et al.* 2003) and breeding/foraging success (e.g. Taylor *et al.* 2001, Ackerman *et al.* 2004). Of particular recent concern is the effect of external antennae, which appears to compromise the swimming energetics of diving birds, with predicted substantial knock-on effects on foraging efficiency and ultimately survival (Wilson *et al.* 2004). Thus, before studies involving PTTs on rehabilitated seabirds are fully implemented, it is germane that the potential deleterious effects of the devices on seabird be assessed.

We conducted work on rehabilitated guillemots *Uria aalge* in captivity and examined the behaviour of birds according to whether they were equipped with dummy PTT packages with, and without, external antennae using a video surveillance system both below and above the water. In addition, in those birds equipped with dummy PTT packages, we used tri-axial accelerometers and depth transducers to help quantify behaviours more precisely. Measures of tri-axial acceleration have been shown to be very powerful for determining both behaviour (e.g. Yoda *et al.* 1999, Shepard & Halsey 2008) and alluding the energy expenditure (Wilson *et al.* 2006, Halsey *et al.* 2009) of equipped animals. We present our findings and consider the extent to which deployment of PTTs is currently appropriate for diving seabirds the size of guillemots for studies of rehabilitated seabirds or otherwise.

Methods

All work was conducted at the Royal Society for Prevention of Cruelty to Animals (RSPCA) facility at Mallydams Wood, Hastings, UK. A total of 39 oil-affected and cleaned guillemots were housed on three external pools prior to release into the wild. All birds had been in care for at least 30 days and were scheduled for release at the time they were involved in the experimentation. For the study, 11 birds were selected and placed on a further freshwater holding tank (dimensions 7 m long x 5 m wide x 1.7 m deep) with access to land (a ledge of dimensions 1.3 m x 5 m). The composition of this flock varied during the course of the work because birds were brought in from the three other holding tanks to replace animals that had been equipped with devices (see below) but which were removed from the experimental set-up after a single deployment. Thus, no individual was equipped with a device more than once.

During experiments, two naïve birds at a time were equipped with devices that mimicked a commercially-available PTT (23 gram solar bird-borne PTT, North Star Science and Technology), with a facility to add, or remove, the antenna (L: 18.5 cm, W: 0.5 cm) that constitutes part of the device and is necessary for normal functioning (Figure 1). The devices were attached to feathers in the dorsal mid-line of the back (cf. Bannasch *et al.* 1994) using tape (Wilson *et al.* 1997) and birds were typically equipped for a number of hours (range 139-1059 min) with, or without, the antenna, after which the situation was reversed (individuals previously equipped with the antenna had it removed and *vice versa*) for another period before the devices were removed. The devices were either 3-axis accelerometers (range 0-6 *g*, 22-bit resolution, sampling rate 16 Hz; JUV Elektronik, Borstel, Germany) or 'Daily Diaries' (DDs) (Wilson *et al.* 2008); multi-channel data-loggers which contained, among other transducers, tri-axial accelerometers coupled with depth sensors (acceleration range 0-6 *g*, depth range 0-5 m, 22-bit resolution, sampling rate 16 Hz; JUV Elektronik, Borstel, Germany). Tri-axial accelerometers recorded acceleration in three axes corresponding to the dorso–ventral, anterior–posterior and lateral axes (hereafter referred to as heave, surge and sway) and can be used to determine posture, movements and energetics (Shepard *et al.* 2008, Watanabe *et al.* 2005, Halsey *et al.* 2009).

The attachment of devices of the different types; DDs and tri-axial accelerometers with, or without, antennae was undertaken randomly so as to preclude any systematic bias. During this procedure, all birds, whether equipped with devices or not, were filmed by a splitter video system consisting of four cameras, three of which were located above the experimental pool and one of which was placed underwater. The base and sides of the pool had been marked with a 1 m grid to help in judging relative movement and calibrations of bird position were undertaken to correct for parallax error in which a life-sized model of a swimming guillemot was held at known positions underwater while filming.

Analysis

Due to inclement weather which led to poor quality video recordings, none of the filmed data was used for proper quantitative analysis although it did help to assess the behaviour of the birds visually and in correspondence with the acceleration data recorded. The acceleration data recorded by the devices were used to derive a proxy for energy expenditure, the Overall Dynamic Body Acceleration (ODBA), following methods described in Wilson *et al.* (2006). In brief, this method uses a running mean (over 1 s (cf. Shepard *et al.* 2008)) on the raw acceleration data from each of the three orthogonal acceleration axes (heave, surge and sway) to derive the static acceleration (acceleration due to gravity) for each axis. These static values are then subtracted from the raw values of acceleration to provide values for the dynamic acceleration of all three axes (stemming from movement of the animal's body). The absolute values of all dynamic values are then summed to provide the proxy for energy expenditure ODBA. Dive events were identified based on the depth profile and/or tri-axial acceleration signature (Figure 2). For each dive, we extracted information about maximum depth (m) and descent duration (s) to then calculate the vertical velocity during the descent phase (m/s). The average, minimum and maximum values of ODBA during the descent were also determined from the DD data.

For the statistical analysis, we differentiated between two major bird groups; (1) birds equipped with devices with antenna and (2) birds equipped with devices without antenna hereafter referred to as 'antenna-equipped' birds and 'non-antenna-equipped' birds, respectively. The diving behaviour and energy expenditure of the birds were compared between the two groups. Firstly, the relationship between the ODBA and the vertical velocity during the descent was assessed using Spearman rank correlation. ODBA statistics (mean, minimum and maximum) were then compared between the non-antenna birds and the antenna birds using a Mann-Whitney U test. Finally, since visual inspection of the video footage indicated differential rolling behaviour for birds resting on the water surface according to whether they were antenna-equipped or not, we examined the frequency distribution of both the static and dynamic components of the sway acceleration (corresponding to acceleration recorded in the lateral axis).

Results

The masses of equipped birds varied between 876 and 944 g (mean ± sd = 918.6 ± 25.3) and devices were deployed for periods between 139 and 1059 minutes.

A total of 26 dives displayed by eight out of the 11 birds could be identified from the acceleration data and depth profile (3 birds did not dive at all during the periods they were equipped) of which 10 were executed by antenna-equipped birds and 16 by non-antenna-equipped birds (Table 1). There was no significant difference in the diving rate between the antenna- and non-antenna-equipped birds (Mann Whitney U test, $z = 0.447$, $P > 0.05$; Table 1). The vertical velocity during the descent could be calculated for only 13 dives (the ones extracted from the DD loggers with the depth profile) of which 11 were from non-antenna-equipped birds (mean ± sd = 0.40 ± 0.06 m/s) and 2 from one antenna-equipped bird (mean ± sd = 0.37 ± 0.08 m/s) yielding no significant relationship between vertical velocity and mean ODBA ($N = 13$, $rs = 0.12$, $P > 0.05$). However, the mean and maximum ODBA values obtained for the descent phase from all 26 dives were approximately 20% higher for the antenna-equipped birds than for the non-antenna-equipped birds (Mann–Whitney U test, $z = 2.82$, $P = 0.003$ and $z = 2.43$, $P = 0.01$ respectively for mean and max ODBA, Figure 3).

Consideration of the frequency distribution of static and dynamic sway between antenna-equipped and non-antenna-equipped birds showed broadly similar patterns but statistically significant differences in peak position (Mann–Whitney U test, $z = 7.844$, $P < 0.001$ and $z = 23.7$, $P < 0.001$ respectively for static and dynamic sway, Figure 4 and Table 2). Our subjective impression from the video recordings was that the antenna-equipped birds tended to roll to a greater degree than the non-antenna-equipped birds.

Discussion

Radio and satellite telemetry are important tools in understanding the biology of wild animals and the use of satellite tracking, in particular, has provided substantial insights into the life and distribution of many elusive and wide-ranging species including seabirds (Burger & Shaffer 2008). The success of wildlife telemetry is, however, tempered by potential negative impacts that tracking devices can have on their bearers (Wilson & McMahon 2006, Vandenabeele *et al.* 2011). Device effects on birds range from behavioural disturbance to physical injuries (Calvo & Furness 1992, Phillips *et al.* 2003, Barron *et al.* 2010) which can ultimately compromise survival (e.g. Paquette *et al.* 1997, Steenhof *et al.* 2006). Ongoing research into miniaturization is allowing devices to become ever smaller and lighter, reducing potential impact (Ropert-Coudert & Wilson 2005, Bridge *et al.* 2011), a process which is enhanced by consideration of device shape so as to reduce drag (Obrecht *et al.* 1988, Bannasch *et al.* 1994, Culik *et al.* 1994). In a demonstration of the importance of drag, a recent study by Pennycuick et al (2012) showed that even the minimal cross-sectional area of a harness increased the drag coefficient of starlings (*Sturnus roseus*) flying in a wind tunnel by nearly 50%. This reinforces the idea that any protuberance, even if relatively small, can disrupt air flow around a body, resulting in increased drag. The density of water makes diving animals particularly susceptible to this, as evidenced by recent studies on penguins wearing flipper bands (Gauthier–Clerc *et al.* 2004, Saraux *et al.* 2011).

Importantly though, and often ignored, drag is not just affected by the shape and size of the main body of transmitters but also by the attached antennae (Wanless *et al.* 1988, Wilson *et al.* 2004, Latty *et al.* 2010) and this may be partially responsible for observed impacts of PTTs on bird wearers (Phillips *et al.* 2003). In fact, in general, relatively few studies have documented the effects of antenna-bearing transmitters including PTTs and even fewer have specifically looked at the effect of antennae (Wanless *et al.* 1988, Wilson *et al.* 2004). This study sought to address this important issue under controlled conditions by examining antenna-related behavioural and energetic changes in the common guillemot.

Our study was limited by the low number of dives recorded which could not be specifically related to device effects due to lack of unequipped controls although we note that previous studies have observed this phenomenon (Ropert-Coudert *et al.* 2000, 2007a). However, even with the low number of dives executed by equipped birds, and in accordance with the predictions made by Wilson *et al.* (2004) on penguin models, we found that the presence of an antenna did indeed appear to increase the energy expenditure, with a higher ODBA occurring during the descent phase of shallow dives. ODBA has been shown to be linearly related to metabolic rate for a number of species of birds (Halsey *et al.* 2009), including diving birds swimming underwater (Gómez-Laich *et al.* 2011), and although lack of a calibration between VO_2 and ODBA precludes us from deriving the precise increment in power associated with diving, it seems safe to conclude that antennae do increase the metabolic costs of diving auks during the descent phase of dives, even at the low descent speeds (*ca.* 0.4 m/s) observed in our study. Given that drag is proportional to the square of the speed (cf. Lovvorn *et al.* 1991, 1999) and that wild guillemots descend the water column at 1.5-2 m/s (Piatt & Nettleship 1985, Watanuki & Sato 2008), we would expect free-living birds to experience much higher energetic costs if they maintained normal foraging patterns. Similarly, wild birds have an extended bottom phase to their dive (Croll *et al.* 1992, Thaxter *et al.* 2010), something that was not exhibited by our birds, which, being powered, would presumably also incur higher energetic costs in antenna-equipped birds. The ascent phase in guillemots is, however, passive, with birds being forced to the surface by their buoyancy (Lovvorn *et al.* 1999, Watanuki *et al.* 2003) so we do not expect the power costs associated with it to increase although over long ascent phases the increased drag of antenna-equipped individuals may reduce vertical velocity and hence increase transit time.

In addition to energetic considerations, the balance of the antenna-equipped birds when diving or resting at the surface appeared to be compromised, even in the still pool in which the birds were housed, with birds exhibiting a tendency to roll more than the non-antenna-equipped birds. Balance problems have already been observed in little penguins *Eudyptula minor* fitted with dorsally-mounted loggers and are presumed to increase energy expenditure as birds attempt to correct for this. (Healy *et al.* 2004, Chiaradia *et al.* 2005). We assume that such problems would be exacerbated for birds resting at the surface of an unstable ocean. Although projecting antennae normally have small mass compared to the main tag body, the farther they project from the carrier's centre of gravity, the greater the force they exert due to the moment arm effect and we believe that our observations of increased rolling were primarily due to this. This moment arm effect may also be important underwater where the projecting antenna could act as a rudder tending to make the bird's trajectory angle more towards the surface. Finally, we also note that antennae in moving fluid systems can sometimes be meta-stable, tending to vibrate with movement (Weaver 1964). We do not know if this is a problem but it deserves consideration. Beyond the specifics of our study, external antennae may result in entanglement and occasionally bird mortality in passerines (Dougill *et al.* 2000, Hill & Elphick 2011).

Quite how wild guillemots might respond to the increasing energy expenditure effects associated with antennae is unclear. Among the most common compensatory behaviours displayed by wild diving birds equipped with various external units are reduced swim speeds (see above), decreased dive depths and/or duration, and increased in surface pause, all of which lower foraging efficiency (Wilson *et al.* 1986, Croll *et al.* 1991, Taylor *et al.* 2001, Ropert-Coudert *et al.* 2007b). As a presumed knock-on consequence of such behaviours, reproductive success (Paredes *et al.* 2005, Whidden *et al.* 2007, Wanless *et al.* 2008, Beaulieu *et al.* 2010) and survival rate can be altered (Calvo & Furness 1992, Paquette *et al.* 1997, Saraux *et al.* 2011).

Given the necessity of external antennae for the proper functioning of so many VHF-dependent systems such as PTTs (Fancy *et al.* 1988, Mech & Barber 2002), we accept that some researchers may regard them as a 'necessary evil' in some studies, but it is hard to justify if the device itself causes the bird to behave abnormally. Recommendations can be made that should reduce their deleterious effect based on our understanding of external antennae increasing drag and producing a force which tends to make birds roll more due to the moment arm effect. In both cases, the deleterious effects should be reduced with shorter antennae as well as by having antennae that are angled backwards rather than projecting perpendicularly. Where length and perpendicular projection are critical for appropriate signal transmission, antennae could be constructed to be thinner (which should decrease both drag [cf. Wilson *et al.* 2004] and the force developed by the moment arm) and made flexible so that as the birds swim underwater (or fly), the antennae tend to lie backwards, thus decreasing drag by having a reduced projecting cross-sectional area. Indeed, it would seem appropriate in these times that are so defined by exciting technological advances in animal telemetric systems (e.g. Ropert-Coudert & Wilson 2005), that we maintain similarly progressive views on animal well-being (Calvo & Furness 1992, Wilson & McMahon 2006, Vandenabeele *et al.* 2011).

Acknowledgements

We thank the Royal Society for Prevention of Cruelty to Animals (RSPCA) for having provided equipment and access to their facilities at the Mallydams Wildlife Centre (Hastings, UK). We are grateful to all the people who helped with the project. This study received the financial support from the California Department of Fish and Game's Oil Spill Response Trust Fund (through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California,

Davis) and the RSPCA (Wilberforce Way, Southwater, Horsham, West Sussex, RH13 9RS, United Kingdom).

