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Meta-analysis of transmitter effects on avian behaviour and ecology

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Summary

1. Researchers often attach transmitters and other devices to free-living birds without a clear understanding of potential deleterious consequences to their study organisms, and thus to their data. Studies investigating this topic have generally been limited to a single species or type of device.

2. To achieve a broader understanding we used a meta-analysis of 84 studies to ask: (1) Do devices have an overall effect on birds? (2) Which aspects of avian behaviour and ecology are affected? (3) What attributes of birds influence transmitter effects? (4) What attributes of devices influence their effects? (5) Are effects partially a consequence of capture and restraint?

3. We found a significant negative effect of devices on birds, both overall and for 8 of the 12 specific aspects analysed. The most substantial effects were that birds with devices had markedly increased energy expenditure and were much less likely to nest.

4. Effects were independent of attributes of the birds (sex, age, primary method of locomotion and body mass). We also found no evidence that proportionally heavier devices had greater effects, although researchers generally avoided using heavy devices. Breast-mounted and harness attachments increased device-induced behaviours such as preening, however, and the risk of device-induced mortality differed between attachment methods.

5. Other than foraging behaviours, no effects were a consequence of capture or restraint.

6. *Synthesis and applications.* We provide the first comprehensive evidence that transmitters and other devices negatively affect birds and may bias resulting data. Researchers should balance the benefits of using these techniques against potential costs to the birds and reliability of the data obtained.

Key-words: birds, capture and restraint, datalogger, device attachment, energetic expenditure, locomotion, radio tracking, reproduction, survival, telemetry

Introduction

The development of miniature radio transmitters helped ecologists overcome the challenges of following free-roaming animals (Lemunyan *et al.* 1959; Cochran & Lord 1963). Decreases in transmitter size and increased battery life expanded the pool of suitable species and made the technology especially useful for studying birds. Growing use of telemetry in avian research (Fig. 1) makes it increasingly important that we understand how transmitters affect birds. Researchers using radio telemetry are often uncertain about the potential deleterious effects of transmitters on their study organisms, and thus about possible biases in the data they collect. Here we use a meta-analytical approach to investigate the effects of transmitters on birds.

Researchers are clearly aware of the potential for transmitters to have negative effects because almost 80% of studies we reviewed (see below) addressed the topic in some fashion. Although there have been several reviews of transmitter effects on birds (Calvo & Furness 1992; Murray & Fuller 2000), none have been comprehensive. These reviews either evaluated transmitter effects qualitatively, or if a quantitative approach was used it relied on 'vote counting' (the number of studies reporting negative effects is compared with the number reporting no effects), which ignores the influence of sample size on statistical significance (Hedges & Olkin 1980). The meta-ana-

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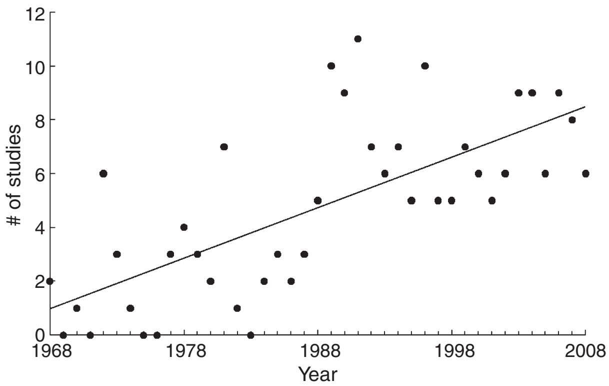

Fig. 1. Number of published studies using transmitters or dataloggers per year.

lytical approach incorporates effect sizes (which provide a measure of the magnitude of a treatment effect) and allowed us to quantitatively analyse results from multiple studies in an unbiased way (Gurevitch & Hedges 1993).

