

## PUBLISHED VERSION

White, Craig R.; Cassey, Phillip Bruce; Schimpf, Natalie G.; Halsey, Lewis G.; Green, Jonathan A.; Portugal, Steven J.

[Implantation reduces the negative effects of bio-logging devices on birds](#)

Journal of Experimental Biology, 2013; 216(4):537-542

© 2013

### PERMISSIONS

[http://download.cell.com/images/EdImages/cellreports/information\\_for\\_authors.pdf](http://download.cell.com/images/EdImages/cellreports/information_for_authors.pdf)

### Author Rights

(these rights are retained when publishing an Open Access article)

Authors remain the owners of the copyright to the article and retain the following non-exclusive rights (for further details, please refer to the license agreement that accompanies article proofs):

[...]

(3) authors may post a copy of the article on their website, provided that it has already been published by the journal and is linked to the journal's website.

*13 August 2013*

<http://hdl.handle.net/2440/78985>

## METHODS & TECHNIQUES

### Implantation reduces the negative effects of bio-logging devices on birds

Craig R. White<sup>1,\*</sup>, Phillip Cassey<sup>2</sup>, Natalie G. Schimpf<sup>1</sup>, Lewis G. Halsey<sup>3</sup>, Jonathan A. Green<sup>4</sup> and Steven J. Portugal<sup>5</sup>

<sup>1</sup>School of Biological Sciences, The University of Queensland, St Lucia, Queensland 4072, Australia, <sup>2</sup>School of Earth and Environmental Sciences, The University of Adelaide, Adelaide, South Australia 5005, Australia, <sup>3</sup>Department of Life Sciences, University of Roehampton, Holybourne Avenue, London SW15 4JD, UK, <sup>4</sup>School of Environmental Sciences, University of Liverpool, Liverpool, Merseyside L69 3GP, UK and <sup>5</sup>Structure and Motion Lab, The Royal Veterinary College, The University of London, Hawkshead Lane, North Mymms, Hatfield, Herts AL9 7TA, UK

\*Author for correspondence (craig.white@uq.edu.au)

#### SUMMARY

**Animal-borne logging or telemetry devices are widely used for measurements of physiological and movement data from free-living animals. For such measurements to be relevant, however, it is essential that the devices themselves do not affect the data of interest. A recent meta-analysis reported an overall negative effect of these devices on the birds that bear them, i.e. on nesting productivity, clutch size, nest initiation date, offspring quality, body condition, flying ability, foraging behaviours, energy expenditure and survival rate. Method of attachment (harness, collar, glue, anchor, implant, breast-mounted or tailmount) had no influence on the strength of these effects but anchored and implanted transmitters had the highest reported rates of device-induced mortality. Furthermore, external devices, but not internal devices, caused an increase in ‘device-induced behaviour’ (comfort behaviours such as preening, fluffing and stretching, and unrest activities including unquantifiable ‘active’ behaviours). These findings suggest that, with the exception of device-induced behaviour, external attachment is preferable to implantation. In the present study we undertake a meta-analysis of 183 estimates of device impact from 39 studies of 36 species of bird designed to explicitly compare the effects of externally attached and surgically implanted devices on a range of traits, including condition, energy expenditure and reproduction. In contrast to a previous study, we demonstrate that externally attached devices have a consistent detrimental effect (i.e. negative influences on body condition, reproduction, metabolism and survival), whereas implanted devices have no consistent effect. We also show that the magnitude of the negative effect of externally attached devices decreases with time. We therefore conclude that device implantation is preferable to external attachment, providing that the risk of mortality associated with the anaesthesia and surgery required for implantation can be mitigated. We recommend that studies employing external devices use devices that can be borne for long periods, and, wherever possible, deploy devices in advance of the time period of interest.**

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/216/4/537/DC1>

Key words: bio-logging, device, meta-analysis, mortality, survival, telemetry.

Received 21 June 2012; Accepted 17 October 2012

#### INTRODUCTION

In recent years, hundreds of studies on thousands of individuals have been conducted using animal-borne logging or telemetry devices. Such devices either transmit or store data that otherwise would be difficult or impossible to collect from free-ranging animals. This approach has provided information on location, movement, activity patterns, diving behaviour, body temperature and heart rate (for reviews, see Cooke, 2008; Hart and Hyrenbach, 2009; Ropert-Coudert et al., 2009; Rutz and Hays, 2009; Bograd et al., 2010). For information gathered by such techniques to be valuable, however, it is crucial that the devices used to transmit or record the data do not themselves influence the data. To understand the effect of devices on animals, Barron et al. (Barron et al., 2010) recently presented a meta-analysis of the effects of externally attached and internally implanted devices on the behaviour and ecology of birds. Barron et al. (Barron et al., 2010) demonstrated an overall negative effect of these devices on the birds that bear them, and concluded that the benefits of using these devices should be balanced against the costs to the birds and the risk of biasing the data. However, they