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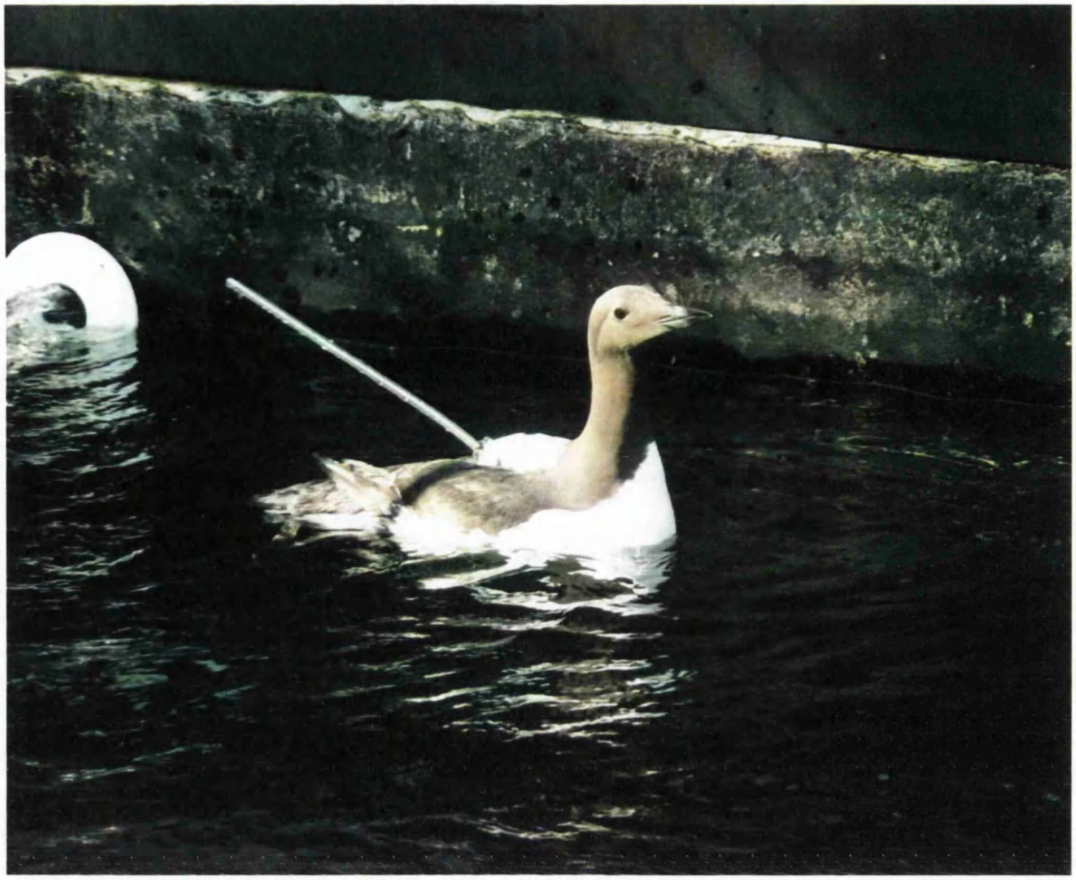

Figure 1. Photo of a captive guillemot fitted with a data- logger plus antenna resting at the water surface in an outdoor pool facility at the RSPCA wildlife centre, Mallydams woods, Hastings, UK.

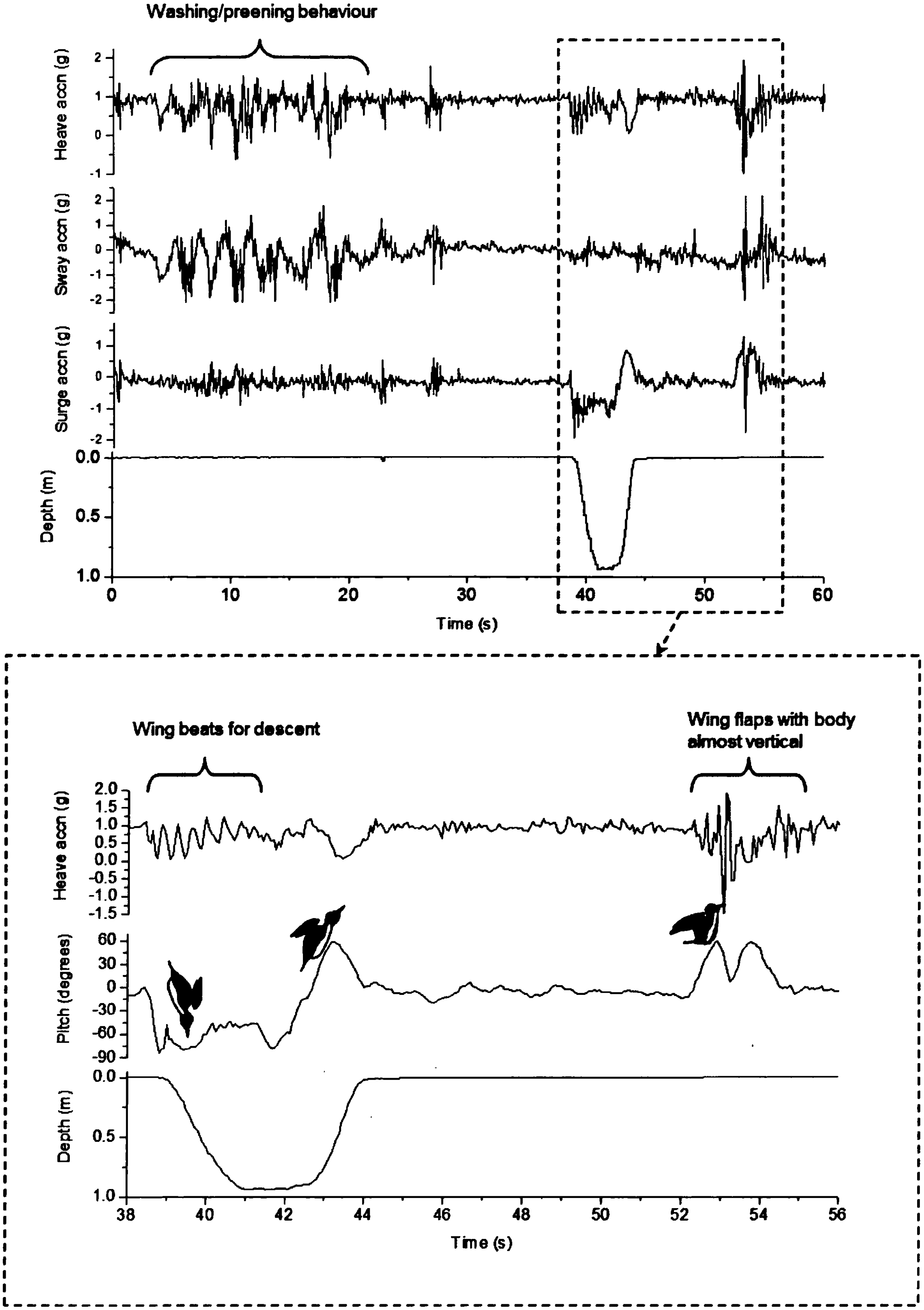

Figure 2. Example of guillemot behaviour recorded by a Daily Diary logger (Wilson *et al.* 2008) showing the tri-axial acceleration signature during a single dive as well as washing, preening and wing-flapping.

Table 1. Details about the captive guillemots their diving activity during the experiment.

Bird ID	Treatment	Mass (g)	Deployment duration (h)	Total nb dives	Diving rate (nb dives /h)
1	No antenna	944	2h30	1	0.4
2	No antenna	922	9h18	10	1.1
3	No antenna	903	1h49	2	1.1
4	No antenna	937	15h31	2	0.13
5	No antenna	876	15h31	1	0.06
6	Antenna	937	2h01	1	0.5
7	Antenna	903	15h42	7	0.45
8	Antenna	–	2h07	2	0.94

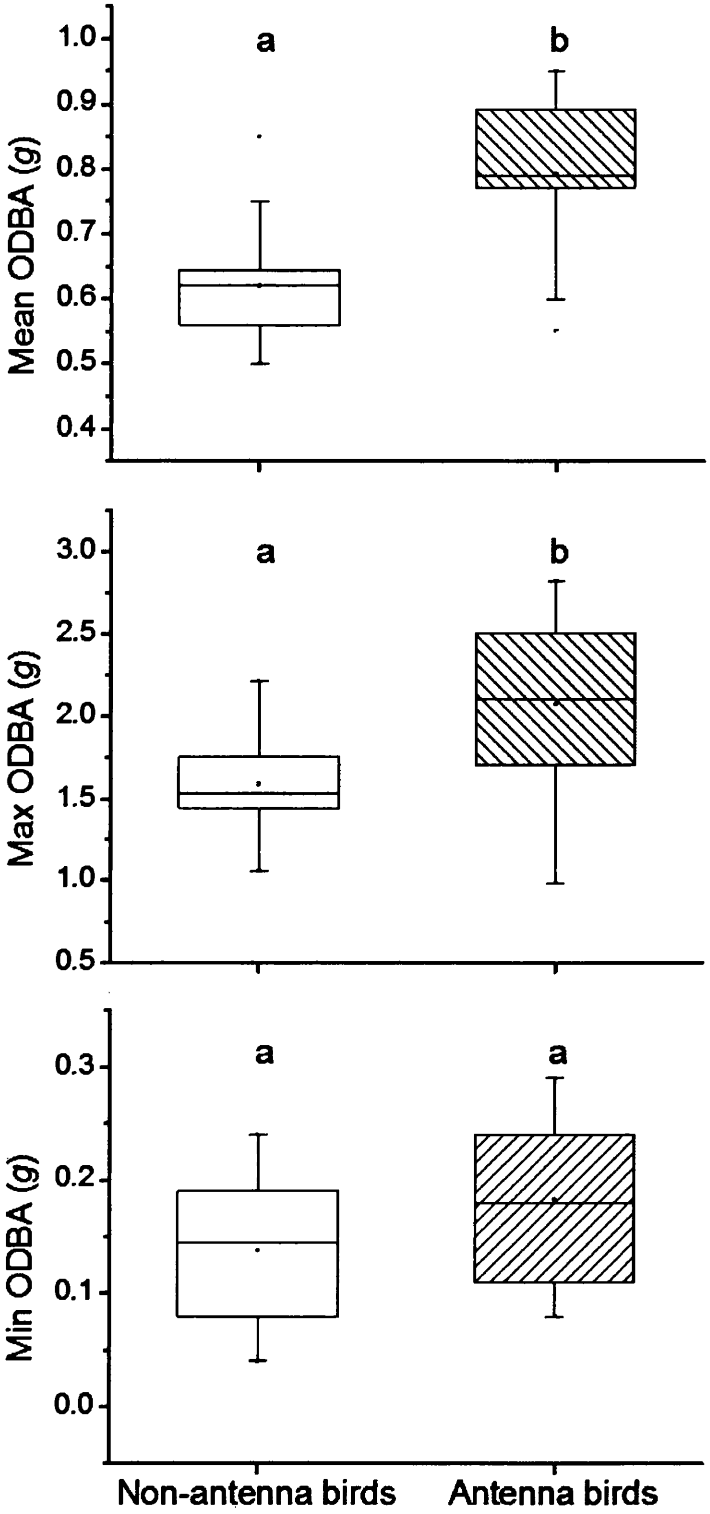

Figure 3. Box-plots of the minimum, maximum and mean values of the Overall Dynamic Body Acceleration (ODBA, proxy for energy expenditure derived from acceleration data) calculated for guillemots fitted with devices with and without antenna. Two different letters indicate a significant difference between the two groups (Mann-Whitney U test, see text). Acceleration unit is in *g* force or m/s^2.

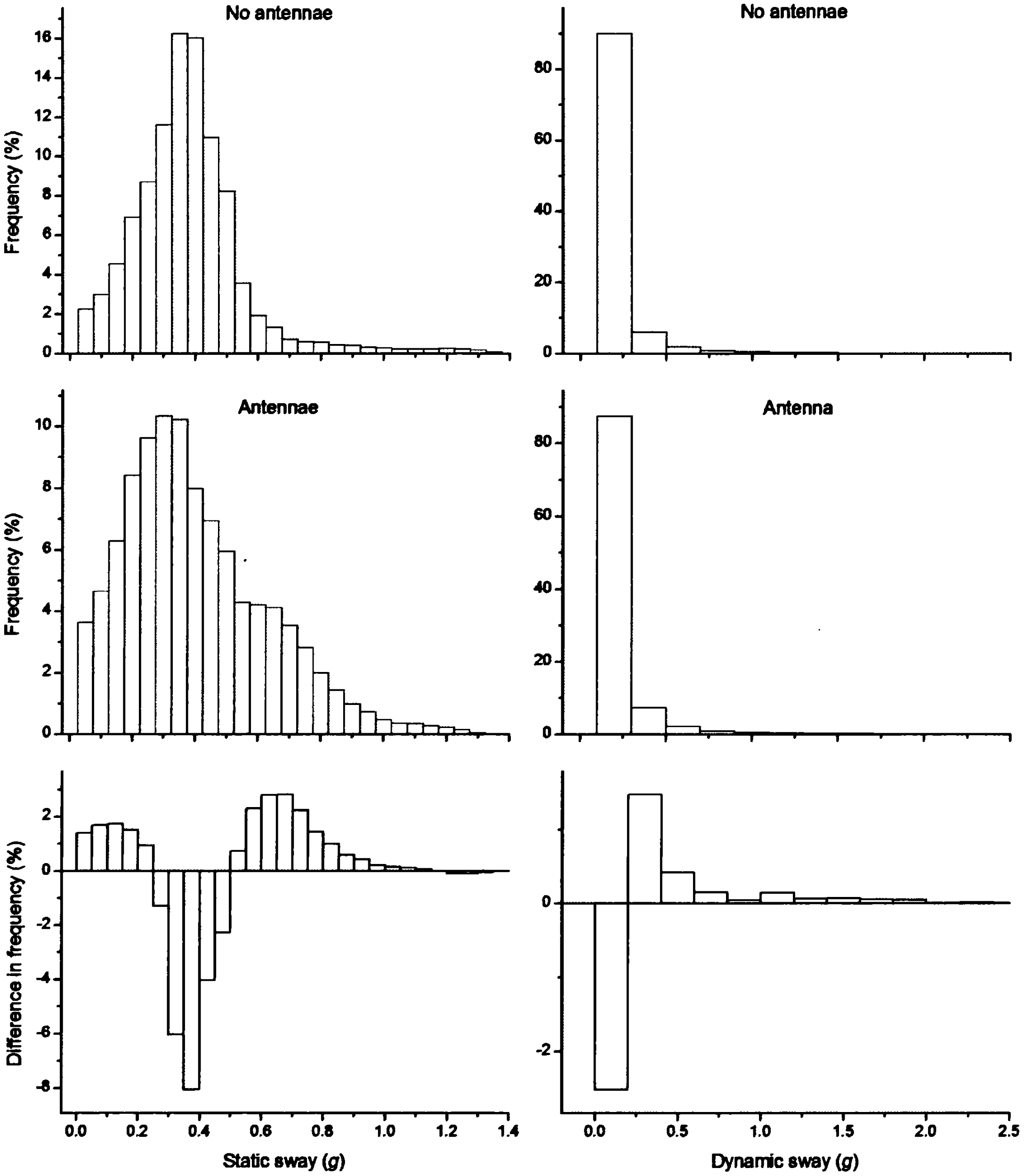

Figure 4. Frequency distribution of the static (left column) and dynamic (right column) components of the lateral acceleration (i.e. sway) recorded on guillemots fitted with devices that included, or not, an antenna. The static sway informs about the posture whereas the dynamic sway indicates movement. The difference between antenna-equipped birds and non-antenna-equipped graphically represented at the bottom row appeared significant (see text and Table 2 for details).

Table 2. Statistics for the static and dynamic components of sway (i.e. lateral acceleration) calculated for birds equipped with devices but no antenna or devices with antenna. This is to look at the difference in rolling behaviour between the two groups of birds during periods of motion (dynamic sway) and resting (static sway).

Treatment	Acceleration component	Mean	Standard deviation	Minimum	Median	Maximum
Non-antenna equipped birds	Static Sway (*g*)	0.35	0.18	0.00	0.34	1.35
	Dynamic Sway (*g*)	0.09	0.18	0.00	0.04	2.99
Antenna-equipped birds	Static Sway (*g*)	0.38	0.23	0.00	0.33	1.37
	Dynamic Sway (*g*)	0.11	0.21	0.00	0.05	3.03

Note: Acceleration unit is in *g* force or m/s^2.

Chapter 8:

Weight-watching for birds; inappropriate placement of tags on gannets changes flight patterns

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SPV, SCV and SCP conducted the study on wild gannets. SPV, with help from EG, analysed the data. SPV wrote the manuscript with inputs from MIF, EG, SCV, AG and RPW.
Submitted to Journal of the Royal Society Interface

Abstract

Devices attached to birds can hugely enhance our understanding of their behavioural ecology for periods when they cannot be observed directly. For this, scientists routinely attach units to either birds' backs or their tails. However, inappropriate payload distribution is critical in aircraft and, since birds and planes are subject to the same laws of physics during flight, we considered aircraft aerodynamic constraints to explain flight patterns displayed by northern gannets *Sula bassana* equipped with (small *ca.* 14 g) tail- and back-mounted accelerometers and (larger *ca.* 30 g) tail- and back-mounted GPS units. Tail-mounted GPS-fitted birds showed significantly higher cumulative numbers of flap-glide cycles and a higher pitch angle of the tail than control birds, indicating problems with balancing inappropriately placed weights with knock-on consequences relating to energy expenditure. These problems can be addressed by carefully choosing where to place tags on birds according to the mass of the tags and the lifestyle of the subject species.

