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PERSPECTIVE

Externally attached biologgers cause compensatory body mass loss in birds

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Abstract

1. Animal-borne logging devices are now commonly used to record and monitor the movements, physiology and behaviours of free-living animals. It is imperative that the impacts these devices have on the animals themselves are minimised.
2. One important consideration is the interaction between the body mass of the animal and the mass of the device.
3. Using captive homing pigeons, we demonstrate that birds lose the equivalent amount of body mass compared to that of the logging device attached. With our experiments, we calculated that the compensatory mass loss because of the logging device equates to a total loss of 1,140 kJ of energy to the bird, over the 25-day period. This equates to 32% per day of their total daily energy budget.
4. We suggest that practitioners of biologging give due consideration to the possibility of a device-induced decrease in body mass when making decisions regarding device size, and when considering the period of the time of the year at which devices are attached.
5. It appears, based on the results of the present study, that device attachment is likely to be most disruptive during periods of regulated mass change, especially when periods of mass gain precede periods in which stored energy reserves are extensively utilised.
6. These findings have significant consequences for anyone using biologging technology on both wild and captive volant animals. Further studies utilising captive birds are now needed to fully understand how context- and species-dependent physiological responses to externally attached devices are.

KEYWORDS

biologging, GPS, homing pigeon, logger effects

1 | INTRODUCTION

Devices that measure the global positioning, acceleration, heart rate and body temperature of animals have uncovered remarkable feats concerning animal movement ecology that were not previously possible to record before the invention of such technology (Wilmers et al., 2015). These miniaturised devices have revealed incredible animal migratory feats (Bishop et al., 2015; Klaassen et al., 2011), demonstrated physiological and aerodynamic energy-saving mechanisms (Handrich et al., 1997; Portugal et al., 2014) and monitored the movements of critically endangered species (Block et al., 2011; Sims et al., 2008). The number of published studies deploying biologging devices now number in the thousands (Bodey et al., 2017; Williams et al., 2020; Yoda, 2019) covering a multitude of animal groups including birds (e.g. Voelkl et al., 2015), mammals (e.g. Curtin et al., 2018), amphibians (e.g. Halsey & White, 2010), reptiles (e.g.

Gutowsky et al., 2016), fish (e.g. Kawabata et al., 2014) and invertebrates (see Batsleer et al., 2020).

As the deployment of biologging technology has become more commonplace, so too has an awareness of the ethical considerations involved with tagging animals (Williams et al., 2020). A combination of experimental (Bowlin et al., 2010; McIntyre, 2014; Paredes et al., 2005; Tomotani et al., 2019; Vandenabeele et al., 2012, 2015) and meta-analytical approaches (Barron et al., 2010; Bodey et al., 2017; Portugal & White, 2018; White et al., 2013) has demonstrated the deleterious impacts that externally attached devices can have on traits such as breeding productivity, offspring quality, energy expenditure and survival rate. These impacts have been particularly well documented in birds, where the effects of logging devices can be intensified due to the increased mass and higher drag created by the device during flight and/or diving (Bowlin et al., 2010; Paredes et al., 2005; Vandenabeele et al., 2014, but see also Authier et al., 2013; Brlik et al., 2020; Lamb et al., 2017). Empirical studies have demonstrated, for example, that upon the application of biologgers, birds flying in a wind tunnel experience increased costs of transport (Schmidt-Wellenburg et al., 2008), while diving cormorants experienced an increase in power requirements during diving (Vandenabeele et al., 2012, 2015). While such studies have been pivotal in quantifying potential issues accompanying logger deployments, it has been more difficult to tease apart the relative contributions of the increased drag and additional mass, or to understand the regulatory responses employed by instrumented birds with respect to a sudden increase in mass. This lack of knowledge regarding body mass regulation post instrumentation is largely due to the nature of biologging studies of wild birds. Once the animal is fitted with the biologging device the individual is released, and as consequence, immediate monitoring of parameters such as body mass is either not feasible or is likely to cause further sustained stress. Causing extra stress through subsequent handling of the birds to regularly monitor body mass will likely exacerbate the negative impact of the device itself.