Our first goal was to determine whether transmitters have any effect on birds and if so, whether improved techniques have decreased the magnitude of these effects over time. Second, we identified specific aspects of avian behaviour and ecology affected by transmitters. A 'catch 22' problem when assessing telemetry effects is that often the behaviours of interest can only be quantified using telemetry. Despite this limitation, we identified a number of aspects where there were sufficient studies of birds with and without transmitters to allow robust analysis: nest success, nesting productivity, clutch size, nesting propensity, nest initiation date, offspring quality, body condition, flying ability, foraging behaviours, device-induced behaviours, energetic expenditure, survival rate, nest abandonment, physical harm and device-induced mortality. Our third objective was to identify attributes of the birds (sex, age, primary mode of locomotion and body mass) that contributed to transmitter effects. Our fourth goal was to determine whether the relative mass of the transmitters or how they were attached contributed to their effects. A rule of thumb is that transmitters weighing less than 5% of an animal's body mass have negligible effects. This '5% rule' has no empirical basis and appears to have originated from a suggestion by Brander & Cochran (1969) regarding transmitter weights. Aldridge & Brigham (1988) probably performed the best test of this rule by comparing variable loads on bats and found that manoeuvrability decreased as load mass increased. Numerous studies have compared multiple device masses within a single species of bird, but there are frequent inconsistencies within and between studies (e.g. Greenwood & Sargeant 1973; Pennycuick, Fuller, & Mcallister 1989; Gessaman, Workman, & Fuller 1991). We asked whether there is evidence for a threshold effect across bird species that would support the '5% rule' (or the '3% rule' adopted recently by some researchers). We also considered whether the method of attachment influences transmitter effects because previous assessments of this issue produced contradictory results (e.g. Small & Rusch 1985; Osborne, Frawley, & Weeks 1997).

Finally, we assessed whether any negative effects of transmitters may be partially a result of capture and restraint (Cox & Afton 1998). If so, transmitters should appear to have a greater effect when birds with transmitters are compared with uncaptured birds than when compared with procedural controls. Ultimately, our goal is to provide information to help researchers design studies that involve attaching devices to birds in a way that minimizes unwanted effects on both birds and research.

Materials and methods

LITERATURE SEARCH

We conducted a literature search current to March 2009 using ISI Web of Science (http://apps.isiknowledge.com) and Google Scholar (http://www.scholar.google.com). Topic words were radio transmitter, transmitter effects/impacts, radio telemetry, radio tagging, device attachment, radio attachment, instrument attachment and load attachment. As dataloggers and satellite transmitters are similar in shape and methods of attachment to radio transmitters, we included them by replacing 'radio' with 'datalogger' or 'satellite' in our literature search. Hereafter, we refer to transmitters, dataloggers, etc. collectively as 'devices' or 'transmitters'. We included additional studies found in literature reviews (Calvo & Furness 1992; Samuel & Fuller 1994; Murray & Fuller 2000; Godfrey & Bryant 2003; Phillips, Xavier, & Croxall 2003) or in the literature cited by published studies. Although this approach inevitably overlooked some papers, it should have provided an unbiased method of collecting relevant studies.

Our initial sample included 192 studies. To be included in our analysis, however, a study had to quantitatively compare birds with devices to birds without devices and allow us to estimate effect sizes. The latter requirement meant that studies had to report sample sizes, direction of the effect, and one of the following statistics: mean and standard deviation, *F*-statistic, *t*-statistic, *Z*-statistic, chi-squared value or *P*-value. A total of 84 studies met these criteria. All studies that were used in analyses but were not directly cited in the main text are available as Supporting Information (see Appendix S1).

DATA COLLECTION

After compiling the usable studies, we determined the types of data to include in each aspect of behaviour and ecology (Table 1) and established rules for extracting relevant data from each study. When results were divided (among study sites, years, etc.) without a combined analysis, we used the first result provided; so, only one result was taken from each study for a given question. If a study used devices that differed in mass and the effects were analysed separately we used only the largest mass. However, if devices with different masses were combined in the analyses, we used their mean mass. We used multiple values from a given study only if separate analyses were provided for different variables of interest (e.g. attachment type, species and sex). Such studies typically used separate controls for each analysis; therefore, potential lack of independence should have little effect on our results (Gurevitch & Hedges 1993). When results were provided in a graph we obtained exact values using GetData Graph Digitizer 2.24 (http://getdata-graph-digitizer.com).