Keywords: tracking; payload; tag placement; aerodynamics; energetics; flying birds

Introduction

Although folklore would have storks flying with babies dangling from their beaks, a more likely modern stork would be carrying a tracking device attached to its back (e.g. Papi *et al.* 1997). Indeed, the development of Platform Transmitter Terminals (PTTs) and Global Positioning Systems (GPS) to follow wildlife in the 80s-90s (Cohn 1999, Gillespie 2001, Rodgers 2001) has led to a plethora of satellite tracking studies, particularly on migratory birds (Guan & Higuchi 2000) such as storks (Papi *et al.* 1997, Berthold 2001).

Despite the unquestionable progress in our understanding of wild bird movements through the miniaturization of remote-sensing devices, the extra mass that these devices represent for their carriers has been cause for concern (Gessaman & Nagy 1988, Bowlin *et al.* 2010). To deal with this, Kenward (2001) suggested that birds should not be fitted with devices representing more than 3% of their body mass, and although this is an important first step, a recent study modelling bird flight indicated that the matter is not that simple as other factors such as device-induced drag can influence the degree of impact that tags may have on their carriers (Vandenabeele *et al.* 2012). Besides, major differences in morphologies, wing loadings and life-histories between bird species suggest that device mass effects should perhaps best be considered at a family or group level (Vandenabeele *et al.* 2012). Although this study has helped refine our thinking with respect to how extra mass might impact flying birds, it does not address the important issue of device placement. Common sense would dictate, in agreement with basic laws of physics about stability in flight (Taylor & Thomas 2002), that tags should be placed as closely as possible to the centre of gravity where it would least destabilize the birds (Wanless *et al.* 1989, Powell *et al.* 1998). However, this solution is somewhat at odds with suggestions made for diving birds, for example, where the explicit recommendation has been to place tags most posteriorly to minimize drag (cf. Bannasch *et al.* 1994). Indeed, such arguments would appear particularly germane in the extreme case of plunge-diving birds, such as gannets (Sulidae), where the force applied to the tag as the bird enters the water is likely to be extreme (Nelson & Busby 1978, Del Hoyo *et al.* 1992). Not only will such force presumably impact the bird but it makes the attachment of devices problematic. One technique that seems to have solved, or at least reduced, this plunging impact problem is the practice of fixing tags to the underside of the tail using tape (e.g. Hamer *et al.* 2007, Stauss *et al.* 2012). This appears to result in the tag being protected by the feet during the plunge and has resulted in tags being attached for periods extending from days to weeks (e.g. Hamer *et al.* 2007, Votier *et al.* 2011). The effect of this deviation from the bird's centre of gravity, however, is unknown.

In aircraft, the weight distribution has to be carefully managed to ensure the position of the centre of gravity is within specified limits. Since a significant proportion of the aircraft weight is payload (cargo and/or passengers), the weight balance has to be calculated for every flight and adjusted by moving the location of payload as necessary (Federal Aviation Administration 2007). For long range aircraft the weight of fuel is also significant and distribution amongst the multiple on-board fuel tanks may be adjusted to ensure the weight is balanced (Raymer 2006). There are two main reasons why the centre of gravity is controlled so carefully in aircraft. First, in straight and level flight the aircraft is *trimmed* so that the aerodynamic forces, moments and weight are in equilibrium. In practice, the angle of the elevator and/or horizontal tail is adjusted to maintain altitude; if the centre of gravity is outside the specified limits then either the tail is unable to generate sufficient force to maintain equilibrium, or the drag penalty is too high. Secondly, moving the centre of gravity aft reduces the longitudinal static stability of the aircraft (Stevens & Lewis 2003). This makes the aircraft more responsive but also more difficult to fly. These considerations of weight balance in aircraft should be just as applicable to birds and so we used it as a framework to investigate the effects of tags, and therefore payload mass and position in birds.

For this, we attached accelerometers to northern gannets (*Sula bassana*), a species that habitually plunge-dives to capture prey (Del Hoyo *et al.* 1992), and which has been subject to an appreciable number of tracking studies using both back- and tail-mounted devices (e.g. Ropert-Coudert *et al.* 2004, Garthe *et al.* 2007, Votier *et al.* 2011). Since accelerometers can give information on both body posture (Watanabe *et al.* 2005, Shepard *et al.* 2008b) and the energy invested in movement (Wilson *et al.* 2006, Green *et al.* 2009, Halsey *et al.* 2009), we sought to define a protocol to identify the extent to which back- and tail-mounted tags may differentially affect birds with a view to minimizing potential device effects. Our point of departure is that non-centrally mounted payloads will affect flight capacity in these birds in the same manner that it does in aircraft since the principles of flight in both birds and planes are comparable (Pennycuick 2008).

Methods

Study site and device deployment

The study was conducted during July-August 2011 and 2012 at the breeding colony of northern gannets located on Grassholm island, Wales, UK (51°43'N, 05°28'W). A total of 20 chick-rearing gannets was caught on the nest at change and equipped with data-loggers attached to the feathers using waterproof Tesa tape (Wilson & Wilson 1989, Wilson *et al.* 1997). Fourteen birds were fitted with a tri-axial accelerometer on the back (X6-2mini accelerometers, Gulf Coast Data Concepts LLC, Waveland, US) and of these, 5 had a dummy GPS tag (with the same dimensions and mass as i-gotU GPS Travel Logger GT-600 (Maplin Electronics Ltd, which is used widely in this species) on the back, 4 a dummy GPS on the tail and 5 with no further device (Table 1). In addition, to look at detailed tail posture and movements, 6 birds were fitted with an accelerometer under the tail with, and without the presence of a GPS tag (Table 1). Accelerometers consisted of a circuit board and battery that had been removed from their original housing and coated with epoxy-resin. Once programmed via USB connection and just prior to deployment, they were sealed in a waterproof heat-shrink tubing package. The whole system (waterproof case included) weighed between 13 and 15 g. With the dummy GPSs weighing between 28 and 30 g, birds carried a total mass ranging from 13 g (accelerometer alone) to 45 g (accelerometer plus dummy GPS) accounting for 0.4 to 1.5 % of the bird's body mass for an adult bird of *ca.* 3 kg (Nelson & Busby 1978, Montevecchi & Piatt 1984), depending on the type of devices deployed (Table 1). The lateral compression and positioning of all attached devices were assumed to have minimal impact on the bird's streamlining. The placement of the device on the back was carefully chosen based on the results of a wind-tunnel study which looked at the effect of tag position on drag (Vandenabeele & Wilson 2012). The acceleration of the bird was recorded continuously at a sampling rate of 40 Hz in each of the 3 main orthogonal axes (dorso–ventral [heave axis], anterior–posterior [surge axis] and lateral [sway axis]) with 16-bit resolution for the duration of at least one foraging trip. When back on the nest, the birds were recaptured and the equipment removed.

Data analysis

Once the devices were retrieved, data were downloaded to a computer and analysed using Origin- (version 8.5.1, OriginLab Corp., USA) and Excel (version 2010, Microsoft inc., USA) software. The different behaviours could be identified based on the frequency and amplitude of the accelerometry signal in the three axes (Figure 1). The first part of the analysis focused on periods of 10 minutes of regular flight extracted between 30 minutes to an hour after departure from the breeding colony, a period when the birds had an empty gut since changeover occurs after birds have conducted long periods of incubation or chick-rearing and foraging does not normally occur until a considerable distance from the colony. To analyse data of birds which had not fed ensured that flying behaviour would not be affected by food load. An approximation of the static (gravity-based) acceleration was derived from the raw acceleration recorded by the loggers using a running mean over 2 s (cf. Shepard *et al.* 2008a). Simple trigonometry was used to derive the pitch angle of the bird body during flight using the anterio–posterior axis (cf. Wilson *et al.* 2008) after correcting for possible variance in attachment angle by using the angle when the gannet was resting on the sea surface as zero. This was done using the acceleration data collected from the devices attached on the back to assess body posture and movements as well as those placed under the tail to look at tail posture.

The acceleration data collected on the back of the birds was subjected to further analysis to determine flight energetics. For this, we derived a proxy for movement-based energy expenditure termed the Overall Body Dynamic Acceleration (ODBA) (Wilson *et al.* 2006). For this, the static acceleration for each of the orthogonal acceleration axes was first subtracted from the relevant raw acceleration values to obtain the dynamic component of acceleration. The absolute values of these dynamic acceleration data were then summed over the 3 channels to get the ODBA (Wilson *et al.* 2006, Shepard *et al.* 2008b). ODBA was determined for the same periods of 10 minute flight previously considered.

Running variance to identify behavioural signatures

During flight, flapping and gliding exhibit distinct acceleration profiles in both the surge and heave axis (Figure 1). We used a running variance of the surge acceleration so as to identify flapping from gliding phases. The running variance is the average residual which was calculated over periods of one second according to:

$$\sigma_{2w}^{2}(x_n) = \frac{1}{w}\sum_{i=n-w}^{n+w}(x_i - \mu_w(x_n))^2 \tag{1}$$

where *2w* is the time window considered, *x* is the data value at index *n* and $\mu_w(x_n)$ is the mean value over the same time window.

Taking the average variance across the whole 10 min flight period (*σ(X)*) and using it to compute a binary classification gives an accurate signal representing the 2 flight states:

$$b(x) = \begin{cases} 1 & if\ \sigma_w(x_n) > \sigma(X) \\ 0 & otherwise \end{cases} \tag{2}$$

where a value of 1 represents flapping behaviour and 0 represents gliding behaviour (or, specifically, not flapping, which we assume to be gliding as the animal was in flight for the whole period) (Figure 2). Based on this binary classification of the flight data, it was then possible to describe and compare profiles of flapping and gliding behaviours between the birds.

Results

All 20 birds came back to their nest although 4 individuals had lost their tags fitted on the back. These 4 birds were all part of the same group, of 5 individuals, carrying accelerometers plus GPS units on their backs ('Acc+GPSback'; Table 1). This left just one bird with data from this group, which, due to the low sample size, was therefore excluded from the analysis. In addition, 1 accelerometer, fitted to a bird from the 'AccBack' (Table 1), failed to record. Consequently, data from 14 birds was collected of which, 4 with accelerometers on the back ('AccBack' thereafter referred as non-GPS birds) and 4 with accelerometers on the back plus GPS units under the tail ('AccBack+GPStail' thereafter referred as GPS birds), were analysed. Although, the major part of the analysis dealt with these 2 groups (non-GPS birds and GPS birds), 6 other birds were included in the analysis which carried accelerometers on their tail with, or without, GPS ('AccTail' and 'Acc+GPStail' respectively; see Table 1) and served to look specifically at the pitch of the tail.

The duration of foraging trips ranged from 7 to 51 hours and appeared significantly shorter for GPS birds (Mann-Whitney U test, $z = -2.32$, $P = 0.02$; mean ± sd = 32 ± 16.7 h for non-GPS birds and 12 ± 8 h for GPS birds). The small sample size of 8 birds as well as the noise observed in raw acceleration data rendered any analysis difficult, offering little immediate insight into flight behaviour and potential differences between the 2 groups of non-GPS birds and GPS birds. However, the running variance method (see Methods) performed on the surge acceleration signal allowed identification and comparison of flapping and gliding behaviours between the birds.

No clear difference was revealed in the amount of time spent flapping *per se* or relative to gliding (Mann-Whitney U test, $P > 0.05$; see Table 2). However, we did observe that the GPS birds executed more transitions between the 2 states than did non-GPS birds, resulting in a larger number of flap/glide cycles (Mann-Whitney U test, $z = 2.31$, $P = 0.03$; see Table 2 and Figure 3). This lead to clear separation between the 2 groups with, however, more variation exhibited amongst the cluster of non-GPS birds than for birds with tail-fitted GPS. This was reflected in the number of flap/glide cycles per minute, which appeared significantly higher for GPS birds than for non-GPS birds (Mann-Whitney U test, $z = 2.12$, $P = 0.03$; Figure 4) as well as more constant (Levene test, $P = 0.011$; Figure 4).

By examining the ODBA signal for each bird in relation to the tri-axial acceleration signals, we could associate each ODBA peak with a specific part of the wingbeat and flap-gliding cycle (Figure 5). In frequency histograms of ODBA for both bird groups, there appeared to be 3 main modes (Figure 6). The first ODBA mode matched to the gliding phases whereas the second and third peaks matched the upward and downward movement of the wing beats during flapping, respectively (see Figures 5 and 6). Both experimental bird groups showed a broadly similar pattern in their frequency distributions of ODBA but with tail-mounted birds (GPS birds) presenting a greater proportion of high ODBA values (i.e. values > 0.75 *g*; Figure 6), corresponding to flapping, than non-GPS birds with a significant difference being detected (Mann-Whitney U test, $z = 6.42$, $P < 0.001$) which, however, may be due to the power of the non-parametric test performed on a large dataset. .

The flight pitch angle of the birds did not obviously change between experimental groups (Mann-Whitney U test, $P > 0.05$; see Figure 7a and 7b) but was significantly different at the tail level with the birds carrying the heaviest payload (accelerometer + GPS) showing a higher pitch than the other birds carrying just an accelerometer under the tail (Mann-Whitney U test, $z = 294.9$, $P < 0.001$; Figure 7c and 7d).

Discussion

This study considered the middle back and the tail as two common locations for the tags. The addition of tags at different positions on a bird has two major aeronautical effects, aerodynamic and inertial. The middle back location will increase the drag of the bird slightly (and hence the energy requirements) but should not significantly affect the lift, which is generated mainly by the wings (Anderson 2005). The tail location has more potential to disrupt the flow depending on the size of the device relative to the size of the tail. The location under the tail will effectively reduce the camber of the tail and, in aeronautical terms, should reduce the lift from the tail.

The inertial properties are changed in two significant ways. The increased mass means that the GPS birds have to generate more lift to fly, and hence use more energy through increased induced drag (Anderson 2005, Pennycuick 2008). The devices are limited to <3% of the bird mass (Kenward 2001) and hence this effect should be relatively small. The second effect is to move the centre of gravity rearwards, and hence the trim of the bird (when the total forces and moments are zero) will have to change. The middle back location will be approximately above the centre of gravity and hence will have little effect on the trim. The mass of the device at the tail location will cause a significant pitch-up moment that would have to be matched through an increase of lift from the tail. Given also that the device aerodynamics will give a decrease in lift from the tail, this means that the angle of attack of the tail would have to be increased significantly, resulting in increased drag from the tail.

Despite the limited dataset, the results support the predictions that tail-mounted devices will affect the flight patterns of foraging gannets, even though we used no tag system that exceeded the 3% limit proposed by Kenward (2001, but see Vandenabeele *et al.* 2012). Birds with tail-fitted GPS units had a significant change in the pitch of their tail implicating a higher level of energy expenditure associated with flapping. The running variance analysis did not reveal any clear difference in the flap/glide behaviour of the birds either in terms of the amount of time spent flapping *per se* or relative to gliding (flap/glide ratio). However, birds carrying GPS under their tail appeared to execute more transitions between flapping and gliding phases and therefore presented higher total number of flap/glide cycles over the 10 min flight period compared to non-GPS birds. This increase in the number of flap/glide cycles is likely linked to the required change in trim predicted for birds with tail-located devices (see above). Since the birds were not used to the devices, they may initially set their tails to the expected angle, which would cause a pitch-up moment with a corresponding increase in height and decrease in speed. An appropriate response to this would be to start flapping to prevent stalling. Similarly, initiation of flapping could be linked to an increase in the sink rate during gliding resulting from the attached tags. Calculations using free-access software (Flight 1.24 software accessible at *http://www.bristol.ac.uk/biology/people/colin-j-pennycuick/index.html*; cf. Pennycuick 2008), indicates that GPS-equipped northern gannets should experience an increase of 6.3% in their sink rate (being 0.64 m/s compared to 0.60 m/s for GPS birds and non-GPS birds, respectively).