Body mass is an important component of the cost of flight in birds, both at the intraspecific and interspecific levels (Tobalske et al., 2003) while also impacting the energetic costs and speed compromises associated with flying with other individuals (Sankey et al., 2019). Body mass not only impacts the energetic costs of flight, but can also dictate breeding success (Bryant, 1988; Croll et al., 1991), flight performance (Blem, 1976; Metcalfe & Ure, 1995), over-winter survival (Rogers, 1987) and numerous physiological processes (Hiebert, 1991; Portugal et al., 2011). Moreover, mass can determine, or interact with, behavioural components such as dominance (e.g. French, 2005; Portugal et al., 2017), personality (e.g. Bouwhuis et al., 2013; Ost et al., 2015), leadership (e.g. Pettit et al., 2016) and group dynamics (e.g. Funghi et al., 2015; Sankey et al., 2019). For many bird species, body mass is highly dynamic, varying substantially throughout the annual cycle in response to key life-history events such as breeding (Bryant, 1988; Croll et al., 1991), moult (van der Jeugd et al., 2003; Portugal et al., 2007) and migration (Blem, 1976; Johnston, 1966). Thus, mass is a tightly regulated physiological factor, both at a daily (e.g. Rogers, 1987) and annual (e.g. Dittami & Gwinner, 1985) scale, with significant implications for overall survival if the optimal mass is not achieved and maintained (Piersma, 2002). Therefore, the addition of mass in the form of a biologger, even when keeping within the generally agreed 5% limit (Barron et al., 2010), is likely to have implications for body mass regulation in birds. To understand whether birds adapt their body mass—both over a short- and long-term time scale—in response to the addition of biologgers, we studied a captive flock of homing pigeons *Columba livia*.

2 | MATERIALS AND METHODS

2.1 | Birds and housing

A group of 18 homing pigeons (here in referred to as pigeons) were housed at Royal Holloway University of London (Egham, UK). All birds were a minimum of 15 months old and had lived together since hatching. The sex of the birds was a 55/45% split (males/females; mean body mass at start of the study, 590 ± 75.6 (*SD*) g). Birds were kept in a pigeon loft (dimensions 3.6 m (long), 2.4 m (wide)) with ad libitum access to food and water (see Portugal, Ricketts, et al., 2017; Portugal, Sivess, et al., 2017 for further husbandry details). Wooden perches ($n = 20$) were attached to the sides of the loft, in arrangements of six perches in horizontal rows at three heights (1, 1.30 and 1.60 m), plus two additional single perches (1.30 m). All procedures described were conducted in accordance and with approval of the appropriate national regulations and approved by Royal Holloway University of London ethics board. This work was deemed as exempt from requiring a Home Office Licence.

2.2 | Body mass measurements and artificial mass attachment

Birds were weighed twice weekly for 4 weeks, by being placed in a cotton bag and weighed using digital scales (0.1 g accuracy, Scales and Balances, Thetford, UK), before each pigeon was fitted with artificial mass in week 5. The artificial devices mimicked the size and mass of typical logging devices (30 g, 3.7 × 2.4 × 0.8 cm), both those that are generally used for studies with birds and those which have been used previously with homing pigeons (Pettit et al., 2016; Taylor et al., 2019; Usherwood et al., 2011).

The artificial mass was attached to the back of the pigeons using Velcro strips and epoxy glue (total package mass 30–31 g, 5% of the mean body mass of the pigeon group at start of the study; see Sankey and Portugal (2019) and Sankey et al. (2021) for further details on logger attachment to the pigeons). Birds were then weighed twice weekly for the next 18 days (see Figure 1). On day 18, the artificial loggers were removed, and birds were again weighed twice weekly for a 4-week period. Following the 4-week period, 10 birds were randomly selected to have the artificial loggers reattached, with the remaining 8 birds having no devices attached. All birds were then weighed twice weekly for further 21 days (Figure 1).