also reported that implanted devices caused no increase in what they classified as ‘device-induced behaviour’ (comfort behaviours such as preening, fluffing and stretching, and unrest activities including unquantifiable ‘active’ behaviours), whereas some external devices resulted in an increase in this category. Method of attachment (harness, collar, glue, anchor, implant, breast-mounted or tailmount) had no influence on the strength of effects for nesting productivity, clutch size, nest initiation date, offspring quality, body condition, flying ability, foraging behaviours, energy expenditure or survival rate, but anchored and implanted transmitters had the highest reported rates of device-induced mortality (Barron et al., 2010).

In our own work on the energetics of a range of species, we have employed both implanted (e.g. Green et al., 2009b; Portugal et al., 2009; Halsey et al., 2010; White et al., 2011) and externally attached devices (e.g. Green et al., 2009a; Halsey et al., 2009; Halsey et al., 2011). Much of this work used the heart rate technique for estimation of energy expenditure over relatively long time scales [see Green (Green, 2011) for a comprehensive review of this technique] and the loggers were internally implanted under anaesthesia. Implantation

might be considered preferable to external attachment for long-term studies because external attachment can increase mortality (e.g. Paton et al., 1991; Saraux et al., 2011), decrease reproductive output (e.g. Paton et al., 1991; Ackerman et al., 2004) and cause increases in the cost of both flight (e.g. Gessaman and Nagy, 1988; Obrecht et al., 1988) and swimming (e.g. Culik and Wilson, 1991; Culik et al., 1993; Schmid et al., 1995). The effect of device implantation on birds has been investigated in a range of studies, most of which have not reported negative effects of the devices. There was no effect of implanting a device on thermoregulation in ducklings *Anas platyrhynchos* (Bakken et al., 1996); no effect on growth or survival for wild turkey *Meleagris gallopavo* poults (Bowman et al., 2002); no effect on laying dates, clutch sizes or hatching success for female common eiders *Somateria mollissima* (Guillemette et al., 2002); no effect on over-wintering survival rates, arrival date or mass at the beginning of the breeding season for macaroni penguins *Eudyptes chrysolophus* (Green et al., 2004); higher resighting rates 2 years after implantation (80% resighted) for 10 implanted great cormorants *Phalacrocorax carbo* compared with 15 non-implanted control birds marked with metal rings (60% resighted) (Grémillet et al., 2005); no effect on maintenance behaviours, agonistic behaviours, reproductive behaviours, blood values designed to test for infection or implant rejection, or circulating corticosterone levels in chukars *Alectoris chukar* (O’Hearn et al., 2005); no effect on nest initiation dates, clutch size or mean egg volume in Canada geese *Branta canadensis* (Hupp et al., 2006); and no effect on percentage of time spent at sea or the number and duration of overnight trips of 2–5 or 6–26 days in little penguins *Eudyptula minor* (Ritchie et al., 2010). However, implantation can cause birds to abandon their nests (Meyers et al., 1998), and implanted birds have been shown to swim more slowly than non-implanted controls and have significantly reduced energy expenditure during swimming (Culik and Wilson, 1991). Further, there was a significant migration delay for implanted Canada geese during years with unfavourable wind conditions, although there was no difference between implanted and non-implanted birds in years with favourable conditions (Hupp et al., 2006) and implanted little penguins undertook fewer trips of less than 1 day duration than non-implanted birds (Ritchie et al., 2010). These findings, that implantation has little effect on a range of traits, contrast with the conclusion of Barron et al. (Barron et al., 2010) that method of attachment had no influence on the strength of effects for a range of traits (nesting productivity, clutch size, nest initiation date, offspring quality, body condition, flying ability, foraging behaviours, energy expenditure or survival rate), perhaps because implantation was only one of multiple attachment methods considered, and subdivision into multiple

attachment categories reduced power to detect differences in mean effect size among categories.

In the present study, we present a meta-analysis designed to examine the effect of externally attached and implanted devices on a range of traits, including condition, energy expenditure and reproduction, and test for an association between the duration of a deployment and the effect of devices. In contrast to Barron et al. (Barron et al., 2010), we focus explicitly on determining if there is a benefit to using externally attached devices compared with implanted ones, or *vice versa*, and therefore compare only two broad categories of device attachment: implanted or externally attached.