We consider that the mechanical and energetic constraints are the likely cause of the reduced variability in flight behaviour observed amongst GPS birds with respect to the flap/glide cycle pattern. Equipment of northern gannets with such tail-mounted packages may compromise their capacity to travel efficiently the long distances they cover during foraging (Garthe *et al.* 2007, Hamer *et al.* 2009) with possible knock-on effects relating to their capacity to exploit highly variable prey abundance and distribution (Hamer *et al.* 2007).

Thus, the case of how to equip plunge-diving birds would appear problematic, with back-mounted tags increasing drag, especially during the plunge (where deceleration can be up to 6 *g*; Figure 1 middle panel with surge acceleration), and being subject to device loss as a result, while tail-mounted units likely upset both the trim of the bird and the tail angle with all the problems that these engender. Perhaps the best way forward is to work on centrally mounted tags with minimum drag and enhanced stability (Healy *et al.* 2004, Adams *et al.* 2009), which can be designed using Computational Fluid Dynamics and Computer Aided Design (Vandenabeele *et al.* in prep.) in combination with more robust attachment procedures such as bird-friendly Silastic® harnesses (Vandenabeele *et al.* in press) which hold units in place more securely than do simple tag/feather attachment systems (Anderka *et al.* 1992). Either way, it is clear that we should not continue attaching tags to birds without giving the consequences of tag placement more thought.

Acknowledgements

We thank all the people who more or less directly contributed to this study including; the fieldworkers who were present on Grassholm Island conducting various work on the gannets; Dr Samantha Patrick as well as the RSPB wardens of Ramsey Island, Lisa and Greg, for their help and kindness; Tim who despite being anti-pop-up tent is a terrific skipper; and Mike Fowler for his constructive comments. This study would have not been carried out without the financial support from the California Department of Fish and Game's Oil Spill Response Trust Fund (through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis) and the Royal Society for Prevention of Cruelty to Animals (RSPCA, Wilberforce Way, Southwater, Horsham, West Sussex, RH13 9RS, United Kingdom). Prof. Friswell acknowledges the support of the European Research Council under the European Union's Seventh Framework Programme (FP/2007-2013) / ERC Grant Agreement n. [247045].

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Table 1. Details of the device deployment conducted on adult (chick-rearing) gannets (*Sula bassana*) as to examine the effects of the position of extra mass on their flying behaviour. Of the 14 birds equipped with accelerometer on the back, 8 (4 in the 'AccBack' group and 4 in the 'AccBack+GPStail' group) could be included in the analysis. Another 6 birds were included in the analysis which had been fitted with accelerometers on their tail, with, and without, GPS ('Acc+GPStail' and 'AccTail' group respectively).

Group	**Number of birds**	**Device deployed**	**Position**	**Device mass**
AccBack (Non-GPS birds)	5	Accelerometer	Middle back	13-15 g
Acc+GPSback (excluded after deployment failure)	5	Accelerometer Dummy GPS	Middle back	13-15 g 28-30 g
AccBack+GPStail (GPS birds)	4	Accelerometer Dummy GPS	Middle back Tail	13-15 g 28-30 g
AccTail	3	Accelerometer	Tail	13-15 g
Acc+GPStail	3	Accelerometer Dummy GPS	Tail	43-45 g

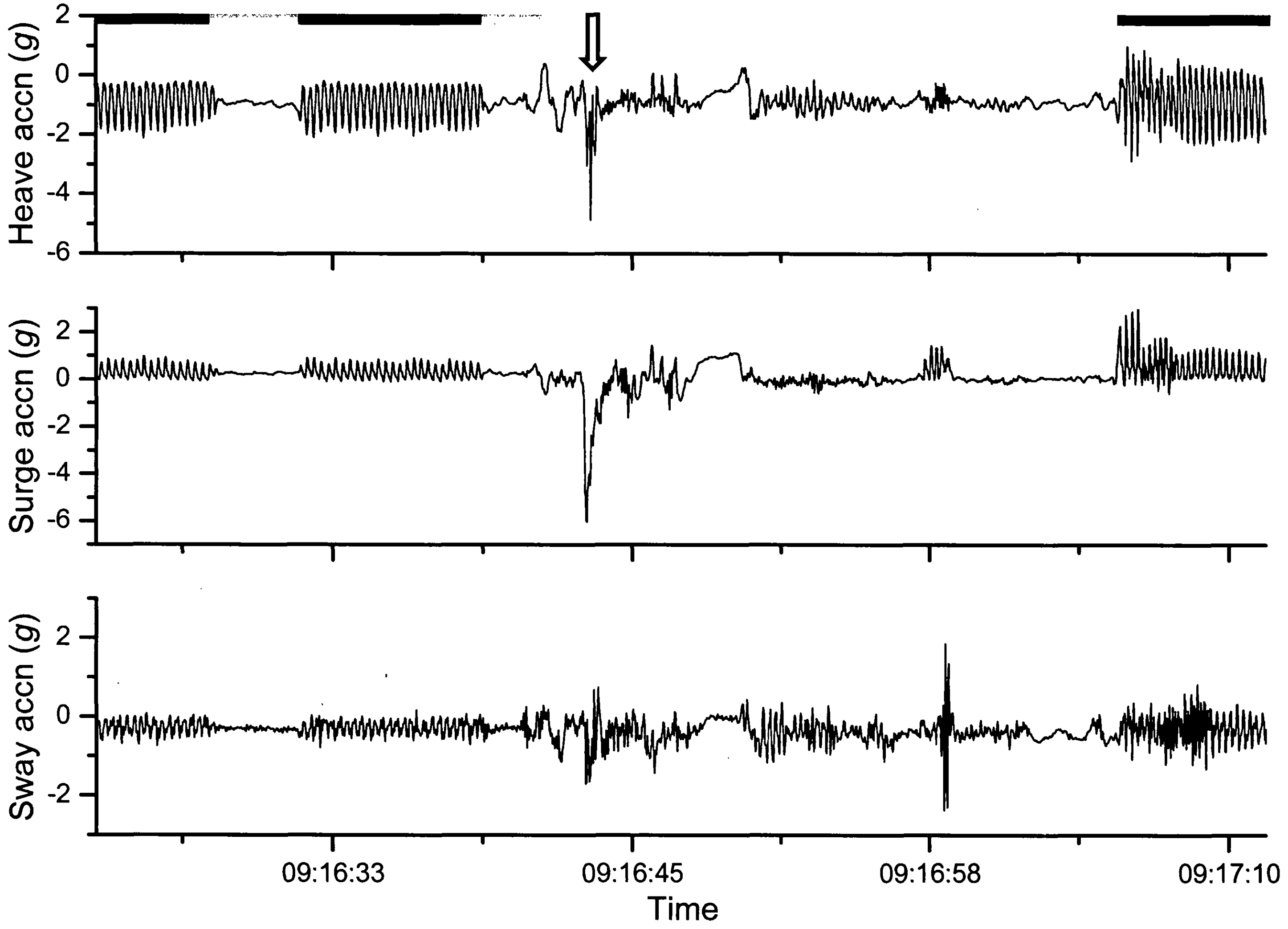

Figure 1.

Example of gannet behaviour recorded by a data-logger (X6-2mini accelerometers, GCDC LLC, Waveland, USA) showing the tri-axial acceleration signature during flight (flapping – black horizontal bars and gliding - grey bars) just before and after a plunge dive (indicated by the arrow followed by phase on sea surface before flapping to take-off).

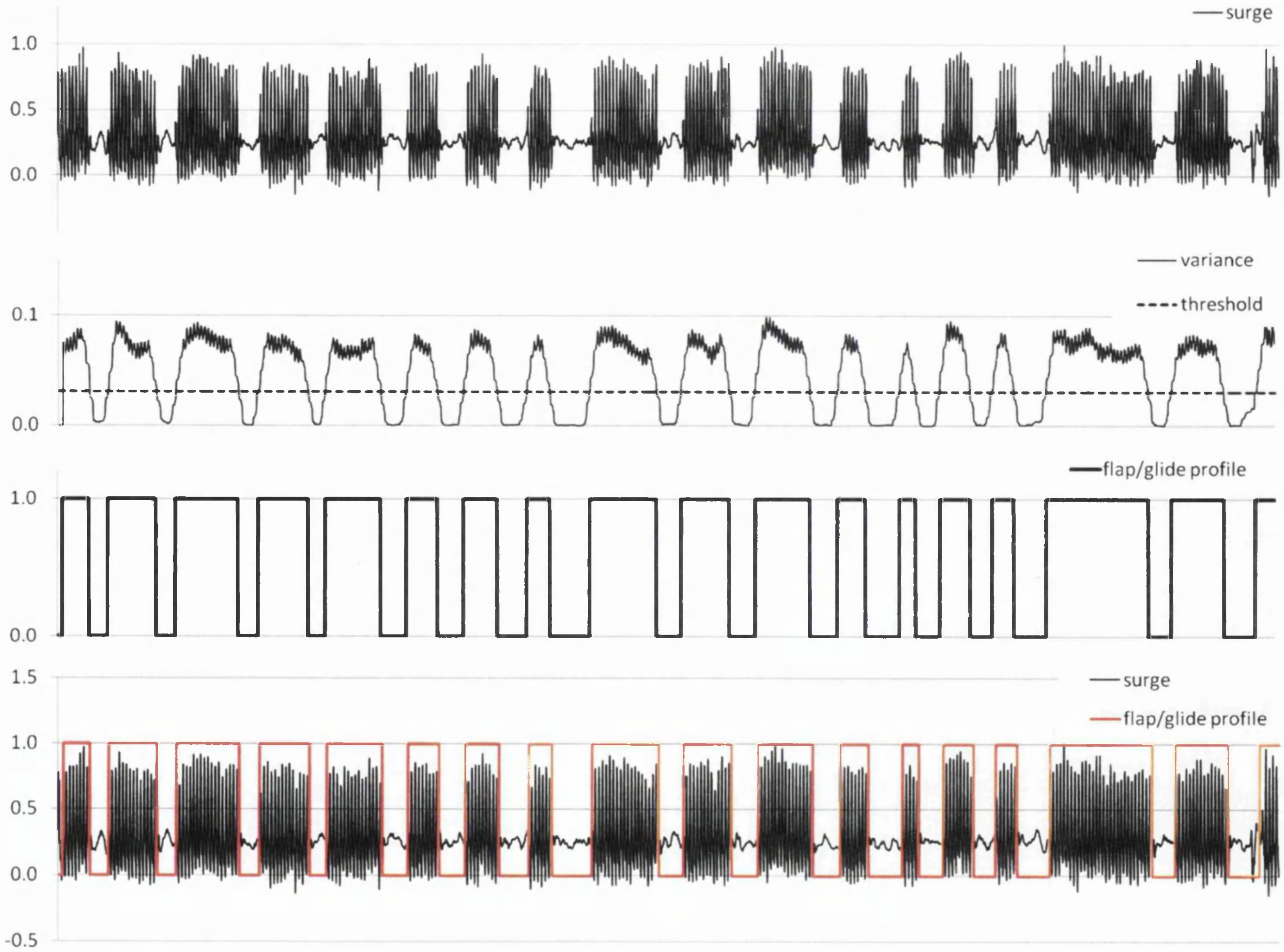

Figure 2.
Flapping and gliding behaviours recorded in the surge (antero-posterior) acceleration axis by an accelerometer fitted to the back of a northern gannet (*Sula bassana*) (top) are separated by the running variance (middle-top), producing a binary signal (middle-bottom).
The alignment of this signal with the raw data supports the behavioural classification (for details see text).

Table 2. Statistics for the flying behaviour of 8 gannets during a 10 minute flight period including the ratio of flapping duration related to gliding duration and the total number of flap/glide cycles. The birds were equipped with a miniature tri-axial accelerometer on their back (Non-GPS birds) and with, or without, a dummy-GPS on their tail (GPS birds). The numbers in bold highlight the difference between the 2 groups (see text).

	Birds	**Total number of flap/glide cycles**	**Flap/glide duration ratio**	**Total time flapping duration**
Non-GPS birds	64	90	1.61	352 s
	68	75	3.19	440 s
	Smiley	65	3.38	443 s
	Emily	89	1.55	352 s
GPS birds	Bully2	**98**	2.17	392 s
	Bully3	**93**	4.86	475 s
	Mini	**97**	2.26	400 s
	Samy	**106**	1.52	345 s

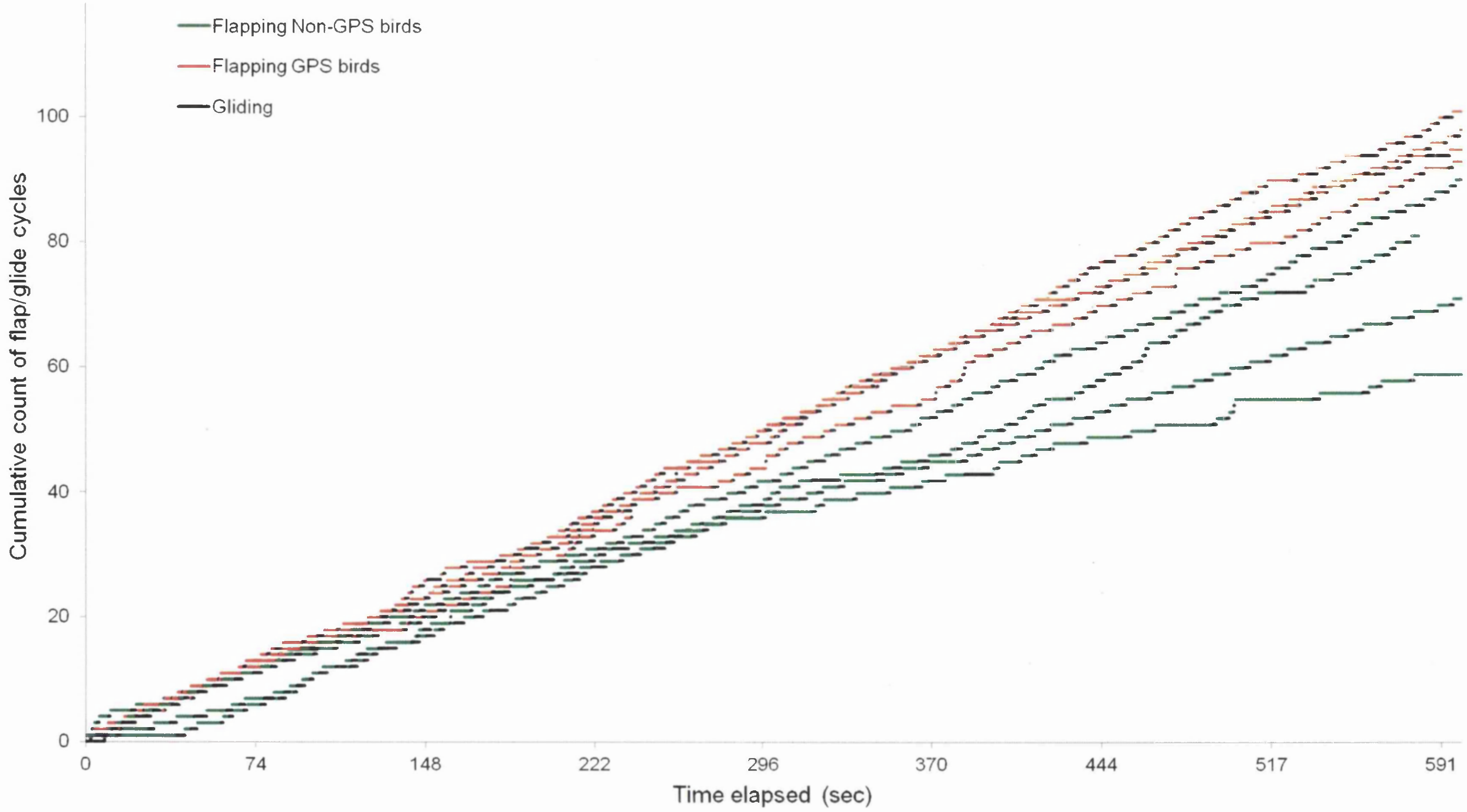

Figure 3. Cumulative count of flap/glide cycles over time measured for 8 gannets during a 10 minute flight after their departure from the breeding colony. The birds were equipped with miniature tri-axial accelerometers on their backs (Non-GPS birds) with, or without, a dummy-GPS on their tail (GPS birds). The duration of the flapping period (in green or red depending on the bird group) is also shown relative to the duration of the gliding period (in black).