We grouped categorical attributes of birds (sex, age and primary mode of locomotion) and devices (attachment type) into discrete categories (Table 2), and recorded the body mass of birds and the per cent body mass of devices. We noted whether studies compared birds with

Table 1. Types of data used to investigate each aspect of behaviour and ecology and the proportion of studies reporting these data types

Aspect	Data type	Proportion of studies (%)
Nest success	% of nests fledging young	69
	Daily survival rate	31
Nesting productivity	Fledglings per pair	29
	Hatching success	21
	% of pairs fledging young	14
	Fledglings per female	7
	No. of fledglings	7
	Fledglings per egg	7
	No. of clutches	7
	% abandoning young	7
Clutch size	No. of eggs laid	100
Nesting propensity	% breeding	80
	% producing second clutch	20
Nest initiation date	Julian date of first nest	78
	Time between device attachment and nest initiation	22
Offspring quality	Growth rate	50
	Mean chick mass	38
	Brood mass	13
Body condition	Body mass	63
	Body mass change	37
Flying ability	Flight or swimming speed	86
	Wing beat rate	14
Foraging behaviours	Foraging duration	53
	Offspring provisioning rate	26
	Food consumption	11
	Prey mass	5
	% of nest visits with prey	5
Device-induced behaviours	% of time in comfort behaviours (e.g. preening, fluffing and stretching)	83
	% of time in unrest activities (unquantifiable 'active' behaviours)	11
	Preening at device	6
Energetic expenditure	Daily energy expenditure	46
	Cost of transport	23
	CO_2 production	15
	Energy expended during flight	8
	Flight metabolism/resting metabolic rate	8
Survival rate	Estimated by return, recapture, recovery, and recruitment rates	100

devices with uncaptured birds or with captured procedural controls to determine the effect of capture and restraint. If studies reported results from both procedural control and uncaptured birds, we included only comparisons with procedural controls. Finally, we categorized foraging behaviours as foraging for self or offspring.

STATISTICAL ANALYSES

We transformed test statistics (see above) to a common product–moment correlation *r* (see Rosenthal 1991), using the MetaCalc Statistical Calculator within the program MetaWin (Rosenberg, Adams, & Gurevitch 2000). Correlation coefficients and sample sizes were used with MetaWin to calculate the effect size, Fisher's *z*-transformation, and its variance for all variables from each study. This approach was chosen because studies often presented summary information in different forms and the statistics provided were often insufficient to calculate Cohen's *d*, or related statistics (Rosenthal 1991). We appointed directionality to the effect sizes, with negative values in the direction considered detrimental.

For each analysis we used a random effects model in MetaWin (Rosenberg, Adams & Gurevitch 2000) because it accounts for a random component of variation in effect sizes between studies and is considered more appropriate for ecological data than the more restrictive fixed effects model (Gurevitch & Hedges 1993). In the omnibus analysis we combined all aspects of behaviour and ecology, using one analysis per study. If a study analysed more than one aspect we included the one with the largest sample size. We bootstrapped 95% confidence intervals of the mean effect size with 999 iterations and considered mean effect sizes significant if confidence intervals did not overlap zero. Categorical attributes of the bird or device could be analysed only if they had two or more categories, and each category contained two or more studies (required to calculated mean effect size). To detect differences among group effect sizes (described by Q) in the categorical attributes and to determine whether slopes (b) of

Table 2. Description of designations for each categorical attributes of the bird or device

Attribute	Category	Description
Attachment method	Harness	Backpacks, harnesses
	Collar	Collars, necklaces, pendants
	Glue	Glue and tape, whether alone or combined with sutures, cable ties, or Velcro
	Anchor	All methods of anchoring subcutaneously
	Implant	All methods of implantation
	Breast-mounted	Attached to the breast
	Tailmount	Attached to tail
Locomotion	Walk	Shorebirds, galliforms, rails
	Swim	Penguins
	Various	Waterfowl
	Fly	All other birds
Sex	Male	Males only
	Female	Females only
	Both	Males and females
	Unknown	Unknown sex
Age	Adult	Reproductively mature
	Juvenile	Non-reproductively mature

Although 'walking' species fly during migration, studies primarily used non-migrating individuals.

continuous attributes plotted against effect sizes were different from zero we estimated probability values from randomization tests with 999 iterations. We report effect sizes and confidence intervals that are transformed from Fisher's z-transformation to Cohen's d (using the MetaCalc Statistical Calculator within the program MetaWin, Rosenberg, Adams & Gurevitch 2000), allowing us to use Cohen's (1988) interpretation of these values: less than 0·5 indicates a 'small' effect, 0·5–0·8 a 'medium' effect and $>0{\cdot}8$ a 'large' effect.