## MATERIALS AND METHODS

Data were compiled from peer-reviewed literature sources identified using searches conducted on Google Scholar (<http://scholar.google.com>) and the ISI Web of Knowledge (<http://apps.isiknowledge.com>). We identified potential studies using combinations of search terms including logger, biollogger, transmitter, radiotransmitter, effect and impact. Having identified a number of studies, we then expanded the search by examining the reference lists of impact studies for additional studies, as well as by examining the studies that cited those that we identified. Studies were included in the data set only if they provided data for groups with and without devices, as well as sample size and an estimate of variance (s.d., s.e.m. or 95% CI). A total of 440 estimates from 55 studies of 49 species were available for birds, so the analysis was restricted to this subset. We then established the direction of detrimental effects by scoring each effect; this was done independently by five of the authors of the present study, and is necessary because for some effects an increase is detrimental (e.g. metabolic rate during flight or swimming), whereas for others a decrease is detrimental (e.g. survival); effects were retained in the data set only if four of the five authors that scored them agreed on the direction of a detrimental effect. This yielded a total of 183 estimates of device impact from 39 studies of 36 species (see supplementary material Table S1). For each measure of effect, Cohen’s *d* was calculated as a standardised estimate of effect size (Hedges and Olkin, 1985). Cohen’s *d* represents the difference in means between the groups with and without devices, standardised by the pooled standard deviation, and therefore represents the difference between the groups in units of standard deviations. Because plots of the relationship between effect size and sample size were ‘funnel’-shaped and showed convergence with increasing sample size (Fig. 1), values of *d* used for the calculation of the mean effect size were weighted by the square root of sample size. This

Table 1. Mean and 95% confidence interval (2.5th, 97.5th percentiles) of the 200 resampled mean effect sizes and correlations between effect size and deployment duration for externally attached and internally implanted devices

	Sample size			Mean effect size	Correlation with deployment duration
	Estimates	Studies	Species		
All data	440	55	49		
Analysed data	185	40	37		
External	131	35	32	−0.36 (−0.48, −0.23)	0.23 (0.09, 0.35)
External (reproduction and survival)	74	19	19	−0.23 (−0.37, −0.10)	0.10 (−0.06, 0.26)
External (metabolic)	23	7	6	−0.65 (−0.98, −0.31)	0.34 (−0.02, 0.79)
External (condition)	34	13	13	−0.58 (−0.86, −0.10)	0.08 (−0.16, 0.26)
External (short)	30	13	13	−0.55 (−0.71, −0.36)	
External (medium)	57	17	16	−0.50 (−0.66, −0.33)	
External (long)	44	8	8	−0.03 (−0.14, 0.07)	
Internal	54	8	8	0.04 (−0.16, 0.30)	0.09 (−0.30, 0.74)
Internal (no outlier)	53	8	8	−0.03 (−0.23, 0.15)	0.19 (−0.25, 0.74)

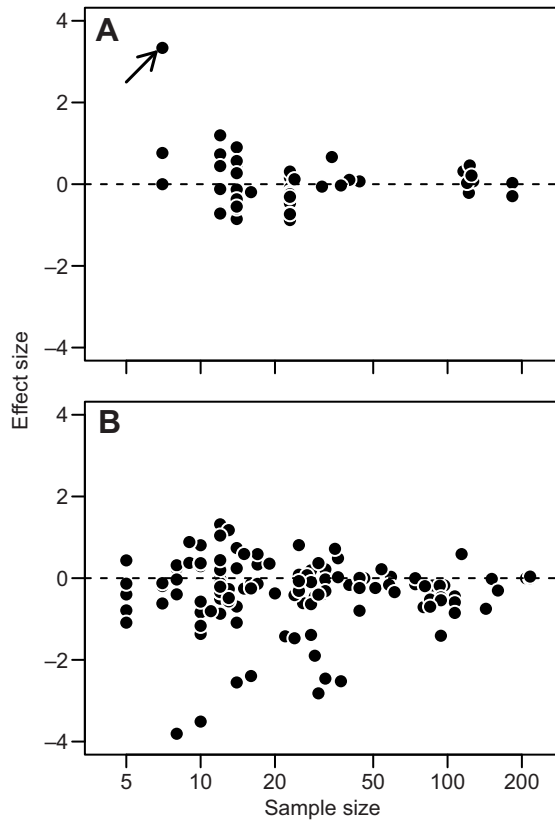


Fig. 1. Relationship between sample size and effect size for (A) internally implanted and (B) externally attached devices. Negative effects are those considered to be detrimental to the bird. Sample size is the pooled number of control and treatment (device-bearing) birds examined. The effect size indicated with an arrow was excluded from some analyses because of an unbalanced design (two implanted individuals and five non-implanted individuals).

