

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

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22 **Short Title:**

23 Meta-analysis of device effects

24

25 **Keywords:**

26 Bio-logging, device, meta-analysis, mortality, survival, telemetry

27

28 **Summary**

29 Animal-borne logging or telemetry devices are widely used for the measurements of physiological
30 and movement data from free-living animals. For such measurements to be relevant, however, it is
31 essential that the devices themselves do not affect the data of interest. A recent meta-analysis
32 (Barron et al. 2010; *Methods Ecol Evol.* 1:180-187) reported an overall negative effect of these
33 devices on the birds that bear them, i.e. on nesting productivity, clutch size, nest initiation date,
34 offspring quality, body condition, flying ability, foraging behaviours, energy expenditure or
35 survival rate. Method of attachment (Harness, Collar, Glue, Anchor, Implant, Breast-mounted,
36 Tailmount) had no influence on the strength of these effects but anchored and implanted
37 transmitters had the highest reported rates of device-induced mortality. Furthermore, external
38 devices, but not internal devices, caused an increase in ‘device-induced behaviour’ (comfort
39 behaviours such as preening, fluffing and stretching, and unrest activities including unquantifiable
40 ‘active’ behaviours). These findings suggest that, with the exception of device-induced behaviour,
41 external attachment is preferable to implantation. In the present study we undertake a meta-analysis
42 of 183 estimates of device impact from 39 studies of 36 species of bird designed to explicitly
43 compare the effects of externally-attached and surgically-implanted devices on a range of traits,
44 including condition, energy expenditure, and reproduction. In contrast to Barron et al., we
45 demonstrate that externally-attached devices have a consistent detrimental effect (i.e., negative
46 influences on body condition, reproduction, metabolism, and survival), whereas implanted devices
47 have no consistent effect. We also show that the magnitude of the negative effect of externally
48 attached devices decreases with time. We therefore conclude that device implantation is preferable
49 to external attachment, providing that the risk of mortality associated with the anaesthesia and
50 surgery required for implantation can be mitigated. We recommend that studies employing external
51 devices use devices that can be borne for long periods, and, wherever possible, deploy devices in
52 advance of the time period of interest.

53

54 **Introduction**

55 In recent years, hundreds of studies on thousands of individuals have been conducted using animal-
56 borne biologging or telemetry devices. Such devices either transmit or store data that otherwise
57 would be difficult or impossible to collect for free-ranging animals. This approach has provided
58 information on location, movement, activity patterns, diving behaviour, body temperature, and heart
59 rate (see reviews: Cooke, 2008; Hart and Hyrenbach, 2009; Ropert-Coudert et al., 2009; Rutz and
60 Hays, 2009; Bograd et al., 2010). For information gathered by such techniques to be valuable,
61 however, it is critical that the devices used to transmit or record the data do not themselves

62 influence the data. To understand the effect of devices on animals, Barron et al. (2010) recently
63 presented a meta-analysis of the effects of externally attached and internally implanted devices on
64 the behaviour and ecology of birds. Barron et al. (2010) demonstrated an overall negative effect of
65 these devices on the birds that bear them, and concluded that the benefits of using these devices
66 should be balanced against the costs to the birds and the risk of biasing the data. However, they also
67 reported that implanted devices caused no increase in what they classified as ‘device-induced
68 behaviour’ (comfort behaviours such as preening, fluffing and stretching, and unrest activities
69 including unquantifiable ‘active’ behaviours), whereas some external devices resulted in an increase
70 in this category. Method of attachment (Harness, Collar, Glue, Anchor, Implant, Breast-mounted,
71 Tailmount) had no influence on the strength of effects for nesting productivity, clutch size, nest
72 initiation date, offspring quality, body condition, flying ability, foraging behaviours, energy
73 expenditure or survival rate, but anchored and implanted transmitters had the highest reported rates
74 of device-induced mortality (Barron et al., 2010).