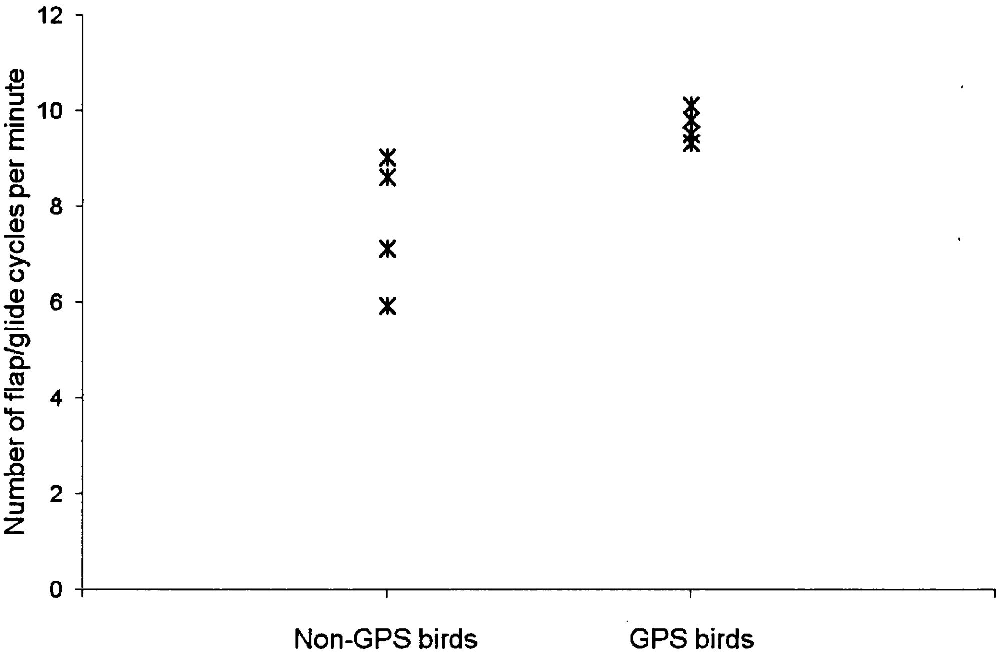

Figure 4. Difference in the slope obtained for the plot of the cumulative number of flap/glide cycles over time during the 10 minute flight period (see Figure 3) performed by 8 gannets, 4 of which were fitted with only an accelerometer on their back (Non-GPS birds) and the other 4 with both an accelerometer on the back and a dummy GPS on the tail (GPS birds). A significant difference was revealed with the slopes of the flap/glide profiles of GPS birds being steeper but less variable (see text).

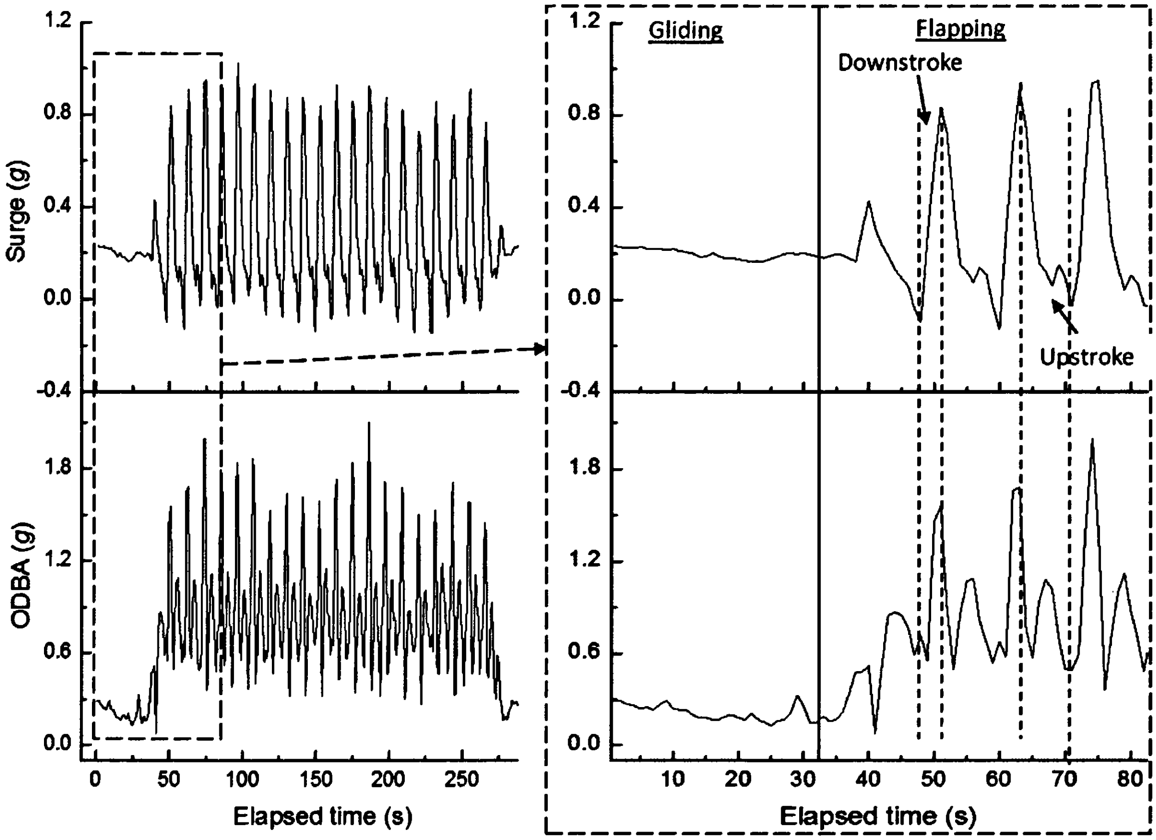

Figure 5. Temporal match between the proxy for energy expenditure ODBA (see Wilson *et al.* 2006) and the wing movements of a flying gannet illustrated by the surge (antero-posterior) acceleration. The acceleration data show the body movements which, during flapping, moves in a direction opposite to that of the wings (i.e. the body goes up during the downstroke and down during the upstroke).

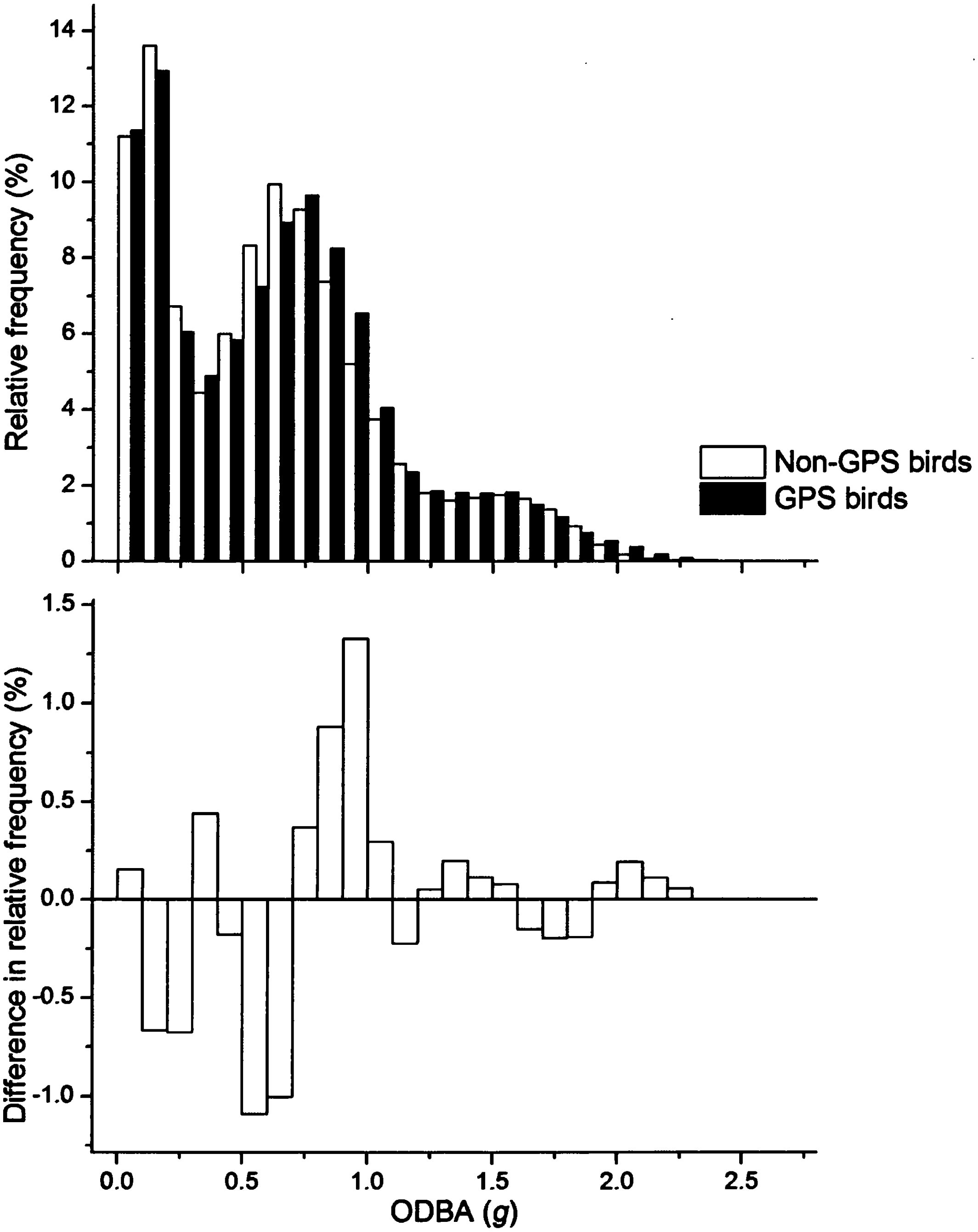

Figure 6. Frequency distribution (top graph) of ODBA-values (a proxy for energy expenditure; Wilson *et al.* 2006) calculated for flying gannets fitted with accelerometers with (black bars), and without, a GPS under the tail (white bars). The first peak corresponds to the gliding phase, the second and third peaks to two different parts of the wing beat cycle during flapping (see Figure 5).

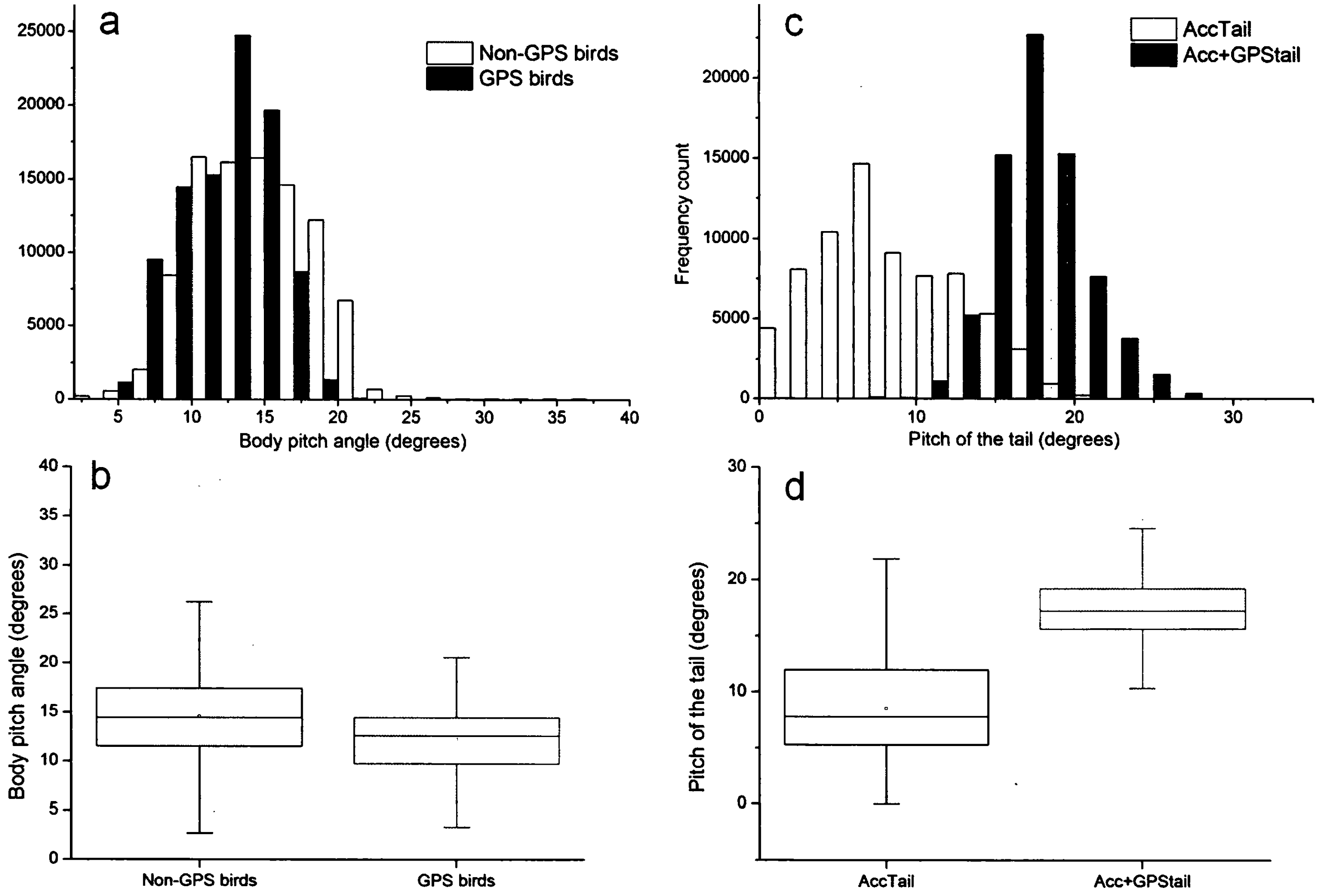

Figure 7.

Frequency distributions (a, c) and box plots (b, d) of the body pitch angle of gannets (see text for full explanation) calculated over 10 minute flight period and while carrying different payloads at different positions.

(a, b) Non-GPS birds (N = 4) were fitted with 15 g accelerometers on their back as were GPS birds (N = 4) which, in addition, carried a 30 g dummy GPS also under the tail. No significant difference was revealed between the 2 groups.

(c, d) AccTail birds (N = 3) were fitted with 15 g accelerometers under their tail as were Acc+GPStail birds (N = 3) which, in addition, carried a 30 g dummy GPS also under the tail. The difference between the 2 groups is significant (Mann-Whitney U test, $z = 294.9$, $P < 0.001$).