was accomplished by multiplying each value of  $d$  by the accompanying weight, summing these values for each resample, and then dividing by the summed weights for the resample. The sign of  $d$  was set so that detrimental effects on traits were scored as negative. For example, an increase in energy expenditure during swimming or flying was coded as negative and a decrease was coded as positive; a decrease in body mass was coded as negative, as was a decrease in survival or reproductive output. Based on the information provided in the studies from which effect sizes were sourced, we also estimated the mean duration that an individual in each study bore a device; the duration of device deployment was coded as 365 days for those studies that spanned multiple years. See supplementary material Table S1 for a full list of all data, including the traits considered and the direction considered to be detrimental in the present study.

Effect sizes for externally attached devices were subdivided into broad categories according to the trait considered (body condition, reproduction, survival and metabolism; there were too few unique studies to subdivide the effect sizes for internally implanted devices) (Table 1). To minimize the bias that might arise from including multiple non-independent effect sizes from a single study, we adopted a re-sampling methodology that randomly chose (with uniform probability) only one effect size per category from each study, following Blackburn et al. (Blackburn et al., 2009). For each resample, we then calculated the mean effect size for each category,

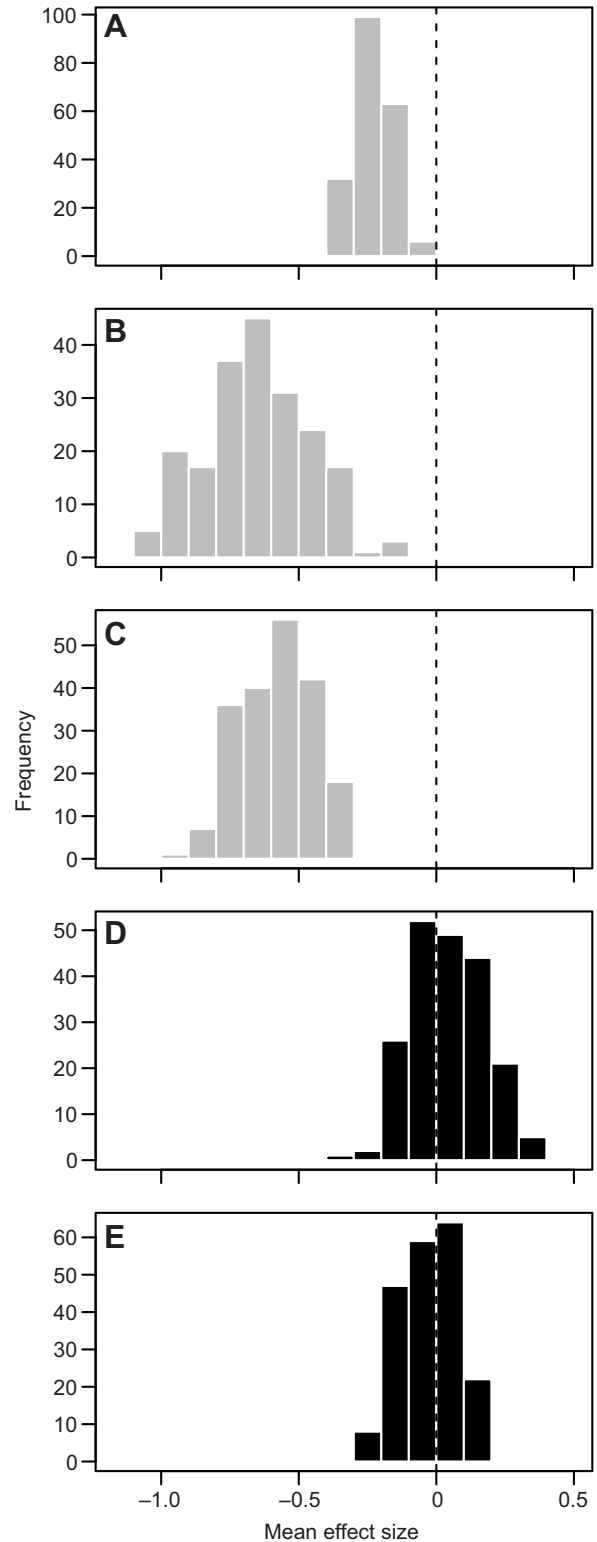


Fig. 2. Frequency distributions of 200 resampled mean effect sizes for (A–C) externally attached and (D,E) internally implanted devices. Mean effect sizes for internal loggers are shown with and without a study that included an  $N$  of 2 for implanted individuals (D and E, respectively; the excluded value is indicated with an arrow in Fig. 1A). Effects for externally attached devices are sub-divided into traits related to reproduction and survival (A), metabolism (B) and condition (C). Sufficient data were not available to subdivide traits for internally implanted devices. Vertical dashed lines in all panels correspond to a mean effect size of zero.