75 In our own work on the energetics of a range of species, we have employed both implanted
76 (e.g. Green et al., 2009b; Portugal et al., 2009; Halsey et al., 2010; White et al., 2011), and
77 externally-attached devices (e.g. Green et al., 2009a; Halsey et al., 2009; Halsey et al., 2011). Much
78 of this work used the heart rate technique for estimation of energy expenditure over relatively long
79 time scales (see Green, 2011 for a comprehensive review of this technique) and the loggers were
80 internally implanted under anaesthetic. Implantation is considered preferable to external attachment
81 for long-term studies because external attachment can increase mortality (e.g. Paton et al., 1991;
82 Saraux et al., 2011), decrease reproductive output (e.g. Paton et al., 1991; Ackerman et al., 2004),
83 and cause increases in the cost of both flight (e.g. Gessaman and Nagy, 1988; Obrecht et al., 1988)
84 and swimming (e.g. Culik and Wilson, 1991; Culik et al., 1993; Schmid et al., 1995). The effect of
85 device implantation on birds has been investigated in a range of studies, most of which have not
86 reported negative effects of the devices. There was no effect of implanting a device on
87 thermoregulation in ducklings *Anas platyrhynchos* (Bakken et al., 1996); no effect on growth or
88 survival for wild turkey *Meleagris gallopavo* poults (Bowman et al., 2002); no effect on laying
89 dates, clutch sizes, or hatching success for female common eiders *Somateria mollissima*
90 (Guillemette et al., 2002); no effect on over-wintering survival rates, arrival date and mass at the
91 beginning of the breeding season for macaroni penguins *Eudyptes chrysolophus* (Green et al.,
92 2004); higher resighting rates two years after implantation (80% resighted) for 10 implanted great
93 cormorants *Phalacrocorax carbo* compared to 15 non-implanted control birds marked with metal
94 rings (60% resighted) (Grémillet et al., 2005); no effect on maintenance behaviours, agonistic
95 behaviours, reproductive behaviours, blood values designed to test for infection or implant
96 rejection, and circulating corticosterone levels in chukars *Alectoris chukar* (O’Hearn et al., 2005);

97 no effect on nest initiation dates, clutch size, and mean egg volume in Canada geese *Branta*
98 *canadensis* (Hupp et al., 2006); no effect on percentage of time spent at sea or the number and
99 duration of overnight trips of 2–5 days or 6–26 days in little penguins *Eudyptula minor* (Ritchie et
100 al., 2010). However, implantation can cause birds to abandon their nests (Meyers et al., 1998),
101 implanted birds have been shown to swim more slowly than non-implanted controls and have
102 significantly reduced energy expenditure during swimming (Culik and Wilson, 1991); there was a
103 significant migration delay for implanted Canada geese during years with unfavourable wind
104 conditions, although there was no difference between implanted and non-implanted birds in years
105 with favourable conditions (Hupp et al., 2006) and implanted little penguins undertook fewer trips
106 of less than 1 day duration than non-implanted birds (Ritchie et al., 2010). These findings, that
107 implantation has little effect on a range of traits, contrast with the conclusion of Barron et al. (2010)
108 that method of attachment had no influence on the strength of effects for a range of traits (nesting
109 productivity, clutch size, nest initiation date, offspring quality, body condition, flying ability,
110 foraging behaviours, energy expenditure or survival rate), perhaps because implantation was only
111 one of multiple attachment methods considered (Harness, Collar, Glue, Anchor, Implant, Breast-
112 mounted, Tailmount), and subdivision into multiple attachment categories reduced power to detect
113 differences in mean effect size among categories.

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

120

121 **Materials and Methods**

122 Data were compiled from peer-reviewed literature sources identified using searches conducted in
123 Google Scholar (<http://www.scholar.google.com>) and ISI Web of Knowledge
124 (<http://apps.isiknowledge.com>). We identified potential studies using combinations of search terms
125 including logger, biologger, transmitter, radiotransmitter, effect, and impact. Having identified a
126 number of studies, we then expanded the search by examining the reference lists of impact studies
127 for additional studies, as well as by examining the studies that cited those which we identified.
128 Studies were included in the data set only if they provided data for groups with and without devices,
129 as well as sample size and an estimate of variance (s.d., SE, or 95% CI). A total of 440 estimates
130 from 55 studies of 49 species were available for birds, so the analysis was restricted to this subset.
131 We then established the direction of detrimental effects by scoring each effect; this was done