Chapter 9:

From cubic and functional to sleek and comfortable; animal tag styles come of age

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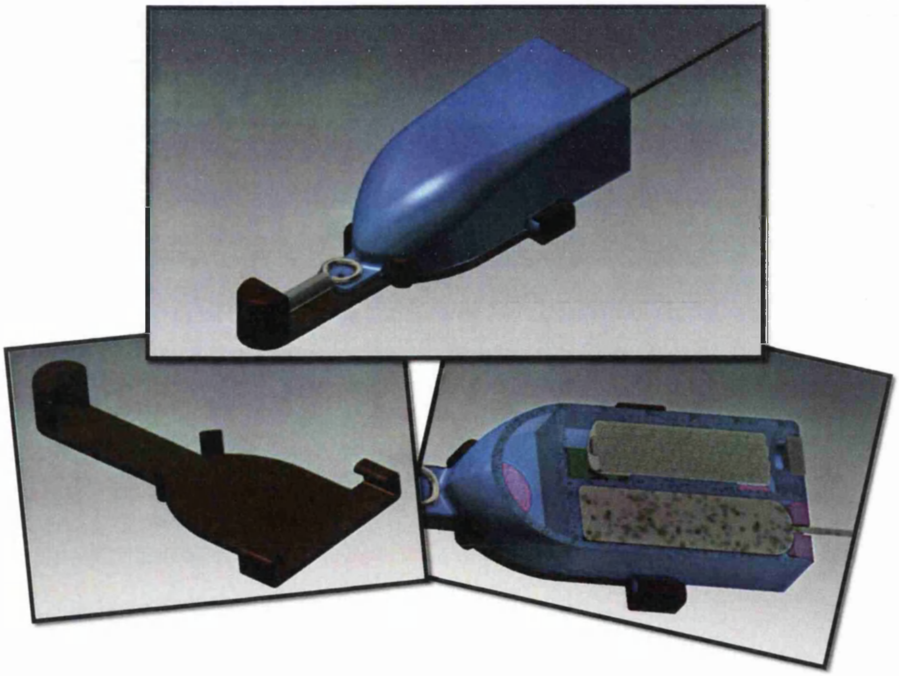
& Rory P. Wilson



SPV, DLPT, OB, NE and RPW worked on the designs of the units. SPV wrote the manuscript with contributions from OB, NE and RPW.
In preparation for Animal Biotelemetry

Abstract

Years of animal tagging using increasingly powerful electronic technology have led to many important revelations, although advances in miniaturization coupled with increased capacity mean that circuit boards and electronic components are ever more sensitive to interference if not properly protected. Thus, the qualities of the tag housing are increasingly important, an issue that is doubly critical in view of increasing numbers of studies documenting detrimental tag effects on their bearers. We present here a novel approach based on Computer-Aided-Design and 3-D printing technology as cutting-edge tools for fabrication of optimal tag housings. Three examples are presented, dealing with different challenges according to the subject species; (1) a plunge-diving seabird, where a hydrodynamic shape is pivotal, (2) a terrestrial mammal, where the size and robustness of the tag are important and (3) a turtle, where the tag needs to be waterproof and streamlined. The relative ease with which bespoke tags can be produced using this approach should enable us to generate large quantities of idealized tags with minimum impact on the bearer and maximum protection of the recording and/or transmitting system.

Keywords: animal tags, devices, packaging, impact, computer design, 3D technology

Introduction

It has been 50 years since the first transmitting (smart) tag was put on a free-living animal (Cochran & Lord 1963) and the value of the approach has now become unquestionable. Such tags have allowed us to document extraordinary physiological feats, such as the non-stop trans-Pacific migration of the bar-tailed godwit (*Limosa lapponica*) (Gill *et al.* 2005, 2009) and the ability of sperm whales (*Physeter catodon)* to dive to depths in excess of 2000 m (Watkins *et al.* 1993), and they have enhanced our understanding of animal space use (e.g. Matthiopoulos *et al.* 2004, Burdett *et al.* 2007), inter- and intra-specific interaction (e.g. Douglass 1976, Biggins *et al.* 2005) and have even contributed to understanding the operating energetics of free-living animals (e.g. Froget *et al.* 2004, Halsey & White 2010).

But the euphoria of the first deployments of these animal-attached smart tags has been increasingly tempered by concerns about how tags might affect animal behaviour (e.g. Hawkins 2004, Wilson & McMahon 2006). Indeed, it is becoming ever more apparent that even small changes in tag design can make a large difference in the way animals behave (e.g. Culik *et al.* 1994, Ropert-Coudert *et al.* 2007, Casper 2009), with increasing pleas for standardized rules and procedures with regard to tag size, mass and attachment mechanism (e.g. McMahon & Wilson 2006, Sherill-Mix *et al.* 2006, Vandenabeele *et al.* 2012). This, in itself, is a complicated issue since particularities of some tags that might affect a number of species greatly might be minimal in others. For instance, while there is a recommendation that birds should not be equipped with tags that weigh more than 3% of their body mass (Kenward 2001), the carriage of this amount of extra mass is trivial for penguins (cf. Wilson 1994) for whom drag is, however, critical (Wilson *et al.* 1986, Bannasch *et al.* 1994).

What is clear, however, is that many aspects of tag deployment can be approached with basic 'common-sense'. These aspects include; device mass (Kenward 2001, Vandenabeele *et al.* 2012), drag (Bannasch et al 1994, Watson & Granger 1998, Hazekamp *et al.* 2010), colour (Burley *et al.* 1982, Wilson *et al.* 1990) and 'fit' to the animal. In addition, tags have to withstand the environmental pressures within the animal's operating milieu, in addition to withstanding the attention of the tagged animal itself.

This manuscript presents a new philosophy for the design of animal tags based on using Computer Aided Design (CAD) (Groover & Zimmers 1983, Joshi & Ranade 2003), whereby housings for smart tags, also encompassing single housings for multiple tags (e.g. Andrew 1998, Gleiss *et al.* 2009, Shepard *et al.* 2011), can be created virtually, and tested within a computer-based framework (including with regard to common sense) before being printed out in 3D using rapid-speed processing technology (Yan & Gu 1996, Pham & Gault 1998) after which they can be deployed on animals. This approach should give researchers deploying commercially available tags the option of modifying the tag housings so that they best interface with the study animal and thereby minimize aberrant behaviour or any unwanted tag-induced effects.

The concept of developing appropriate housings for animal tags is illustrated below through one prime example, although two other examples are presented very briefly to give an indication of the general applicability and adaptability of the approach. The main study project involves the conceptual design of tags to be attached to plunge-diving seabirds, which, by virtue of their foraging methods, are exposed to substantial impact when they hit the water during dives (Nelson 1978, Ropert-Coudert *et al.* 2004) and so should benefit from a particularly well-streamlined device. The brief cases also mentioned are; (a) a collar attachment procedure for terrestrial mammals, which may subject tags to a great deal of force, either by biting (Lee & Mill 2004, Christiansen & Adolfssen 2005) and simple physical impact and (b) turtles, which dive to appreciable depths (van Dam & Diez 1996, Blumenthal *et al.* 2009) and so require device housings that are watertight despite being exposed to appreciable hydrostatic pressure from saltwater, a medium that is particularly hostile to electronics.

Methods

For all three housing types; seabirds, mammals and turtles, the aim was to design housings that would provide suitable protection for the electronic component(s) of the tag given the environmental conditions to which it may be exposed, as well as to make it of minimal impact for the animal. Amongst the main aspects that had to be considered were the material used and the size and shape of the housing. Each housing type is described as a single case study.

Plunge diving seabird tag - Northern gannets (Sula bassana)

Gannet tags are conventionally attached to the tail using tape (cf. Garthe *et al.* 2000, Ropert-Coudert *et al.* 2004). Using this as a start point, the overall shape of this housing was designed using CAD software (Autodesk® Inventor® 3D CAD software) with the aim for it to incur minimal drag and maximum robustness, so as to minimally impede the descent speed (particularly sub-surface) and withstand the impact during plunge diving, the normal feeding method of this species (Nelson 1978, Del Hoyo *et al.* 1992; see Chapter 9). In order to minimize the drag, the cross-sectional area of the operational part of the tag was kept to minimum height and width values (Figure 1). In addition, since wind tunnel measurements have shown that device-induced drag can be greatly decreased by incorporating an elongated nose (Obrecht *et al.* 1988; see Chapter 4), the housing was designed to have a frontal shape consisting of a cone with an angle of 25° and a length of 4.8 cm (although reduced to 4.6 cm after the extremity was smoothed to prevent injuring the bird; Figure 2), this being a compromise between having a maximally acute angle to minimize drag and the practical consideration of the size of the gannet back (cf. Bannasch *et al.* 1994; Figure 1). Tag dimensions were 107 x 37 x 21 mm with a mass of 15.7 g (41 g with the logger inside). Finally, because the ventral surface of the tag was to be in contact with the bird, it was made slightly concave so that the housing followed the body contours. In the print-out of the housing, we selected white material since this accords with the colour of the bird's plumage at the site of attachment.

In order to verify the advantages of the final design, a similar housing was designed, but this time incorporating an essentially rounded leading end. This led to the tag housing having final dimensions of 88 x 37 x 21 mm (the length being the minimum possible for complete insertion of the data-loggers) and a mass of about 16 g (42 g with the logger inside; Figure 2). The final housings were built from ABS Plus material by rapid-prototyping using a Hewlett Packard Design Jet 3D Printer (see *http://www.cartridgesave.co.uk/news/a-roundup-of-3d-printers/* for details).

Projected field tests

Both tag housings were conceived to be deployed on free living gannets during 2012, and incorporating a specific tri-axial accelerometer (X2-6mini accelerometer; Gulf Coast Data Concepts, Waveland, USA), which was to be set to record at very high sampling rates (up to 320 Hz). Consideration of the acceleration signals would allow a fine description of the behaviour (e.g. Watanabe *et al.* 2005, Shepard *et al.* 2008) and energetics (e.g. Wilson *et al.* 2006, Halsey *et al.* 2009, 2011) of birds carrying both housing types. In this configuration, particular attention would have been paid to the plunging behaviour (e.g. see Figure 3), with close examination of the deceleration apparent in the dive signal as the birds hit the water.

Unfortunately, despite frequent attempts to secure a position on field trips involving gannets during 2012, this proved impossible.

Terrestrial Mammal Tag

The housing for deployment on a typical terrestrial mammal was designed to fit onto a leather collar, as is usual in such studies (Böhm *et al.* 2009, Fuller & Fuller 2012) although the design of the housing was intentionally generic, to make it useful for as many mammal species as possible without the need for any redesign. The housing consisted of three parts, a leather collar, the main housing and a cover plate. The use of a cover plate allowed access to the devices within the main housing. The design and production of the housing utilised CAD and 3D printing technology. 3D printing is useful in this context, because the same generic design can be produced in a number of materials (e.g. Nylon, ABS or Titanium) depending on the strength requirements for the study in question. For instance, for a housing intended to be deployed on carnivores, the strength of their jaws (Christiansen & Adolfssen, 2005) necessitates that stronger materials (such as titanium) be used in order to prevent damage to the devices within. The use of CAD technologies enables the estimation of housing strength for a given material before production is undertaken. The printed housing could be waterproofed by using silicon sealant around the joint between the housing main and cover plate.

The specific dimensions of the unit printed tested were 130 x 32 x 35 mm, with the housing designed to contain specific spaces for a Daily Diary device (Wilson *et* *al.* 2008) a radio release mechanism (Bytesnap, UK) and a VHF transmitter to aid recovery (Biotrack Pip tag), as well as batteries for the various devices (Figure 4).The units were built from the same material and using the same process as for the gannet tag housings (see above). With all the components inside, the tag total mass was 94.35 g. Slots were printed into the final housing design to prevent the devices from changing position relative to the animal, which is particularly germane for studies which utilise accelerometers (Gleiss *et al.,* 2010).

Projected field tests

This unit will be deployed on badgers and deer in 2013.

Turtle tag

The turtle tag was designed for attachment on immature turtles foraging in the inner lagoon of an atoll with maximum depth of 30 m. The certainty of the maximum diving depth and the field location affected the selection of material, housing closures and retrieval devices for the tag. The housing for the turtle deployment was designed using CAD to contain 5 components; a Daily Diary (Wilson *et al.* 2008) connected to an external ambient pressure and temperature transducer, a VHF transmitter and antenna (to aid recovery), a power source (Lithium battery), and an external Galvanic Timed Release (GTR) to allow the system to release from the base plate after 3 days' deployment in sea water of approximately 25°C (Figure 5a). The main housing, base plate and closure caps were constructed from Nylon Polyamide 12 using a plastic laser-sintering system (EOS FORMIGA P110 3D printer) which produces functional prototypes. This type of 3D product was selected to be watertight with O-ring seals between (i) the pressure transducer and the housing, (ii) the closure caps and the housing of each of the 2 compartments (Figure 5b). This housing was mounted with a small sledge rail system onto a baseplate, being held in place by the corroding GTR (e.g. Gleiss *et al.* 2009). The baseplate was conceptualized for attachment to the turtle carapace using marine epoxy glue (Hays *et al.* 2003, Schofield *et al.* 2007). Once the GTR has corroded, the main unit will slip back and float to the surface whereupon the VHF signal can be picked up (radio-waves do not travel in salt water) so that the unit can be located (see e.g. Watanabe *et al.* 2012). Besides the main compartment containing the 5 elements, an anterior chamber was modelled into the housing to allow the unit to be balanced with lead shot to ensure that it floats so that the VHF antennae protrudes vertically from the water surface. The desired weight of lead shot was calculated after trials in sea water using all the components.

The specific dimensions of the housing unit printed were 115 x 40 x 43 mm. The maximum baseplate dimensions were 75 x 57 x 12 mm, adding 3 mm to the overall length and height of the housing unit when the turtle tag was assembled. The main posterior compartment contained a Daily Diary (Wilson *et al.* 2008) connected to external pressure and temperature transducer (Keller Series 4LD sensor capsule with I^2C signal 20 bar Absolute) powered by a 3.6 V Lithium battery (Eve ER14505). Integrated into the posterior compartment was the VHF receiver and antenna (Advanced Telemetry Systems ATS, 65 mm length plus aerial 350 mm). Similar to other tags, slots were printed into the final housing design to prevent the devices from changing position relative to the animal (Gleiss *et al.* 2010). The main housing weighed 105.5 g when all components were inserted. After trials, it was determined that 46.7 g lead shot should be added to the anterior chamber in order to provide sufficient buoyancy for the VHF aerial to stand proud of the sea surface. The relatively long antenna of 350 mm was considered necessary for the signal to reach the shore receiver during rough sea conditions.

Projected field tests

The turtle tags are scheduled to be deployed on Hawksbill turtles (*Eretmochelys imbricata*) in a shallow inner lagoon environment during 2013.

Discussion

Technical difficulties in accessing the gannet colony precluded me from testing the plunge-diving seabird housing design during 2012 so that the success of the approach cannot be verified within this thesis, although tests will be conducted during 2013. The other two tag designs are scheduled for proper testing during 2013 anyway. Nonetheless, the potential advance that this technology represents means that it is important to present as a critical future development.

Perhaps the most important element of this approach is that it will allow the physical attributes and effects of devices to be simulated before they are actually deployed on wild animals. This adds another quality control layer to the process of device deployment on wild animals that should reduce detriment while ensuring optimal protection of the tag. Furthermore, with the new 3D scanning technology which now enables modelling even the most complex structures including bodies, the door is opened to an even broader range of possibilities whereby tags can be 'tailor-made' to perfectly mould the contours of the animal.

This is certainly the best way forward to more ethically and scientifically robust tagging research performed in respect with animal welfare and allowing the collection of data which can be assumed to be the true reflection of animals' normal behaviour. Animal welfare is clearly an aspect which has, so far and critically, been overlooked in wildlife telemetry (McMahon *et al.* 2011, Vandenabeele *et al.* 2011) compared to other fields of research such as in laboratories. By using 3D scanning and modelling, it will be now possible to remedy to this and abide to one of the fundamental principles set up to ensure animal well being is maintained known as the 3R's (Flecknell 2002, Richmond 2010), in this case the refinement of the methods of study of the subject animals. Technological progress may not only improve tagging methodology itself but also be the platform for better integration of animal welfare in wildlife telemetry.

Acknowledgements

We would like to thank the ASTUTE team for the fabrication of the tag housings. This work was partially funded by SEACAMS, the California Department of Fish and Game's Oil Spill Response Trust Fund (through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis) and the Royal Society for Prevention of Cruelty to Animals (RSPCA, Wilberforce Way, Southwater, Horsham, West Sussex, RH13 9RS, United Kingdom).

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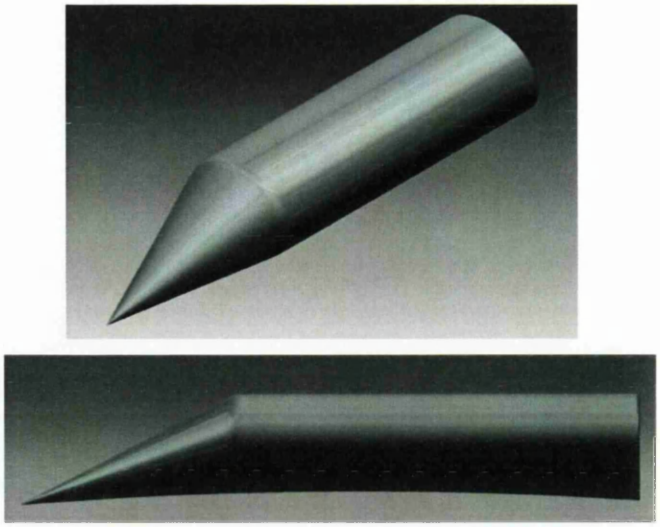


Figure 1. Top and lateral 3D views of the minimal-impact tag housing designed for plunging gannets (*Sula bassana*) using Computer Aided Design software. The minimum cross-sectional area and elongated nose of this housing give it sharp streamlined profile as to reduce device-induced drag to minimum level. The bottom part of the housing was made slightly curved in order to have it following the contours of the bird once attached to its back.