If studies with non-significant results tend to go unpublished, a reporting bias known as the 'file-drawer effect' would result (Sterling 1959). We addressed this problem by calculating Rosenthal's 'fail-safe' numbers (Rosenthal 1979) for an $\alpha = 0{\cdot}05$ in the program MetaWin (Rosenberg, Adams & Gurevitch 2000). This quantity is the number of unpublished studies with a mean effect size of zero required to reduce the combined significance to the specified α value. For example, a fail-safe number of 100 would mean 100 studies with no effect must have gone unpublished to render the results non-significant. If this number is large relative to the number of studies analysed, then the conclusions are relatively robust. We present fail-safe numbers only for marginal results where the outcome would change with a few unpublished studies showing no effect. We could not investigate the potential opposing publication bias (i.e. researchers preferentially publish results showing no impact of devices), but should it occur, our results would be conservative.

To investigate whether attachment method influenced the frequency of nest abandonment, physical harm or device-induced mortality, we could not use a meta-analytical approach because the outcomes of interest were discrete (but ordinal), preventing the calculation of effect sizes. Instead we assigned studies a '2' if they reported at least one occurrence of a negative outcome, '1' if they reported no occurrence and '0' if they did not address the topic. We included the '0' category because negative outcomes might be reported only if they were observed, or alternatively, underreported. Data were gathered from all 192 studies because even those not meeting the criteria for inclusion in the meta-analyses frequently reported deaths, physical harm and nest abandonment. We compiled singly ordered contingency tables for each variable and compared the proportion of studies in each response category for each attachment type with a Kruskal–Wallis test in the program StatXact (Cytel Software Corporation 2004). The null hypothesis of no attachment effect was assessed by estimating exact P-values with a Monte Carlo procedure.

Results

EFFECT OF DEVICES

Overall, birds are significantly negatively affected by devices ($\bar{x} = -0{\cdot}27$, 95% CI = $-0{\cdot}37$ to $-0{\cdot}17$, $n = 84$). Furthermore, we found no evidence that researchers have become better at reducing these effects because the magnitude of effects did not vary with study year ($b \pm \text{SE} = 0{\cdot}003 \pm 0{\cdot}003$, $P = 0{\cdot}26$, $n = 83$). Individual analyses indicated that devices negatively affected every aspect considered except flying ability; 8 of the 12 effects were significant (Table 3). The fail-safe

Table 3. The number of studies (n), estimates of Cohen's d and 95% confidence intervals for each aspect of avian behaviour and ecology

Aspect	n	Cohen's d	95% confidence interval
Nest success	16	−0·33	−0·59 to −0·09
Nesting productivity	14	−0·22	−0·48 to −0·01
Clutch size	14	−0·17	−0·31 to 0·00
Nesting propensity	5	−0·57	−0·81 to −0·30
Nest initiation date	9	−0·12	−0·36 to 0·12
Offspring quality	8	−0·42	−0·95 to 0·02
Body condition	35	−0·38	−0·63 to −0·17
Flying ability	7	0·27	−0·52 to 1·12
Foraging behaviours	38	−0·26	−0·46 to −0·10
Device-induced behaviours	18	−0·37	−0·37 to −0·12
Energetic expenditure	13	−0·96	−1·74 to −0·32
Survival rate	38	−0·18	−0·28 to −0·10

Confidence intervals were obtained by bootstrapping with 999 iterations and are considered significant if not overlapping zero.

value for nesting productivity (9) was smaller than the number of studies included, suggesting that the negative effect could be sensitive to the file-drawer effect. Most effects were 'small', except that birds with transmitters had markedly increased energetic expenditure and were much less likely to nest (Table 3). We detected no difference between foraging behaviours for self versus offspring ($Q_1 = 1{\cdot}23$, $P = 0{\cdot}34$, $n = 38$), indicating that birds with transmitters do not sacrifice self-feeding in favour of current reproduction or offspring feeding in favour of self-preservation.

INFLUENCE OF BIRD ATTRIBUTES

We found little evidence that attributes of the birds influence their response to the device. Birds were similarly affected regardless of age, mode of locomotion and body mass (Table 4). Only sex had some influence, with device-induced behaviours observed more in studies involving both sexes ($\bar{x} = -0{\cdot}83$, 95% CI = −1·08 to −0·38, $n = 4$), than in studies using only females ($\bar{x} = -0{\cdot}18$, 95% CI = −0·39 to 0·06, $n = 9$), only males ($\bar{x} = 0{\cdot}25$, 95% CI = −0·03 to 0·55, $n = 2$) or an undetermined sex ($\bar{x} = -0{\cdot}62$, 95% CI = −3·86 to −0·21, $n = 3$; $P = 0{\cdot}05$; Table 4). If effects differ between the sexes, however, we would have expected studies using both sexes to produce an effect intermediate to those from studies using only males or females. The lack of an ecological explanation for this finding, along with its marginal significance, suggests that gender has little influence on device-induced behaviours.