weighted by the square root of sample size. This resampling procedure was repeated a total of 200 times, and the distribution of mean effect sizes was examined for overlap with the null expectation of a mean effect size of zero. To determine whether effect sizes changed with the duration of deployment, we calculated for each resample the correlation coefficient (weighted by the square root of sample size) for the association between effect size and the duration of deployment, which was square root transformed to reduce skew in the distribution of deployment durations. We then arbitrarily subdivided the data for external devices into short-term ( $\leq 21$  days), medium-term (21–100 days) and long-term ( $>100$  days) deployments, and calculated mean effect size for each category.

A mean effect or weighted correlation was considered significantly different from zero if the 2.5th and 97.5th percentiles of the distribution of resampled effect sizes or correlation coefficients excluded zero. All calculations and analyses were conducted using R v2.15.0 (R Development Core Team, 2012).

### RESULTS AND DISCUSSION

Mean effect sizes for externally attached devices and traits related to body condition, metabolism, reproduction and survival were always negative (Fig. 2A–C) and significantly lower than zero (Table 1), indicating that external attachment of devices was, on average, detrimental.

The distribution of mean effect sizes for internally implanted devices across all traits was not significantly different from zero (Fig. 2D), and continued to be not significantly different from zero following exclusion of a large positive effect of implantation from a study that included only two implanted individuals but a larger number of non-implanted individuals (Culik and Wilson, 1991), and was therefore not adequately standardised by our weighting procedure (i.e. an outlier) (Fig. 2E, Table 1). These findings do not indicate that internal deployment never has a negative effect, or that external attachment always has a negative effect, but instead indicate that the effect of device implantation is consistently neither positive nor negative and on average it is less likely to have a negative effect than external deployment.

This finding that externally attached devices show consistently negative effects whereas internally implanted devices do not contrasts that of Barron et al. (Barron et al., 2010), who found that method of attachment (harness, collar, glue, anchor, implant, breast-mounted and tailmount) had no influence on the strength of effects for a suite of traits (nesting productivity, clutch size, nest initiation date, offspring quality, body condition, flying ability, foraging behaviours, energy expenditure and survival rate). The difference between the conclusions of these studies presumably arises because Barron et al. (Barron et al., 2010) sought to partition variance in effect size among a range of attachment methods, whereas our study sought only to compare internal implantation and external attachment. Based on the clear difference in the distribution of mean effect sizes for implanted and external devices demonstrated in the present study (Fig. 2), we conclude that, on average, implanted devices can be used to obtain reliable data for birds whereas external devices have a consistently detrimental effect. This is an important distinction from the meta-analysis of the effect of transmitters on birds by Barron et al. (Barron et al., 2010). They reported an overall effect of transmitters and other devices, with relatively few differences due to method of attachment.

A surprising outcome of the present study is the finding that although the overall effect of externally attached devices is negative (Table 1), there is a significant positive association between effect size and deployment duration, such that the magnitude of the