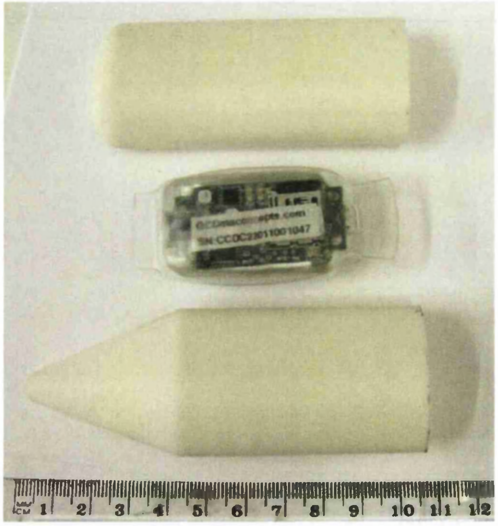


Figure 2. Photos of the 2 tag housing prototypes for gannets (*Sula bassana*) built using rapid prototyping and a miniature tri-axial accelerometer (X2-6mini accelerometer; Gulf Coast Data Concepts, Waveland, USA). One housing incorporates a nose as to make it the most streamlined possible and, therefore, of minimal impact for the bird in opposition to a more common housing with just a blunt front. The objective is to fit an accelerometer inside each housing and deploy them on wild gannets as to compare the impact on the behaviour and energetics of the birds particularly during plunge diving.

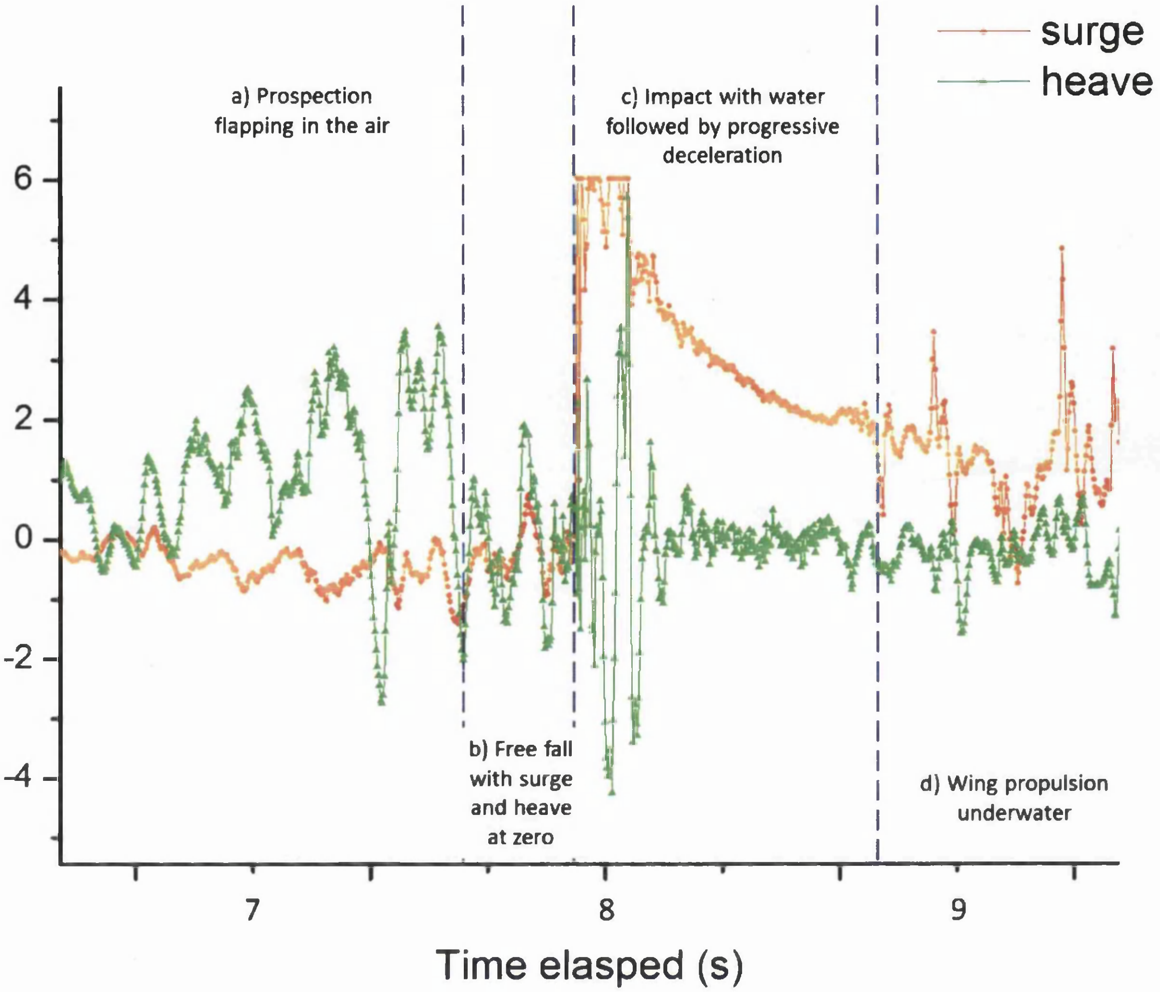


Figure 3. Acceleration signal recorded at 320 Hz in the anterio-posterior (surge) and dorso-ventral (heave) axis of a northern gannet (*Sula bassana*) during a single plunge dive. Before the plunge (a), the heave is at approximately 1 with the surge at approximately 0 (both with a superimposed wave pattern due to the beating of the wings). As the bird turns into a vertical plunge (b), the heave turns to 0. However, since, during the plunge the bird is in free-fall, being accelerated towards gravity, the surge does not change to -1, as would be the case if the bird were stationary with respect to gravity. Instead, the surge continues to have a value of about 0 until the bird impacts the water. At this point, the drag caused by the bird entering the water causes a radical deceleration (c), apparent as a plateau in the surge corresponding to the maximum recording capacity of the sensor. This is followed by a progressive decrease in surge as the bird slows down, while still travelling vertically down the water column, as evidenced by the heave value still at *ca.* 0. Substantial waves in the heave around the time of the impact are certainly due to massive dorso-ventral oscillations as the bird, or just its tail where the device was attached, shudders entering the water at speed. Following the decrease in surge, waves in both the heave and the surge indicate likely wing beating for propulsion (d).

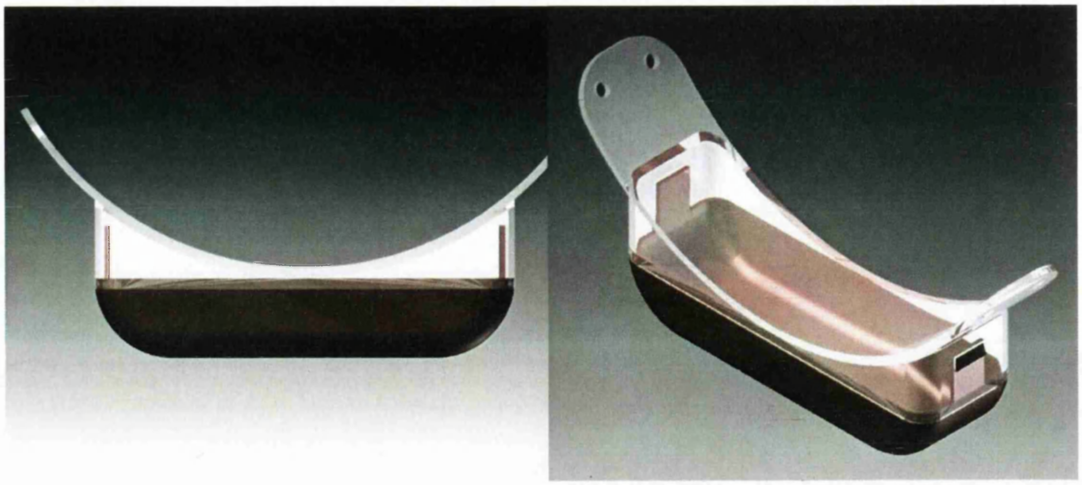
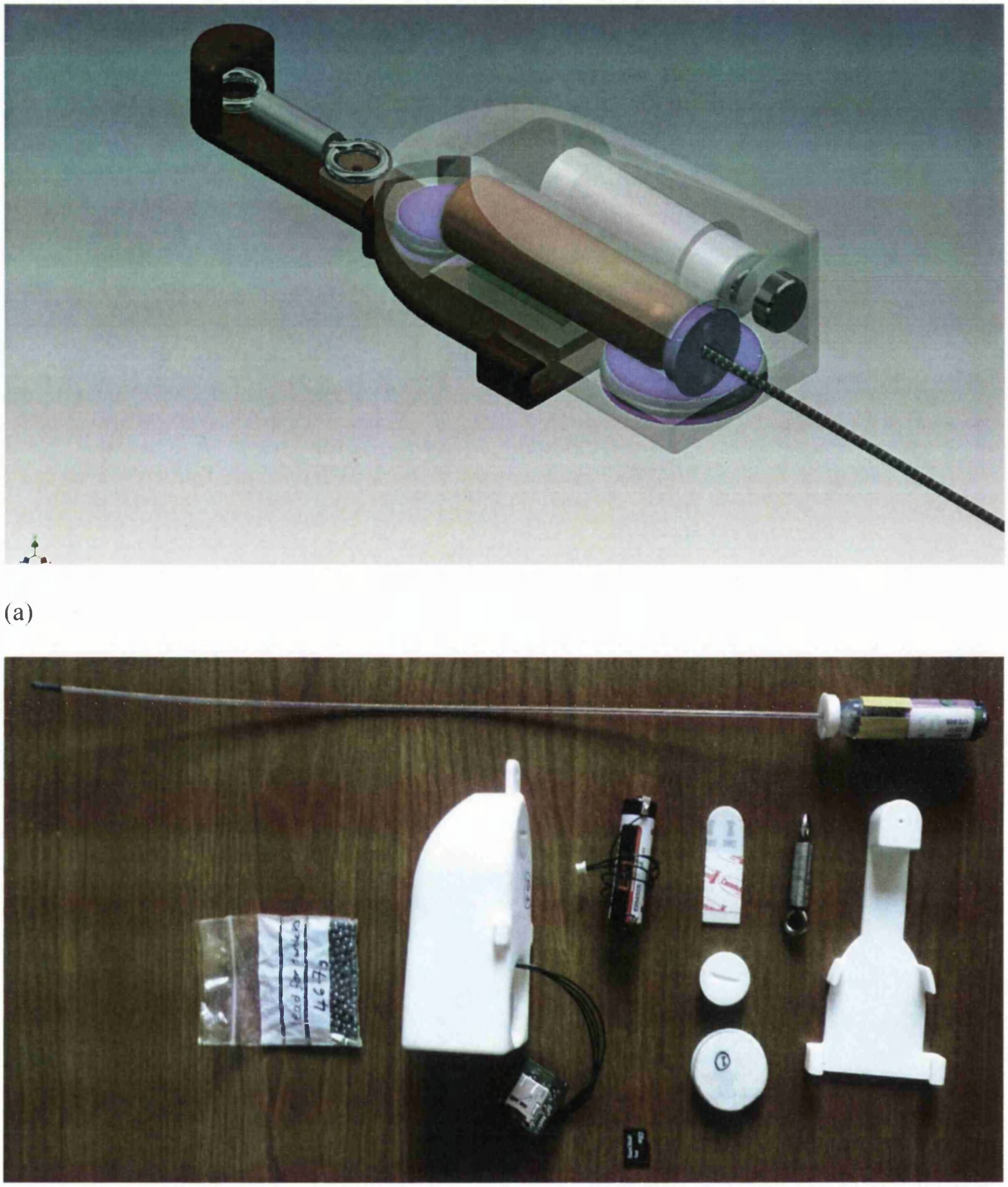


Figure 4. Tri-dimensional view of the housing prototype for deployment of tracking devices on badgers designed using Computer Aided Design software. The curve and holes in the clear bottom part of the housing are here to allow the whole package to be attached around the neck of the badger onto a collar.



(a)

(b)

Figure 5. (a) Tri-dimensional view of the housing prototype designed using Computer Aided Design software, shown with components for deployment of tracking devices on turtles. The main housing casing appears translucent to indicate relative positions of components. The base plate is shown in red. (b) Assemblage of components and printed housing prototype.

Synopsis

The evidence that animal-attached devices can affect their bearers raises ethical issues and may render the quality and reliability of the research performed using this technology questionable (Calvo & Furness 1992, Hawkins 2007, McMahon *et al.* 2011). Based on this, although animal welfare bodies should indeed try to ensure that tagging practises do not compromise the well-being of animals, it would be a mistake if such issues lead to the blanket prohibition of animal tagging studies (also see McMahon *et al.* 2006, Wilson & McMahon 2006, McMahon *et al.* 2007 about the controversy with marking practises, McMahon *et al.* 2012). For a start, tagging studies and their associated actions are arguably nothing new to wild animals. Wild animals regularly have to deal with predators, a process that escalates from the stress experienced from the moment potential danger is perceived (Boissy 1995, McNamara & Buchanan 2005) (and this may be what happens when animals perceive humans watching them, whether part of a tagging study or not; see Putman 1995, Carney & Sydeman 1999) to extreme penalties like injuries or even death if the animal is captured (by predators or, for example, by being netted and restrained by humans; see Lima & Dill 1990, Putman 1995) (Figure 1). Similarly, wild animals 'wear' extraneous material all the time. Soiled bird plumage, feather lice or internal parasites and can make up to, for instance, 0.9 % of a bird's mass (see Vercruysse et al. 1985 who found an average of 11.84 g of parasitic worm per bird weighing *ca.* 1 kg), just above the 0.3% bird body mass tags used by Weimerskirch & Wilson (2000) bird in their study on Wandering albatrosses *Diomedea exulans.* So the fuss may be little more than a question of scale.

But scale is important, and the problem is that tagging scientists have to work in the grey area somewhere between the unacceptable black of radical tag-induced effects (e.g. Peniche *et al.* 2011, Saraux *et al.* 2011) and the wholly natural white of untagged individuals, with little guidance and hard data on which to base acceptability decisions, highlighting the urgent need for appropriate guidelines. Scientists are actually partially to blame for the lack of guidelines since they are often remiss in attempting to assess the impact of their procedures on their study animals, something that one might assume their humanity would lead them to do anyway. Would that it were so simple! And the matter is made ever more complicated by smaller and lighter technology that goads workers into believing that simply because devices are smaller, the associated impact is 'now' minimum and somewhat negligible.

The difficulty is that deleterious device effects are complex (Dixon 2011, Walker *et al.* 2012) and cannot be conveniently summarized within device mass or limited to behavioural aberrations as implied by the '3% rule' (Kenward 2001). In fact, although some devices can almost be 'as small as a louse' or as 'light as a feather', if not used appropriately, they can still impact their carriers deleteriously, as illustrated by recent reports on the effects of flipper bands (Saraux *et al.* 2011). Here, devices constituting less than 0.3% of their carrier's body mass, caused a decrease of 16% in king penguin (*Aptenodytes patagonicus*) survival rate (over 10 years) and a 39% reduction in reproductive success. Similarly, Quillfeldt *et al.* (2012) found that thin-billed prions (*Pachyptila belcheri*), after one year carrying small geolocators of about 1% their body mass, showed relatively high hormonal stress levels.