2.3 | Statistical analysis

Data were analysed using linear mixed models implemented in the LME4 (Bates et al., 2015) package of R v3.2.2 (R Core Team, 2016). The significance of random effects in mixed models was determined using likelihood ratio tests, and the significance of fixed effects in mixed models was determined using t tests with Satterthwaite approximations to degrees of freedom implemented in the LMERTEST package (Kuznetsova et al., 2016). The model included a random intercept for individual identity and a random slope for the effect of time, which varied among measurement blocks. Data for time and mass were mean centred and scaled to unit variance prior to analysis. Full statistical findings are shown in Supporting Information: Statistical Outputs.

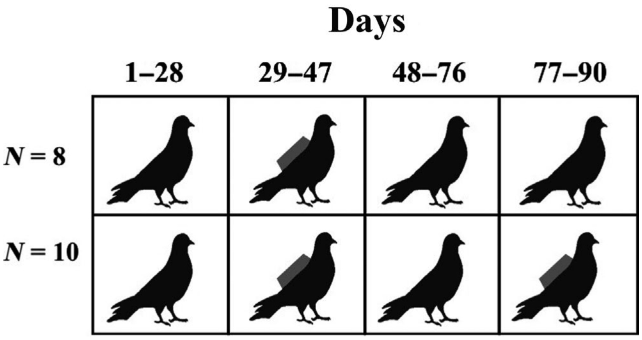

FIGURE 1 Experimental design. 18 homing pigeons were used to determine the effects of artificial mass attachment (see Section 2). The two panels show the different treatments the birds were exposed to. All birds, however, were kept together at the time. The pigeons and loggers are not to scale and are purely for diagrammatic representation

3 | RESULTS AND DISCUSSION

Upon attachment of the artificial mass, all 18 birds lost body mass over the 18-day period (Figure 2a, mean end body mass 560 ± 76.4 (*SD*) g, 5.1 ± % decrease). On day 18, the artificial loggers were removed, and birds were again weighed twice weekly for a 4-week period. All birds gained mass during this period, returning to the body mass measured prior to the attachment of the artificial loggers (591 ± 75.5 g (*SD*); Figure 2). The total amount of body mass the pigeons lost while the artificial biologger was attached matched that of the mass of the artificial device, suggesting the birds were losing body mass in a compensatory fashion. Short flights inside the loft would have provided ample opportunity for the pigeons to experience the instantaneous mass gain, and it is possible the body masses of the birds were responding in a compensatory fashion. The body mass of the birds at the end of the first deployment of artificial biologgers is strongly related to their starting mass ($r > 0.99$, $t_{16} = 56.3$, $p < 0.001$), but the mass that the birds lose is independent of their starting mass ($r = -0.16$, $t_{16} = -0.64$, $p = 0.52$). Moreover, there is no difference in body mass between the last two measurement days of the first deployment on all 18 birds (day 45: mass = 561.2 ± 76.6 g, day 49: mass = 560.6 ± 76.4 g, paired $t_{17} = 22.6$, $p = 0.43$), suggesting the body mass of the birds had stabilised. By the last day of the