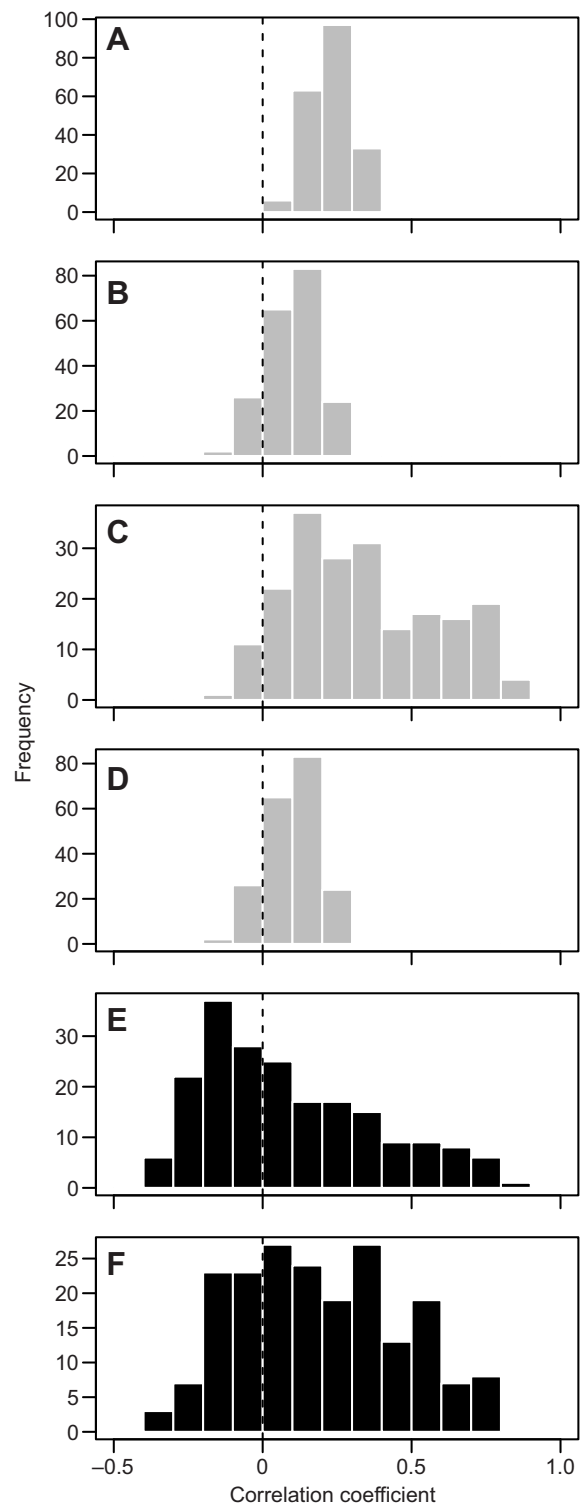


Fig. 3. Frequency distributions of 200 resampled correlation coefficients for the relationship between effect size and the square root of deployment duration for the effect of (A–D) externally attached and (E,F) internally implanted devices. Associations for internal loggers are shown with and without a study that included an  $N$  of 2 for implanted individuals (E and F, respectively; the excluded value is indicated with an arrow in Fig. 1A). Associations for externally attached devices are for all data (A) or data subdivided into traits related to reproduction and survival (B), metabolism (C) or condition (D). Sufficient data were not available to subdivide traits for internally implanted devices. Vertical dashed lines in all panels correspond to a correlation coefficient of zero.



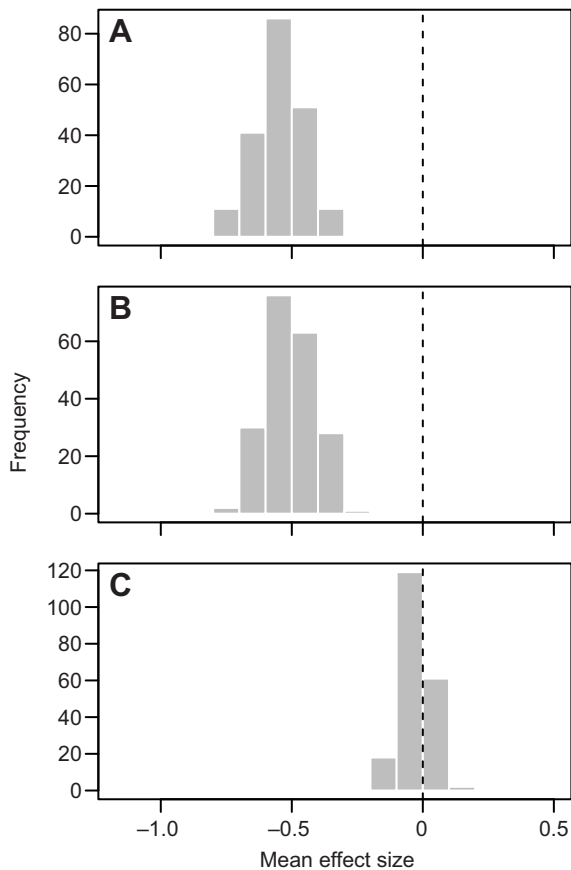


Fig. 4. Frequency distributions of 200 resampled mean effect sizes for externally attached devices. Mean effect sizes are shown for deployments of (A)  $\leq 21$  days, (B) 21–100 days and (C)  $> 100$  days. Vertical dashed lines in all panels correspond to a mean effect size of zero.

negative effect of externally attached devices decreases with the duration of device deployment (Fig. 3A). The association is also positive, but non-significant, if the data for external devices are subdivided into traits related to reproduction and survival, metabolism and condition (Fig. 3B–D, Table 1), though power to detect correlations is limited in these subdivisions. The association between effect size and deployment duration is less positive and also non-significant for internal devices (Fig. 3E,F), though again power is low. When the data for externally attached devices are pooled for all traits, and arbitrarily subdivided into short-term ( $\leq 21$  days), medium-term (21–100 days) and long-term ( $> 100$  days) deployments, the mean effect sizes are negative and significantly different from zero for short- and medium-term deployments, but not for long-term deployments (Fig. 4, Table 1). Given that the magnitude of the negative effect of externally attached devices decreases over time, we therefore suggest that future studies employ devices that can be borne for long periods, and, wherever possible, deploy devices in advance of the time period of interest.