Clearly then, part of the problem in understanding device effects is the difficulty in obtaining hard metrics applicable to this complex topic, which includes notions such as stress, pain and suffering, at least if animal welfare bodies are to be entertained. These latter notions fuel the eternal question of whether animals should be considered sentient organisms (Duncan 2006, Turner & D'Silva 2006) and whether some are 'more' sentient than others, and if so, by how much? Our differential rules with respect to organism type allowed in standard experimental procedures as stated in the Animals Scientific Procedures Act 1986 which, for instance, protects octopuses but not fish (House of Lords 2002) indicate that we already have some opinions on that (Smith 1991, Broom 2007). The prime problem here is that it is characteristically human to attribute our own sentient, essentially unchecked, to animals (Harrison 1991, Kennedy 1992). In fact, it is as much as a mistake to believe that animals 'feel' the way we do as not to, so we should tread carefully when we invoke such subjective concepts in tagging studies.

The goal of this thesis was not to invoke sentient, recognizing its associated discrepancy, but to show that hard-core scientifically based methods can quantify the impact of tags at a variety of levels, including behaviour and energetics (e.g. Ropert-Coudert *et al.* 2000, Wilson *et al.* 2004, Hazekamp *et al.* 2010). There are two levels at which this can be done; (i) by using models and simulations to determine likely physical changes in the complete absence of the animals and (ii) careful use of live animals, either in captivity or in the wild, to document changes in parameters with varying device characteristics, with the hope of extrapolating to the 'no-device' situation. In essence, some aspects of animal biology cannot be studied without tags (Ropert-Coudert & Wilson 2005, Rutz & Hays 2009) but, for instance, the increase in energetics can be calculated as a function of device size with the intercept of the obtained curve representing an estimate of the energetics of an unequipped individual (see Figure 4 in Wilson & McMahon 2006).

This thesis incorporates both these approaches, and uses them to examine the type of detriment that we might expect in birds according to external device size, shape, position and even attachment method (Figure 1). Having looked at these effects on several seabird species the overarching conclusion is that there is no 'cure-all' formula and that species need to be examined on a case-by-case basis. Indeed, even closely related species may differ in their responses to external tags considerably with, for instance, a higher failure rate for tagging studies conducted on saker falcons (*Falco cherrug*) compared to peregrines (*Falco peregrinus*) (A. Dixon, pers. comm.). Happily though, there are some generalities within which the species specifics can be cast. Perhaps the most obvious of these is the duration of the period over which animals are to be tagged because any deleterious effects are likely to be exacerbated over time (Wilson & McMahon 2006, Saraux *et al.* 2011; see Figure 2). It is also generally true to say that almost all species will show periods when they are more susceptible to deleterious device effects than others, with the breeding season being particularly critical due to the increased stress associated with brood provisioning (Ricklefs 1983, Watanuki *et al.* 1992, Paredes *et al.* 2005). Ironically, in seabirds at least, this is also often the only time of the year when many species can be accessed.

How might we best proceed then, in an attempt to minimize tag effects? I would suggest that scientists should be forced to answer questions derived from a proper framework on tag effects. Even though most of the questions will not be answered easily due to lack of data, such an exercise might help change the mind-set of taggers. A rough framework that might help in this was given by Wilson & McMahon (2006), who even went as far as to suggest the creation of a 'discomfort index'. However, based on Wilson & Culik (1992), Kenward (2001), Wilson &

McMahon (2006), Casper (2009), and as well as my work within this thesis, I would suggest that there are 8 major axes to this framework that need to be explicitly referred to by scientists so that they may be aware of the multi-dimensional nature of deleterious effects caused by tags. These are;

(1) Animal physical impairment, where, for example, feather condition underneath a back-mounted tag cannot be maintained, where tags actually rub fur or feathers away and thus compromise function, or where coarse non-elastic harness constricts and wounds the bearer not accounting for substantial change in body size.

(2) Animal operating energetics, influenced by factors such as device drag, mass and position. Here, studies would seek to describe how the energetics of activities varies as a result of the tag (e.g. Culik & Wilson 1991, Gales et al. 2009; Chapters 6, 7 and 8 of this thesis).

(3) Reduction in animal performance capacities where, for example, equipped birds cannot dive as deep or as long wearing tags as they can without (e.g. Taylor *et al.* 2001, Ropert -Coudert *et al.* 2007). This is often related to (2).

(4) Animal consequential energetics, as a result of animals investing time and energy in interacting with the tag (such as preening) or simply engaging less in particular activities because their energetic costs have been exacerbated by the tag. Here, changes in daily energy budgets would be assessed on the premise that a higher proportion of time devoted to removing a tag results in a low proportion of time spent doing something else, such as resting, or that animals simply reduce energetically costly behaviour and thus affect daily energy expenditure.

(5) Behavioural consequences of physical impairment (where certain functions or activities normally engaged in cannot be carried out or appear aberrant). An example of this would be birds with back-mounted devices that cannot mate (A. Dixon, pers. comm.) or harness-equipped birds which were observed walking backward, a behaviour not seen otherwise (Herzog 1979, Nenno & Healy 1979, P. J. Pietz pers. comm.).

(7) Inter- and intra-specific consequences as a result of the tag. This includes undue attention from conspecifics (e.g. Wilson *et al.* 1990, Cuthill *et al.* 1997, Seamans *et al.* 2010) or, for example, predators such as for unusually coloured

pigeons (Palleroni *et al.* 2005) or even harriers (Zuberogoitia *et al.* 2012) which can be singled out by peregrine falcons. Even underwater colour appears to matter with for instance, this report of a harnessed turtle which equipment had been bitten by a shark (Keinath & Musick 1993).

(8) Risks for the equipment, particularly the antenna or the straps of the harness, to get tangled with elements of the surrounding environment with risk to immobilise the animal permanently therefore causing it to die of starvation. This could easily happen during long-term deployment when the attachment system starts deteriorate and can lead to the situation where the animal is left entangled (Millspaugh & Marzluff 2001) or hindered with a partially opened harness (Figure 3).

(9) Effects of the tags on the survival rate of the birds when feasible. Similarly to the study by Bächler *et al.* (2010), it could be relatively easy to quantify the return rates of birds fitted with geolocators compared to ringed birds. In other cases, it appears more difficult to assess the mortality rate associated with tags such as with PTTs when the location signal is lost and it cannot be determined if it is due to bird or tag failure.

Apart from points (7) and (9), all of the above have been examined in this thesis demonstrating how the different aspects can be checked in future studies. By obliging scientists to think about quantifying the potential effects associated with certain study protocols, ethical bodies can hope that tag users will adopt a more animal-friendly mind set, and be stimulated to provide data to build up an exhaustive and solid database populated with solid documentation of how study animals react to being tagged. Tag manufacturers also should be encouraged to assess the effects of their products and try design minimal impact tags. With an increasing database on the effects of tags, ethical committees could weigh the costs against the benefits to help decide if the study should be approved in a manner similar to that adopted in other fields of research. For instance, in medical research, which often involves the use of laboratory animals, workers have adopted the Bateson's cube (Bateson 1986) as a tool to help decisions. This is based on a cost-benefit analysis which considers the likelihood of getting valuable data and the costs implied in getting such data. A recent article by McMahon *et al.* (2012) suggests that such a tool could similarly be successfully applied in wildlife research. Although scientist can, and should, contribute to assessing the potential costs of their procedures, it is the role of experts and committees to then determine what is acceptable (Wilson & McMahon 2006). Only these committees can set up appropriate rules, a process that we might expect to be fraught with inter-country variation anyway, given disparate views on animal rights (e.g. Pifer *et al.* 1994, Veissier *et al.* 2008).

More than just a framework for decision making and future approval upon animal tagging studies, a detailed assessment of the effects caused by animal-attached devices offers the opportunity to refine methodologies of 'how' to best do it. This means that at least one of the founding principles of animal welfare, the 3R's consisting of 'refinement', 'reduction' and replacement (Flecknell 2002, Richmond 2010), can be applied in wildlife research through refinement. This could be the very first step towards integration of animal welfare concepts in wildlife research which should ultimately help ease the conflict between tagging studies on wild animals and animal welfare facilitating regulation rather than prohibition. Perhaps animal conservation is a first and important port of call to wed scientists with welfare officers, where the primary aim is to preserve species, even at the expense of individuals, particularly if, by so doing, it also maintains the ecosystem functioning (Daily *et al.* 1997, Turner *et al.* 2007).

There is thus clear hope for a middle ground where blue-skies science, animal conservation science and animal welfare science can meet together because all parties share the common goal of acquisition of quality knowledge mediated by best practice. Blue-skies scientists need to appreciate that data gained by tagging wild animals will not be representative unless the equipped animals are minimally impacted by the procedure, while supporters of animal welfare need to realise that it is not all about individuals and that the safeguard of animal populations sometimes come at the expense of some disturbance and possibly even (planned) death of few individuals. Somewhere in the middle, conservationists need the best information on tag effects so as to be able to put the delicate balancing act of acquiring critical knowledge with minimal impact into perspective. In this regard, perhaps the recent initiation of the Compassionate Conservation Symposium (held at the University of Oxford in 2010) signals a genuine change in the way we are thinking because it integrates all three elements. It would truly seem that the days of the war pigeons, where birds were so important in human survival, are long gone. It is now time we took what we have learned since those dark war years and turned the tables to help animals using the same approach they used to rescue us.

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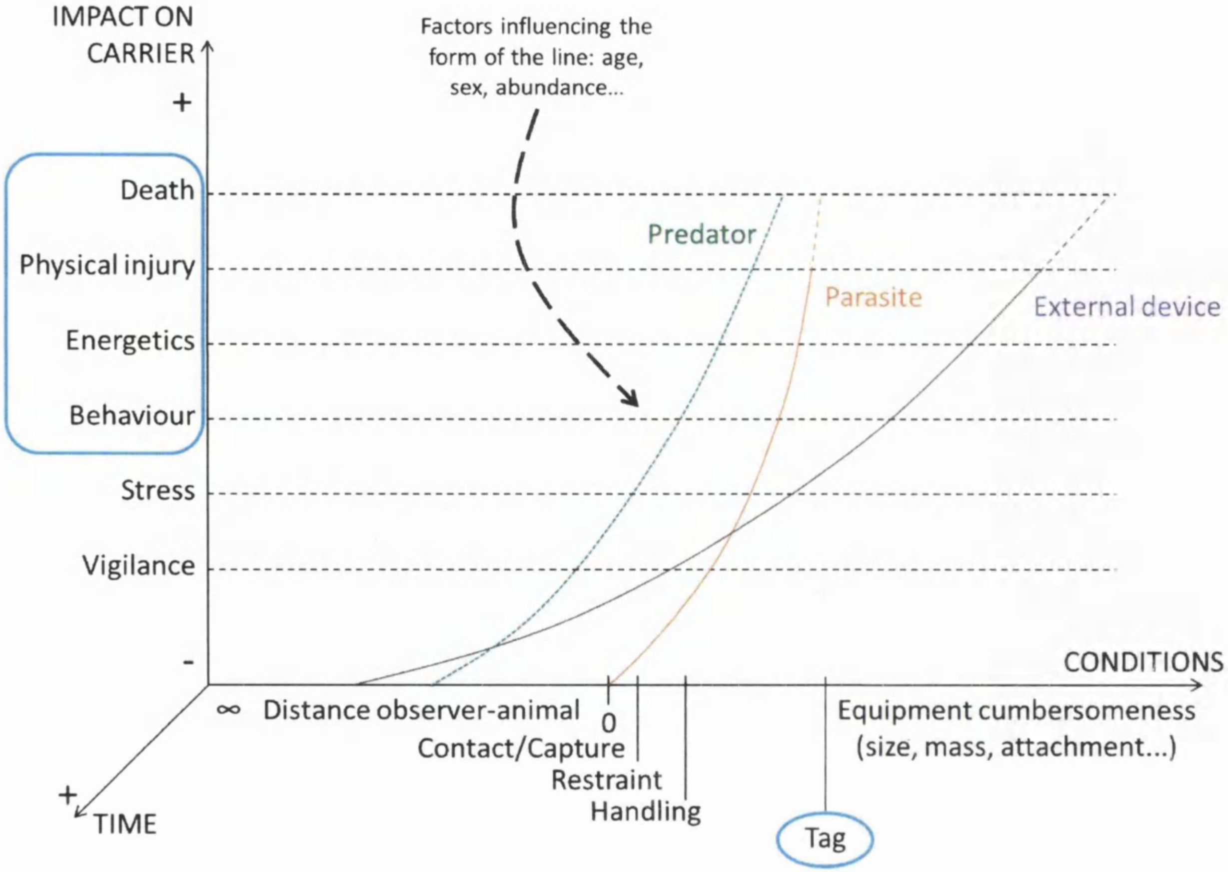

Figure 1.
Schematic representation of the various effects experienced by animals through predation (in green), parasitism (in orange) and tagging (in purple) and drawing analogies with tagging procedures. Disturbance starts when the animal becomes aware that it is being approached and then increases with decreasing distance between predator/human, increasing further, dramatically with capture, restraint and handling. After capture and handling, a successful predator will often kill and eat its prey whereas a parasite will exploit its host, causing damage (e.g. lice feeding on blood) but rarely causing death. The disturbance caused by tags only differs to that elicited by a predator or parasite according to the procedure used and the type of equipment attached. The more cumbersome the device, the greater the impact on the carrier. Effects are likely to be aggravated with time (see below). Potential tag effects are circled in blue.

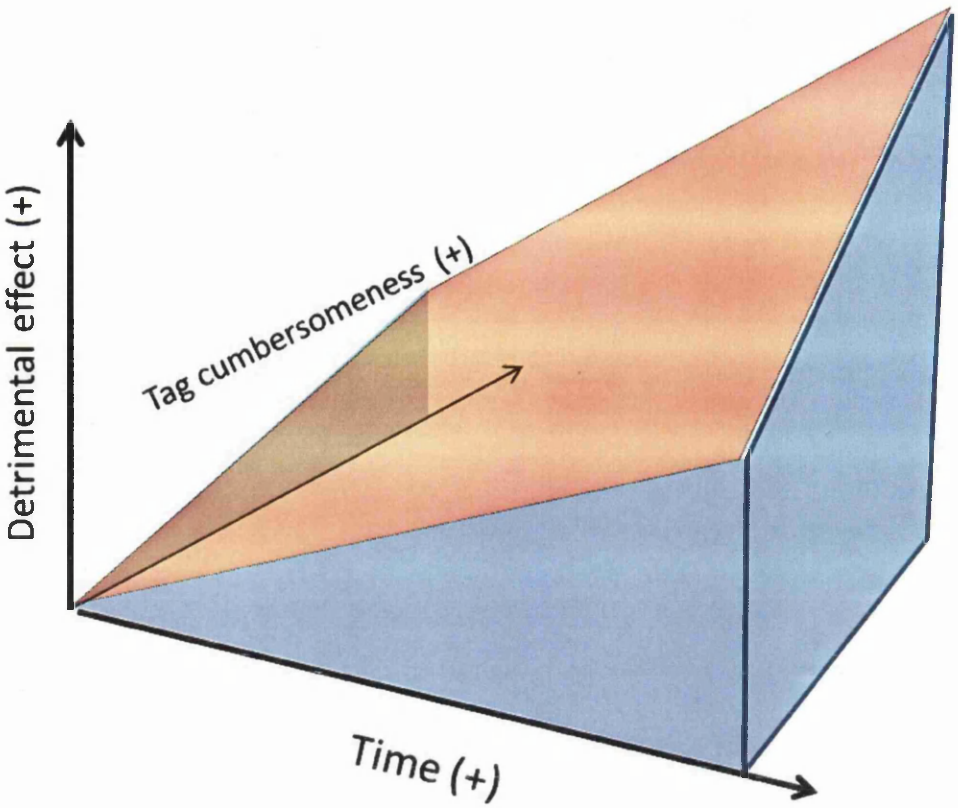

Figure 2. Schematic diagram to illustrate that detrimental tag effects (cf. Figure 1) increase with increasing tag cumbersomeness (tag size, mass, drag, colour, etc.) (e.g. Wilson *et al.* 1986, Ropert-Coudert *et al.* 2000) and that any effect is likely to be exacerbated by increased wearing time (e.g. Saraux *et al.* 2011).

Figure 3. Anonymous photo of a flying goose with a back-mounted tag attached with a harness from which one loose strap has accumulated frozen material and is now dangling from the bird.

Une thèse qui, je l'espère, en incitera plus d'un à poursuivre ses
rêves comme j'ai eu la chance de le faire

(A thesis that, I hope, will incite people to follow their dreams
as I had the chance to do)