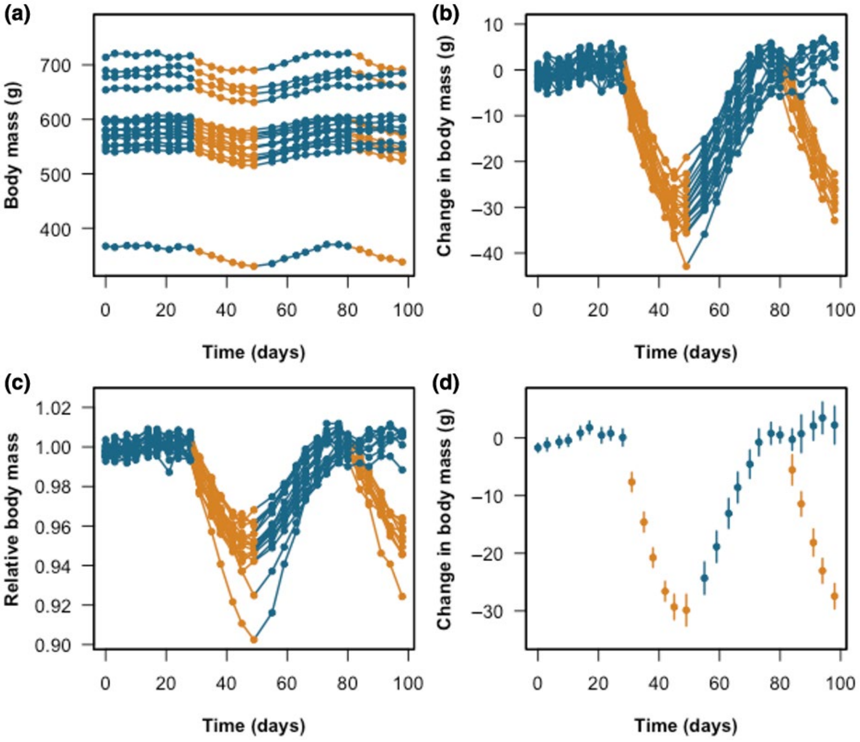

FIGURE 2 The effect of logger deployments on birds. The effect of artificial mass addition on body mass for 18 pigeons (a). Data in (b) are the same data expressed as differences from mean pre-treatment body mass. Data in (c) are the same data expressed relative to mean pre-treatment body mass, and data in (d) are treatments means (± *SEM*) of the data in (b). In all panels, birds with artificial weights added are shown in orange

first deployment of artificial biologgers on all 18 birds, the pigeons had lost an average of 29.9 ± 5.5 g (95% CI: 27.1–32.6 g), which is not significantly different from the mass of the artificial device (30 g; $t_{17} = -0.10$, $p = 0.92$). It is likely the majority of the body mass loss is fat, as the catabolism of fat stores typically account for the majority of initial body mass loss in birds (Blem, 1990). The yield from the complete oxidation of fatty acids is approximately 9 kcal/g (38 kJ/g), so a 30 g reduction in fat content is the equivalent to losing 1,140 kJ in available energy stores (Blem, 1976, 1990). Based on a metabolic rate of 5 ml/min of oxygen (taken from Rashotte et al., 1996) for a resting pigeon, we can calculate that this equates to 0.08 ml O_2 per second, equivalent to 1.675 J/s, based on a standard conversion of 20.1 J/ml O_2 (Taylor et al., 1982), thus 144,720 J/day (144.72 kJ). The total estimate of energy lost through compensatory body mass adjustment is estimated at 1,140 kJ over an approximate 25-day period. Based on the assumption of a relatively constant rate of body mass loss (see Figure 2), this equates to 45.6 kJ/day potential loss through fat catabolism. If a pigeon's total daily energy requirements are 144.72 kJ, a daily loss of 45.6 kJ through mass loss equates to approximately 32% of their total daily energy budget.

To ensure there was not an alternate explanation for the recorded body mass loss in response to artificial logger attachment, 10 birds were randomly selected to have the artificial loggers reattached at the end of the 4-week period, with the remaining eight birds having no devices attached. After 14 days, the 10 selected birds had lost body mass (mean 555.9 ± 27.9 g (*SD*)), whereas the body mass of the remaining eight birds without artificial loggers varied by less than 1% (Figure 2). Further analysis demonstrated that body mass varied significantly among individuals ($\chi^2_1 = 2{,}883.7$, $p < 0.0001$, Figure 2) and the relationship between body mass and measurement day varied among measurement blocks ($\chi^2_1 = 331.8$, $p < 0.0001$; here, measurement blocks are the pre-deployment period, the first deployment period, the recovery period and the second deployment period). In a model including a random intercept for individual identify and a random slope that varied among measurement blocks, there was a significant interaction between measurement day and mass ($t_{250} = -13.1$, $p < 0.001$) indicating that rates of mass change differed among birds fitted with a device and those not fitted with a device. Birds either maintained or gained mass when not fitted with a device, and lost mass when fitted with a device (Figure 2; see Supporting Information: Statistical Outputs, for full details).