INFLUENCE OF DEVICE ATTRIBUTES

Method of attachment influenced the degree of effects for both nest success ($P = 0{\cdot}05$) and device-induced behaviours ($P = 0{\cdot}03$; Table 4). When devices were secured with a subcutaneous anchor-shaped wire (i.e. anchored) birds had the lowest nest success ($\bar{x} = -0{\cdot}75$, 95% CI = −1·14 to −0·41, $n = 3$), followed by those with harness attachment ($\bar{x} = -0{\cdot}33$, 95% CI = −0·99 to −0·08, $n = 5$), whereas glued devices caused no decrease in nest success ($\bar{x} = 0{\cdot}21$, 95% CI = −0·08 to 0·55, $n = 4$). However, this influence on nest success could be an artefact of the file-drawer effect because the fail-safe number (12) is equal to the number of studies in the analysis. Birds performed the most device-induced behaviours when wearing breast-mounted devices ($\bar{x} = -1{\cdot}05$, 95% CI = −1·10 to −0·89, $n = 2$) followed by those with devices attached with a harness ($\bar{x} = -0{\cdot}51$, 95% CI = −1·16 to −0·18, $n = 7$), whereas neither glued ($\bar{x} = -0{\cdot}34$, 95% CI = −0·46 to 0·10, $n = 2$) nor implanted devices ($\bar{x} = 0{\cdot}08$, 95% CI = −0·12 to 0·40, $n = 5$) caused an increase in device-induced behaviour. Method of attachment had no influence on the strength of effects for the other aspects analysed in the meta-analyses (Table 4).

Attachment type did not influence the proportion of studies reporting physical harm ($\chi^2 = 12{\cdot}83$, d.f. = 7, $P = 0{\cdot}70$) or nest abandonment ($\chi^2 = 7{\cdot}64$, d.f. = 7, $P = 0{\cdot}35$), but the proportion of studies reporting device-induced mortality

Table 4. The impact of attributes of the birds and devices on each aspect of behaviour and ecology

	Nest success	Nesting productivity	Clutch size	Nesting propensity	Nest initiation date	Offspring quality	Body condition	Flying ability	Foraging behaviours	Device-induced behaviours	Energetic expenditure	Survival rate
Bird attributes												
Sex	1·62 (3, 15)	2·58 (3, 14)	2·92 (2, 14)	–	–	–	1·39 (4, 35)	–	5·24 (4, 38)	8·50*† (4, 18)	0·19 (3, 12)	4·09 (4, 38)
Age	–	–	–	–	–	–	2·75 (3, 35)	–	0·02 (2, 38)	–	2·19 (2, 13)	0·62 (2, 37)
Locomotion	3·66 (3, 15)	0·97 (2, 13)	2·93 (3, 14)	0·50 (2, 5)	–	0·19 (2, 8)	2·83 (4, 35)	0·22 (2, 7)	0·60 (4, 38)	1·37 (4, 18)	3·35 (4, 13)	0·59 (3, 38)
Body mass‡	0·00 ± 0·00 (16)	0·00 ± 0·00 (14)	0·00 ± 0·00 (14)	0·00 ± 0·00 (5)	0·00 ± 0·00 (9)	0·00 ± 0·00 (8)	0·00 ± 0·00 (35)	0·00 ± 0·00 (7)	0·00 ± 0·00 (38)	0·00 ± 0·00 (18)	0·00 ± 0·00 (13)	0·00 ± 0·00 (38)
Device attributes												
Attachment type	8·48* (3, 12)	0·98 (3, 11)	1·19 (3, 11)	–	0·02 (2, 5)	1·01 (2, 5)	1·32 (3, 30)	0·17 (2, 5)	5·98 (5, 33)	9·90*† (4, 16)	3·27 (3, 12)	2·68 (5, 34)
% Body mass	0·07 ± 0·03*† (16)	−0·03 ± 0·06 (14)	0·01 ± 0·05 (14)	−0·08 ± 0·09 (5)	−0·14 ± 0·09* (9)	−0·01 ± 0·21 (8)	0·03 ± 0·03 (35)	0·00 ± 0·00 (7)	0·00 ± 0·03 (38)	−0·07 ± 0·07 (18)	−0·11 ± 0·07 (13)	0·02 ± 0·02*† (38)