132 independently by five of the authors of the present study, and is necessary because for some effects
133 an increase is detrimental (e.g. metabolic rate during flight or swimming), whereas for others a
134 decrease is detrimental (e.g. survival); effects were retained in the data set only if four of the five
135 authors that scored them agreed on the direction of a detrimental effect. This yielded a total of 183
136 estimates of device impact from 39 studies of 36 species (see supplementary information). For each
137 measure of effect Cohen's d was calculated as a standardised estimate of effect size (Hedges and
138 Olkin, 1985). Cohen's d represents the difference in means between the groups with and without
139 devices, standardised by the pooled standard deviation, and therefore represents the difference
140 between the groups in units of standard deviations. Since plots of the relationship between effect
141 size and sample size were “funnel” shaped and showed convergence with increasing sample size
142 (Fig. 1), values of d used for the calculation of the mean effect size were weighted by the square
143 root of sample size. This was accomplished by multiplying each value of d by the accompanying
144 weight, summing these values for each resample, and then dividing by the summed weights for the
145 resample. The sign of d was set so that detrimental effects on traits were scored as negative. For
146 example, an increase in energy expenditure during swimming or flying was coded as negative and a
147 decrease was coded as positive; a decrease in body mass was coded as negative, as was a decrease
148 in survival or reproductive output. Based on the information provided in the studies from which
149 effect sizes were sourced, we also estimated the mean duration that an individual in each study bore
150 a device; the duration of device deployment was coded as 365 days for those studies that spanned
151 multiple years. See supplementary information for a full list of all data, including the traits
152 considered and the direction considered to be detrimental in the present study.

153 Effect sizes for externally-attached devices were subdivided into broad categories according
154 to the trait considered (body condition, reproduction and survival, metabolism; there were too few
155 unique studies to subdivide the effect sizes for internally-implanted devices; Table 1). To minimize
156 the bias that might arise from including multiple non-independent effect sizes from a single study,
157 we adopted a re-sampling methodology that randomly chose (with uniform probability) only one
158 effect size per category from each study, following Blackburn et al. (2009). For each resample, we
159 then calculated the mean effect size for each category, weighted by the square root of sample size.
160 This resampling procedure was repeated a total of 200 times, and the distribution of mean effect
161 sizes was examined for overlap with the null expectation of a mean effect size of zero. To determine
162 if effect sizes changed with the duration of a deployment, we calculated for each resample the
163 correlation coefficient (weighted by the square root of sample size) for the association between
164 effect size and the duration of a deployment, which was square root transformed to reduce skew in
165 the distribution of deployment durations. We then arbitrarily subdivided the data for external

166 devices into short-term (less than or equal to 21 d), medium-term (21 – 100 d) and long-term (> 100
167 d) deployments, and calculated mean effect size for each category.

168 A mean effect or weighted correlation was considered significantly different from zero if the
169 2.5th and 97.5th percentiles of the distribution of resampled effect sizes or correlation coefficients
170 excluded zero. All calculations and analyses were conducted using R v2.15.0 (R Development Core
171 Team, 2012).

172

173 **Results and Discussion**

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

177 The distribution of mean effect sizes for internally-implanted devices across all traits was
178 not significantly different from zero (Fig 2D), and continued to be not significantly different from
179 zero following exclusion of a large positive effect of implantation from a study that included only
180 two implanted individuals but a larger number of non-implanted individuals (Culik and Wilson,
181 1991), and was therefore not adequately standardised by our weighting procedure (i.e., an outlier)
182 (Fig. 2E, Table 1). These findings do not indicate that internal deployment never has a negative
183 effect, or that external attachment always has a negative effect, but instead indicate that the effect of
184 device implantation is consistently neither positive nor negative and on average it is less likely to
185 have a negative effect than external deployment.

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

200 A surprising outcome of the present study is the finding that although the overall effect of
201 externally attached devices is negative (Table 1), there is a significant positive association
202 between effect size and deployment duration, such that the magnitude of the negative effect of
203 externally attached devices decreases with the duration of device deployment (Fig. 3A). The
204 association is also positive, but non-significant, if the data for external devices are subdivided into
205 traits related to reproduction and survival (Fig. 3B, Table 1), metabolism (Fig. 3C, Table 1), and
206 condition (Fig. 3D, Table 1), though power to detect correlations is limited in these subdivisions.
207 The association between effect size and deployment duration is less positive and also non-
208 significant for internal devices (Fig. 3E-F), though again power is low. When the data for
209 externally attached devices are pooled for all traits, and arbitrarily subdivided into short-term (less
210 than or equal to 21 d), medium-term (21 – 100 d) and long-term (> 100 d) deployments, the mean
211 effect sizes are negative and significantly different from zero for short- and medium term
212 deployments, but not for long-term deployments (Fig 4, Table 1). Given that the magnitude of the
213 negative effect of externally attached devices decreases over time, we therefore suggest that future
214 studies employ devices that can be borne for long periods, and, wherever possible, deploy devices
215 in advance of the time period of interest.