Body mass in the pigeons showed a dynamic response to the addition of the artificial mass. This is despite the birds being limited to a loft for the duration of the study, and only able to undertake very short flights; a maximum of eight wingbeats were possible before landing or turning. The implications on flight itself of logger attachments are less clear, as evidence for the effect of additional mass on flight performance in birds is not ubiquitous, and is not just dependent on total mass added but positioning of the logger itself, and the total frontal area (Pennycuick et al., 2012). Nevertheless, even if birds are able to compensate for the addition of mass through an alteration of flight kinematics, for example, the amount of fuel available to them via their fat stores is still reduced relative to that available to birds without attached devices. Such a reduction in energy stores is likely to result in decreased flight durations and increased requirements for stop overs and refuelling. Previously, it has been demonstrated that even on an intraspecific level, variations in fat storage reflect differences in migration strategy and duration, and whether migratory trajectories are taking place predominately over land or sea (e.g. Åkesson et al., 1992). Fat storage is, therefore, fine-tuned to ensure a successful migration, and the reduction of body fat stores in response to the addition of a biologging device is likely to have deleterious effects on survival rates (Biebach et al., 1986; Newton, 2006). Biebach et al. (1986), for example, demonstrated that small intraspecific differences in body mass upon arrival at key stop over sites prior to- and within the Sahara Desert had significant implications for migration strategies in three species of passerine bird. Individuals that were, on average, 10% lighter spent up to 3 weeks at stop-over sites, in comparison to just one day for those individuals that were heavier. Moreover, only 60% of the individuals who were lighter had sufficient mass to have completed the migration, if they had not been able to stop and re-fuel. It is likely, therefore, that a 5% reduction in body mass for migratory passerines will have an impact on migration range, and stop-over frequency. The impact of compensatory body mass loss is likely to differ depending on the migration strategy of the species, particularly in passerines, and what standard body mass dynamics they exhibit prior to and during migration (Yohannes et al., 2009).

Based on our findings, we suggest the following recommendations for the external attachment of biologging devices, in addition to those typically detailed with regard to both mass and placement of the device.

3.1 | Birds on the borderline

Portugal and White (2018) detailed how the miniaturisation of biologging devices was not helping alleviate the often cited 5% body mass. We suggested that rather than the onset of smaller and lighter biologging technology driving the study of smaller animal species, it would be better to focus on constructing a more robust approach whereby the maximum permissible device mass is more clearly defined, and less commonly exceeded. Our findings in the present study suggest, even more strongly, that (wild) species who are close to this 5% rule should not have biologging devices attached. As of 2018, numerous studies have breached the 5% rule, based on species-level body mass values (Portugal & White, 2018). Individuals within a species will of course be lighter than the published mean body mass, meaning that those individuals in ‘borderline species’ will already be experiencing a >5% addition to their mass, with the deployment of a logger. If these lighter individuals and/or lighter species, then lose a mass of fat equal to the mass of the logger in response to the artificial mass of the biologging attachment, this will dramatically drop their mass well below the recommended 5% level. Thus, we recommend that the 5% rule (although see Brlik et al., 2020) be calculated assuming that, following device attachment, an individual bird will decrease in body mass by an amount equal to the mass of the attached device. Bodey et al. (2017) demonstrated, through meta-analytical approaches, that a logger had to be less than 1% of the body mass of the species to truly detect no deleterious impacts of the device. The authors clarified, however, that a 1% rule was not being promoted, but rather a trade-off recognised between the value of the data gathered and the possible negative effects caused. Other authors have advocated for a possible 3% approach, as a more conservative approach to the more established 5% rule (Phillips et al., 2004; Vandenabeele et al., 2012). A 3% threshold could be particularly helpful for birds that are considered borderline, and based on our findings, may leave more energy for migration and/or moulting (however, see caveats for discussion on the use of arbitrary threshold values).