The value reported for categorical attributes is the variation in effect size explained by the model (Q), with number of categories and number of studies in parentheses. The value reported for continuous attributes is the slope (b) ± 1 standard error, with number of studies included in parentheses. Aspects without an entry could not be calculated because there were not two or more categories containing two or more studies.

*Results significant ($\alpha < 0{\cdot}05$).

†Rosenthal's fail-safe number is much larger than the number of studies in the analysis.

‡All values for the slope and standard error equal 0·00.

differed among attachment types ($\chi^2 = 29{\cdot}37$, d.f. = 8, $P < 0{\cdot}001$). Mortality was most commonly reported in studies using anchors (100%, $n = 2$), followed by implants (57%, $n = 23$), harnesses (52%, $n = 27$), collars (50%, $n = 6$) and glue (31%, $n = 13$), with no mortality reported in studies using tailmounts (0%, $n = 3$).

The mean per cent body mass of devices from all studies was 2·7% (SD 1·6) and there was no change in the relative size of devices across years ($b \pm SE = -0{\cdot}009 \pm 0{\cdot}023$, $P = 0{\cdot}71$, $n = 82$). The effect of devices did not vary with their per cent body mass for most aspects of behaviour and ecology (Table 4). Birds wearing proportionally heavier devices did initiate nests later than those wearing lighter devices ($P = 0{\cdot}03$; Table 4), although the fail-safe number (0) indicates that this result is tenuous. Surprisingly, birds with proportionally heavier devices actually had higher nest success ($P = 0{\cdot}04$) and survival rates ($P = 0{\cdot}05$; Table 4).

EFFECT OF CAPTURE AND RESTRAINT

Transmitter effects on foraging behaviours were more evident when birds with devices were compared with uncaptured birds ($\bar{x} = -0{\cdot}59$, 95% CI = $-0{\cdot}89$ to $-0{\cdot}30$, $n = 12$) than when compared with procedural controls ($\bar{x} = -0{\cdot}02$, 95% CI = $-0{\cdot}26$ to $0{\cdot}22$, $n = 24$; Table 5), suggesting that birds forage less following capture and restraint, independent of the effect of device attachment. On the other hand, no other aspects of the birds' behaviour or ecology were affected by capture and restraint (Table 5), suggesting that the negative effects described above are primarily due to transmitters.

Discussion

Attaching transmitters and similar devices to birds negatively affected most aspects of their behaviour and ecology to some degree. The most substantial effects were increased energy expenditure and decreased likelihood of nesting, whereas six aspects of ecology and behaviour were affected to a lesser extent and four others were unaffected. Although all observed effects were independent of attributes of the birds, the method of device attachment was important. Nest success and device-induced behaviours differed between attachment types and, although the method of attachment did not affect the frequency of nest abandonment or physical harm, certain attachment methods were more likely to cause death. In particular, anchored and implanted transmitters, which generally require anaesthesia, had the highest reported device-induced mortality rates. Machin & Caulkett (2000) showed that anaesthetizing birds with propofol instead of isoflurane reduced threats to the bird's health and decreased the probability of nest abandonment. Harnesses and collars also had relatively high device-induced mortality rates, sometimes because birds became entangled in vegetation. Researchers can minimize this risk by using adjustable harnesses and collars (Dwyer 1972) to custom fit each bird and by adding a weak link that causes the device to detach if entangled (Karl & Clout 1987). Although glue and tailmount attachments had the lowest reported frequency of mortality, low retention rates of these methods on many species (Woolnough *et al.* 2004) can limit their value.