216 While our findings tend to support the use of device implantation where possible, this is
217 clearly not possible in every application. For example it would not be possible record light levels, or
218 swim speed using a turbine from the inside of a bird's body cavity. Furthermore, reported rates of
219 device-induced mortality are higher for implanted than externally-attached devices (Barron et al.,
220 2010). Our conclusion is though that external devices do not represent a clear solution to the
221 problem of mortality associated with surgical implantation of devices, however, because they have
222 a consistent negative effect on survival (Fig. 2D). The benefits accruing from data obtained using
223 implanted devices must thus be balanced against the risk of mortality associated with the
224 anaesthesia and surgery required for implantation. In the same way, the ease of external deployment
225 and reduction of this risk must be balanced against the knowledge that data from external
226 deployments are highly likely to be influenced in some way by the presence of the data logger.

227

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232

233 **References**

- 234 **Ackerman, J. T., Adams, J., Takekawa, J. Y., Carter, H. R., Whitworth, D. L., Newman, S.**
235 **H., Golightly, R. T. and Orthmeyer, D. L.** (2004). Effects of radiotransmitters on the
236 reproductive performance of Cassin's auklets. *Wildl. Soc. Bull.* **32**, 1229-1241.
- 237 **Bakken, G. S., Reynolds, P. S., Kenow, K. P., Korschgen, C. E. and Boysen, A. F.** (1996).
238 Thermoregulatory effects of radiotelemetry transmitters in mallard ducklings. *J. Wildl.*
239 *Manag.* **60**, 669-678.
- 240 **Barron, D. G., Brawn, J. D. and Weatherhead, P. J.** (2010). Meta-analysis of transmitter effects
241 on avian behaviour and ecology. *Methods in Ecology and Evolution* **1**, 180-187.
- 242 **Blackburn, T. M., Cassey, P. and Lockwood, J. L.** (2009). The role of species traits in the
243 establishment success of exotic birds. *Global Change Biology* **15**, 2852-2860.
- 244 **Bograd, S. J., Block, B. A., Costa, D. P. and Godley, B. J.** (2010). Biologging technologies: new
245 tools for conservation. Introduction. *Endangered Species Research* **10**, 1-7.
- 246 **Bowman, J., Wallace, M. C., Ballard, W. B., Brunjes, J. H., IV, Miller, M. S. and Hellman, J.**
247 **M.** (2002). Evaluation of two techniques for attaching radio transmitters to turkey poults. *J.*
248 *Field Ornithol.* **73**, 276-280.
- 249 **Cooke, S. J.** (2008). Biotelemetry and biologging in endangered species research and animal
250 conservation: relevance to regional, national, and IUCN Red List threat assessments.
251 *Endangered Species Research* **4**, 165-185.
- 252 **Culik, B. M. and Wilson, R. P.** (1991). Swimming energetics and performance of instrumented
253 Adelie penguins (*Pygoscelis adeliae*). *J. Exp. Biol.* **158**, 355-368.
- 254 **Culik, B. M., Wilson, R. P. and Bannasch, R.** (1993). Flipper-bands on penguins: what is the cost
255 of a life-long commitment? *Mar. Ecol. Prog. Ser.* **98**, 209-214.
- 256 **Gessaman, J. A. and Nagy, K. A.** (1988). Transmitter loads affect the flight speed and metabolism
257 of homing pigeons. *Condor* **90**, 662-668.
- 258 **Green, J. A.** (2011). The heart rate method for estimating metabolic rate: Review and
259 recommendations. *Comp. Biochem. Physiol. A* **158**, 287-304.
- 260 **Green, J. A., Halsey, L. G., Wilson, R. P. and Frappell, P. B.** (2009a). Estimating energy
261 expenditure of animals using the accelerometry technique: activity, inactivity and
262 comparison with the heart-rate technique. *J. Exp. Biol.* **212**, 471-482.
- 263 **Green, J. A., Tanton, J. L., Woakes, A. J., Boyd, I. L. and Butler, P. J.** (2004). Effects of long-
264 term implanted data loggers on macaroni penguins *Eudyptes chrysolophus*. *J. Avian Biol.*
265 **35**, 370-376.
- 266 **Green, J. A., Boyd, I. L., Woakes, A. J., Warren, N. L. and Butler, P. J.** (2009b). Evaluating the
267 prudence of parents: daily energy expenditure throughout the annual cycle of a free-ranging
268 bird. *J. Avian Biol.* **40**, 529-538.
- 269 **Grémillet, D., Kuntz, G., Woakes, A. J., Gilbert, C., Robin, J.-P., Le Maho, Y. and Butler, P.**
270 **J.** (2005). Year-round recordings of behavioural and physiological parameters reveal the
271 survival strategy of a poorly insulated diving endotherm during the Arctic winter. *J. Exp.*
272 *Biol.* **208**, 4231-4241.
- 273 **Guillemette, M., Woakes, A. J., Flagstad, A. and Butler, P. J.** (2002). Effects of data-loggers
274 implanted for a full year in female common eiders. *Condor* **104**, 448-452.
- 275 **Halsey, L. G., Portugal, S. J., Smith, J. A., Murn, C. P. and Wilson, R. P.** (2009). Recording
276 raptor behavior on the wing via accelerometry. *J. Field Ornithol.* **80**, 171-177.
- 277 **Halsey, L. G., Butler, P. J., Fahlman, A., Bost, C. A. and Handrich, Y.** (2010). Changes in the
278 foraging dive behaviour and energetics of king penguins through summer and autumn: a
279 month by month analysis. *Mar. Ecol. Prog. Ser.* **401**, 279-289.
- 280 **Halsey, L. G., White, C. R., Enstipp, M. R., Wilson, R. P., Butler, P. J., Martin, G. R.,**
281 **Grémillet, D. and Jones, D. R.** (2011). Assessing the validity of the accelerometry
282 technique for estimating the energy expenditure of diving double-crested cormorants
283 *Phalacrocorax auritus*. *Physiol. Biochem. Zool.* **84**, 230-237.