While our findings tend to support the use of device implantation where possible, this is clearly not possible in every application. For example it would not be possible to record light levels or swim speed using a turbine from the inside of a bird's body cavity. Furthermore, reported rates of device-induced mortality are higher for implanted than externally attached devices (Barron et al., 2010). However, our conclusion is that external devices do not represent

a clear solution to the problem of mortality associated with surgical implantation of devices, because they have a consistent negative effect on survival (Fig. 2D). The benefits accruing from data obtained using implanted devices must thus be balanced against the risk of mortality associated with the anaesthesia and surgery required for implantation. In the same way, the ease of external deployment and reduction of this risk must be balanced against the knowledge that data from external deployments are highly likely to be influenced in some way by the presence of the data logger.

#### ACKNOWLEDGEMENTS

Two anonymous reviewers provided comments that helped us greatly clarify earlier versions of the manuscript.

#### FUNDING

C.R.W. is an ARC QEII Research Fellow (project DP0987626); P.C. is an ARC Future Fellow (project FT0991420).

#### REFERENCES

- Ackerman, J. T., Adams, J., Takekawa, J. Y., Carter, H. R., Whitworth, D. L., Newman, S. H., Golightly, R. T. and Orthmeyer, D. L. (2004). Effects of radiotransmitters on the reproductive performance of Cassin's auklets. *Wildl. Soc. Bull.* **32**, 1229–1241.
- Bakken, G. S., Reynolds, P. S., Kenow, K. P., Korschgen, C. E. and Boysen, A. F. (1996). Thermoregulatory effects of radiotelemetry transmitters in mallard ducklings. *J. Wildl. Manage.* **60**, 669–678.
- Barron, D. G., Brawn, J. D. and Weatherhead, P. J. (2010). Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods Ecol. Evol.* **1**, 180–187.
- Blackburn, T. M., Cassey, P. and Lockwood, J. L. (2009). The role of species traits in the establishment success of exotic birds. *Glob. Chang. Biol.* **15**, 2852–2860.
- Bograd, S. J., Block, B. A., Costa, D. P. and Godley, B. J. (2010). Biologging technologies: new tools for conservation. Introduction. *Endanger. Species Res.* **10**, 1–7.
- Bowman, J., Wallace, M. C., Ballard, W. B., Brunjes, J. H., IV, Miller, M. S. and Hellman, J. M. (2002). Evaluation of two techniques for attaching radio transmitters to turkey poults. *J. Field Ornithol.* **73**, 276–280.
- Cooke, S. J. (2008). Biotelemetry and biologging in endangered species research and animal conservation: relevance to regional, national, and IUCN Red List threat assessments. *Endanger. Species Res.* **4**, 165–185.
- Culik, B. M. and Wilson, R. P. (1991). Swimming energetics and performance of instrumented Adelie penguins (*Pygoscelis adeliae*). *J. Exp. Biol.* **158**, 355–368.
- Culik, B. M., Wilson, R. P. and Bannasch, R. (1993). Flipper-bands on penguins: what is the cost of a life-long commitment? *Mar. Ecol. Prog. Ser.* **98**, 209–214.
- Gessaman, J. A. and Nagy, K. A. (1988). Transmitter loads affect the flight speed and metabolism of homing pigeons. *Condor* **90**, 662–668.
- Green, J. A. (2011). The heart rate method for estimating metabolic rate: review and recommendations. *Comp. Biochem. Physiol.* **158A**, 287–304.
- Green, J. A., Tanton, J. L., Woakes, A. J., Boyd, I. L. and Butler, P. J. (2004). Effects of long-term implanted data loggers on macaroni penguins *Eudyptes chrysolophus*. *J. Avian Biol.* **35**, 370–376.
- Green, J. A., Halsey, L. G., Wilson, R. P. and Frappell, P. B. (2009a). Estimating energy expenditure of animals using the accelerometry technique: activity, inactivity and comparison with the heart-rate technique. *J. Exp. Biol.* **212**, 471–482.
- Green, J. A., Boyd, I. L., Woakes, A. J., Warren, N. L. and Butler, P. J. (2009b). Evaluating the prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging bird. *J. Avian Biol.* **40**, 529–538.
- Grémillet, D., Kuntz, G., Woakes, A. J., Gilbert, C., Robin, J.-P., Le Maho, Y. and Butler, P. J. (2005). Year-round recordings of behavioural and physiological parameters reveal the survival strategy of a poorly insulated diving endotherm during the Arctic winter. *J. Exp. Biol.* **208**, 4231–4241.
- Guillemette, M., Woakes, A. J., Flagstad, A. and Butler, P. J. (2002). Effects of data-loggers implanted for a full year in female common eiders. *Condor* **104**, 448–452.
- Halsey, L. G., Portugal, S. J., Smith, J. A., Murn, C. P. and Wilson, R. P. (2009). Recording raptor behavior on the wing via accelerometry. *J. Field Ornithol.* **80**, 171–177.
- Halsey, L. G., Butler, P. J., Fahlman, A., Bost, C. A. and Handrich, Y. (2010). Changes in the foraging dive behaviour and energetics of king penguins through summer and autumn: a month by month analysis. *Mar. Ecol. Prog. Ser.* **401**, 279–289.
- Halsey, L. G., White, C. R., Enstipp, M. R., Wilson, R. P., Butler, P. J., Martin, G. R., Grémillet, D. and Jones, D. R. (2011). Assessing the validity of the accelerometry technique for estimating the energy expenditure of diving double-crested cormorants *Phalacrocorax auritus*. *Physiol. Biochem. Zool.* **84**, 230–237.
- Hart, K. M. and Hyrenbach, K. D. (2009). Satellite telemetry of marine megavertebrates: the coming of age of an experimental science. *Endanger. Species Res.* **10**, 9–20.
- Hedges, L. V. and Olkin, I. (1985). *Statistical Methods for Meta-Analysis*. Orlando, FL: Academic Press.
- Hupp, J. W., Pearce, J. M., Mulcahy, D. M. and Miller, D. A. (2006). Effects of abdominally implanted radiotransmitters with percutaneous antennas on migration, reproduction, and survival of Canada geese. *J. Wildl. Manage.* **70**, 812–822.