Despite wide acceptance of the '5% rule', we found little evidence that negative effects increased as transmitters became proportionally heavier. In fact, no aspect of behaviour or ecology was negatively affected independent of the file-drawer effect, and nest success and survival appeared to improve as transmitters became heavier. The increase in nest success cannot be explained by birds with transmitters perceiving their probability of survival to have declined and therefore investing more in current reproduction (*sensu* Trivers 1972) because survival actually increased. Thus, this result appears best interpreted as a statistical artefact. A shortcoming of our analysis is that wide acceptance of the '5% rule' meant that few studies used heavier devices. Only 10% of studies exceeded this recommendation and the heaviest proportional mass used was 10%, limiting the variability available to search for a threshold (whether 5% or higher) above which effects increase dramatically. However, we did have numerous studies exceeding 3% body mass, and found little evidence to suggest that effects intensified above this value. Although adhering to the '3%' or '5% rule' may be reasonable, further research is required to determine a safe maximum proportional mass.

Another limitation of our study is that we were unable to assess aerodynamic effects of transmitters. Proportional surface area may be more important than proportional mass in determining a device's effects, especially for flying and swimming birds that experience drag (Culik, Bannasch, & Wilson 1994). Researchers can minimize drag by reshaping transmitters, modifying antennas and attaching them in the most caudal position (Obrecht, Pennycuick, & Fuller 1988; Bannasch, Wilson, & Culik 1994; Wilson *et al.* 2004).

Studies examining effects of devices on multiple aspects often conclude that some aspects are affected while others are not. This could result from relationships that exist between

Table 5. The effect of capture and restraint on each aspect of behaviour or ecology, as calculated by contrasting studies comparing birds with devices with uncaptured birds with those comparing with procedural controls

Aspect	n	Q	P
Nest success	16	0·27	0·62
Nesting productivity	14	0·20	0·72
Clutch size	14	0·13	0·79
Nesting propensity	–	–	–
Nest initiation date	9	0·16	0·76
Offspring quality	8	0·35	0·57
Body condition	35	2·78	0·13
Flying ability	–	–	–
Foraging behaviours	36	10·69	0·002
Device-induced behaviours	18	0·03	0·89
Energetic expenditure	13	0·42	0·56
Survival rate	38	0·08	0·80

The values reported are sample sizes (n), the variation in effect sizes explained by the model (Q) and randomized probability values (P). Aspects without an entry could not be calculated because there were less than two studies from one of the categories.

aspects, as illustrated when birds with devices maintain their normal flying ability, foraging behaviours or reproduction at the expense of energy consumption (e.g. Gales, Williams, & Ritz 1990; Godfrey, Bryant, & Williams 2003). Discrepancies frequently exist between studies as well, partially as a consequence of differing sample sizes (as discussed previously). It is also likely that discrepancies are generated from interactions between the environment and device effects, making it possible for environmental conditions to mask effects if the disparity between birds with and without devices is the greatest when resources are at intermediate levels (Pietz *et al.* 1993).

Our results have implications for attaching devices to all birds but are particularly important when studying sensitive or rare birds. Although many aspects of behaviour and ecology we investigated were minimally affected, their cumulative impact could be substantial. For example, reductions in nest success, nesting productivity, nesting propensity and foraging behaviour will decrease reproductive potential. Similarly, reduced foraging, body condition and flying ability along with increased device-induced behaviours and energetic expenditure are likely to increase mortality of birds with transmitters beyond the direct mortality effects reported. Transmitters could also indirectly reduce the fitness of unmarked mates if they compensate for decreased parental investment by the bird with the transmitter (Paredes, Jones, & Boness 2005). As we found little effect of capture and restraint, traditional mark–recapture methods are unlikely to have negative effects. When designing studies, ecologists need to balance the benefits of data acquired using transmitters and other devices against potential harm to the birds and biases in the data we have identified here.

Novice researchers considering the use of transmitters or other devices should use resources available to anticipate and minimize deleterious effects. Good starting points for inquiry into the topic are the previously mentioned reviews, the compilation of literature for this study (see Appendix S1), a recent article proposing guidelines for instrumentation (Casper 2009), Kenward's (2001) radio tagging manual and the guidelines published by the Ornithological Council (Gaunt & Oring 1999). Programs such as Flight 1.11 (Pennycuick 2002) permit theoretical examination of the impact a device will have given certain parameters (Pennycuick 1989, 2008). By varying these parameters (such as mass), researchers are able to optimize the costs and benefits of their devices when designing their study.

Transmitters are likely to have similar effects on other small, volant animals (e.g. bats) and a similar meta-analysis would be useful in determining the nature of those effects. Whenever possible, researchers using transmitters and other devices should report the information necessary for their study to be included in such a future meta-analysis.

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