- 284 **Hart, K. M. and Hyrenbach, K. D.** (2009). Satellite telemetry of marine megavertebrates: the
285 coming of age of an experimental science. *Endangered Species Research* **10**, 9-20.
- 286 **Hedges, L. V. and Olkin, I.** (1985). Statistical methods for meta-analysis. San Diego: Academic
287 Press.
- 288 **Hupp, J. W., Pearce, J. M., Mulcahy, D. M. and Miller, D. A.** (2006). Effects of abdominally
289 implanted radiotransmitters with percutaneous antennas on migration, reproduction, and
290 survival of Canada geese. *J. Wildl. Manag.* **70**, 812-822.
- 291 **Meyers, P. M., Hatch, S. A. and Mulcahy, D. M.** (1998). Effect of implanted satellite transmitters
292 on the nesting behavior of murre. *Condor* **100**, 172-174.
- 293 **O'Hearn, P. P., Romero, L. M., Carlson, R. and Delehanty, D. J.** (2005). Effective subcutaneous
294 radiotransmitter implantation into the furcular cavity of chukars. *Wildl. Soc. Bull.* **33**, 1033-
295 1046.
- 296 **Obrecht, H. H., Pennycuik, C. J. and Fuller, M. R.** (1988). Wind tunnel experiments to assess
297 the effect of back-mounted radio transmitters on bird body drag. *J. Exp. Biol.* **135**, 265-273.
- 298 **Paton, P. W. C., Zabel, C. J., Neal, D. L., Steger, G. N., Tilghman, N. G. and Noon, B. R.**
299 (1991). Effects of radio tags on spotted owls. *J. Wildl. Manag.* **55**, 617-622.
- 300 **Portugal, S. J., Green, J. A., Cassey, P., Frappell, P. B. and Butler, P. J.** (2009). Predicting the
301 rate of oxygen consumption from heart rate in barnacle geese *Branta leucopsis*: effects of
302 captivity and annual changes in body condition. *J. Exp. Biol.* **212**, 2941-2948.
- 303 **R Development Core Team.** (2012). R: A Language and Environment for Statistical Computing.
304 Vienna, Austria: R Foundation for Statistical Computing.
- 305 **Ritchie, W. J., Green, J. A., Dann, P., Butler, P. J. and Frappell, P. B.** (2010). Do implanted
306 data-loggers affect the time spent at sea by Little Penguins (*Eudyptula minor*) during
307 winter? *Emu* **110**, 71-77.
- 308 **Ropert-Coudert, Y., Beaulieu, M., Hanuise, N. and Kato, A.** (2009). Diving into the world of
309 biologging. *Endangered Species Research* **10**, 21-27.
- 310 **Rutz, C. and Hays, G. C.** (2009). New frontiers in biologging science. *Biology Letters* **5**, 289-292.
- 311 **Saraux, C., Le Bohec, C., Durant, J. M., Viblanc, V. A., Gauthier-Clerc, M., Beaune, D., Park,
312 Y.-H., Yoccoz, N. G., Stenseth, N. C. and Le Maho, Y.** (2011). Reliability of flipper-
313 banded penguins as indicators of climate change. *Nature* **469**, 203-206.
- 314 **Schmid, D., Grémillet, D. and Culik, B. M.** (1995). Energetics of underwater swimming in the
315 great cormorant (*Phalacrocorax carbo sinensis*). *Marine Biology* **123**, 875-881.
- 316 **White, C. R., Grémillet, D., Green, J. A., Martin, G. R. and Butler, P. J.** (2011). Metabolic rate
317 throughout the annual cycle reveals the demands of an Arctic existence in Great
318 Cormorants. *Ecology* **92**, 475-486.
- 319
320