- Meyers, P. M., Hatch, S. A. and Mulcahy, D. M.** (1998). Effect of implanted satellite transmitters on the nesting behavior of murre. *Condor* **100**, 172-174.
- O'Hearn, P. P., Romero, L. M., Carlson, R. and Delehanty, D. J.** (2005). Effective subcutaneous radiotransmitter implantation into the furcular cavity of chukars. *Wildl. Soc. Bull.* **33**, 1033-1046.
- Obrecht, H. H., Pennycuik, C. J. and Fuller, M. R.** (1988). Wind tunnel experiments to assess the effect of back-mounted radio transmitters on bird body drag. *J. Exp. Biol.* **135**, 265-273.
- Paton, P. W. C., Zabel, C. J., Neal, D. L., Steger, G. N., Tilghman, N. G. and Noon, B. R.** (1991). Effects of radio tags on spotted owls. *J. Wildl. Manage.* **55**, 617-622.
- Portugal, S. J., Green, J. A., Cassey, P., Frappell, P. B. and Butler, P. J.** (2009). Predicting the rate of oxygen consumption from heart rate in barnacle geese *Branta leucopsis*: effects of captivity and annual changes in body condition. *J. Exp. Biol.* **212**, 2941-2948.
- R Development Core Team** (2012). *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Ritchie, W. J., Green, J. A., Dann, P., Butler, P. J. and Frappell, P. B.** (2010). Do implanted data-loggers affect the time spent at sea by little penguins (*Eudyptula minor*) during winter? *Emu* **110**, 71-77.
- Ropert-Coudert, Y., Beaulieu, M., Hanuise, N. and Kato, A.** (2009). Diving into the world of biologging. *Endanger. Species Res.* **10**, 21-27.
- Rutz, C. and Hays, G. C.** (2009). New frontiers in biologging science. *Biol. Lett.* **5**, 289-292.
- Saraux, C., Le Bohec, C., Durant, J. M., Viblanc, V. A., Gauthier-Clerc, M., Beaune, D., Park, Y.-H., Yoccoz, N. G., Stenseth, N. C. and Le Maho, Y.** (2011). Reliability of flipper-banded penguins as indicators of climate change. *Nature* **469**, 203-206.
- Schmid, D., Grémillet, D. and Culik, B. M.** (1995). Energetics of underwater swimming in the great cormorant (*Phalacrocorax carbo sinensis*). *Mar. Biol.* **123**, 875-881.
- White, C. R., Grémillet, D., Green, J. A., Martin, G. R. and Butler, P. J.** (2011). Metabolic rate throughout the annual cycle reveals the demands of an Arctic existence in great cormorants. *Ecology* **92**, 475-486.