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

323

	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)

324

325 Fig. 1. Relationship between sample size and effect size for internally implanted (a) and externally
326 attached (b) devices. Negative effects are those considered to be detrimental to the bird. Sample
327 size is the pooled number of control and treatment (device-bearing) birds examined. The effect size
328 indicated with an arrow was excluded from some analyses because of an unbalanced design (2
329 implanted individuals and 5 non-implanted individuals).

330

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

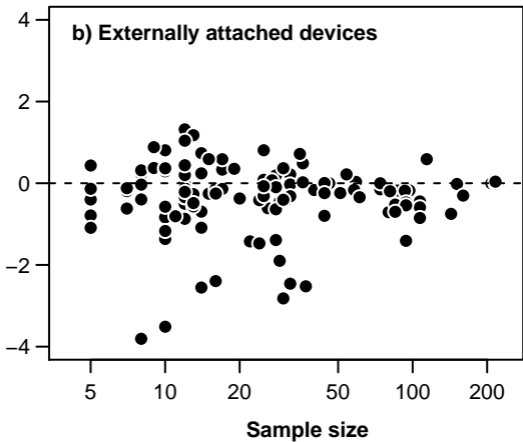
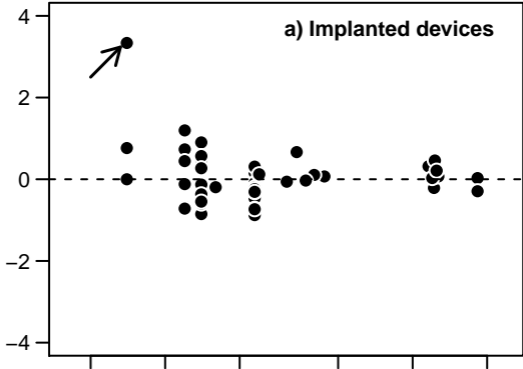
339

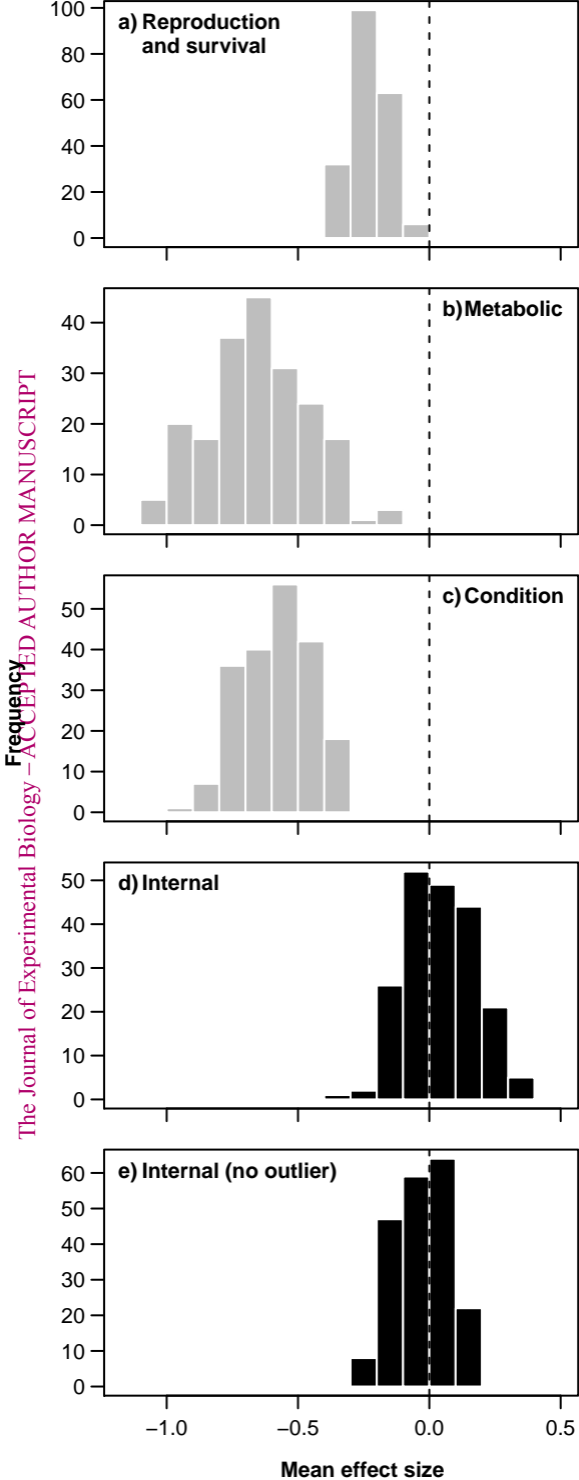
340 Fig. 3. Frequency distributions of 200 resampled correlation coefficients for the relationship
341 between effect size and the square root of deployment duration for the effect of externally attached
342 (panels A-D) and internally-implanted (panels E and F) devices. Associations for internal loggers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

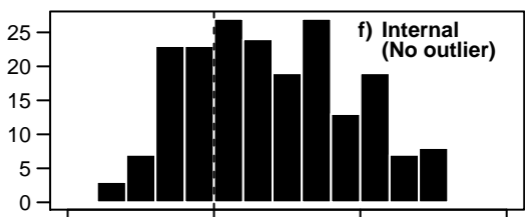
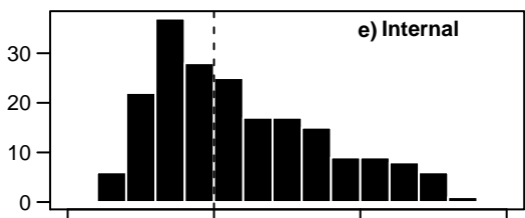
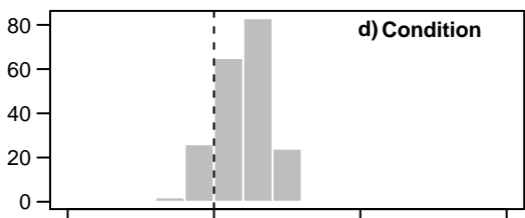
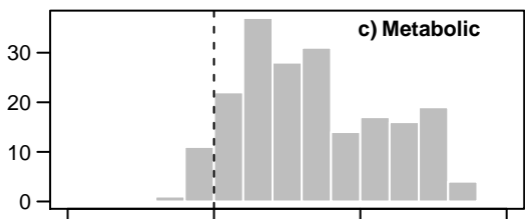
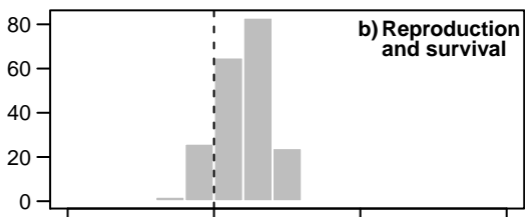
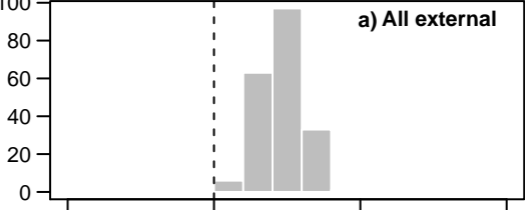
349

350 Fig. 4. Frequency distributions of 200 resampled mean effect sizes for externally-attached devices.
351 Mean effect sizes are shown for deployments of less than or equal to 21 days (panel A), 21 – 100 d
352 (panel B), > 100 d (panel C). Vertical dashed lines in all panels correspond with a mean effect size
353 of zero.

354







-0.5 0.0 0.5 1.0

Correlation coefficient