3.2 | Migratory birds

Migratory birds undergo intense periods of hyperphagia prior to departure, with many species doubling their body mass during this time (Eikenaar, 2017; Guillemette et al., 2012; Ramenofsky, 1990). The function of hyperphagia is to ensure sufficient stores to fuel migration, particularly for species that are undertaking water or desert crossings, where refuelling and stops will not be possible (Barlein, 1985; Goymann et al., 2010; Scott et al., 1994; Weber & Houston, 1997). Body mass dynamics in general are known to have significant impacts on the energetic costs of flight (Pennycuick, 1975); migratory birds in particular have to trade-off the necessary fat storage requirements for fuelling migration against the heightened cost of transporting the increased mass. Body mass and, in particular, body composition, are also known to significantly impact migration strategies (see above), and the frequency of migratory stop overs required (Biebach et al., 1986; Yohannes et al., 2009). Such fine-scale temporal body mass dynamics at these typically two critical junctions of the year (spring and autumn) likely mean that the addition of an artificial mass via a biologger will impact both pre-migratory fattening, and migratory range. The initial deployment of biologgers should, therefore, avoid pre-migratory periods. This should assist in alleviating any potential issues surrounding pre-migratory body mass dynamics. This is particularly pertinent for species which are close to the 5% traditional rule already.

3.3 | Birds which undergo simultaneous flight feather moult

For many groups of birds, moulting their flight feathers involves simultaneously dropping all their feathers at once and entering a flightless period of about 4–6 weeks (Hohman et al., 1992). This moulting strategy is seen in bird groups which can still get to safety while flightless, and access a food source (e.g. Gaviidae, Podicipedidae, Alcidae, Anatidae). Such an approach to moulting is typically associated with aquatic species, although females of the Bucerotidae are an exception, as safety is provided by being holed into a tree cavity during incubation, with food provided by the male (Stanback et al., 2018). For many species, simultaneous flight moult is energetically demanding (Guillemette et al., 2007; Guozhen & Hongfa, 1986; Portugal et al., 2007) and significant decreases in body mass are observed (e.g. Fox et al., 1998). This body mass loss has been interpreted as a response to the increase in metabolic rate (Dolnik & Gavrilov, 1979), the reduced foraging time due to the increased risk of being predated upon (Fox & Kahlert, 1999) and an adaptive strategy to allow the regaining of flight quicker due to the lower body mass (DuBowy, 1985; Geldenhuys, 1983; Sjöberg, 1986). It is evident that simultaneous flight feather moult involves finely tuned temporal dynamics in body mass, and as such, the addition of an externally attached logger at this time may result in a compensatory body mass loss in addition to the mass loss typically observed. Many species of Anatidae, for example, deposit fat prior to flight feather moult (Hohman et al., 1992; Sjöberg, 1986). In captive birds, it has been demonstrated that the daily percentage of time spent resting was positively correlated with initial body mass at the start of wing moult (Portugal et al., 2011), and many species increase mass, in the form of increased fat deposition, prior to moult (Hohman et al., 1992). It is assumed this storage of energy before the start of wing moult helps birds to reduce exposure to the dangers of predation by being able to reduce foraging. Therefore, compensatory body mass adjustments via fat loss could have significant implications for the associated foraging and moulting strategies for species which undergo a simultaneous flight feather moult. The initial attachment of externally attached loggers during simultaneous flight feather moult is therefore not recommended.

3.4 | 'Capital' breeding birds

Birds which are characterised as capital breeders are those which use energy stores acquired prior to reproduction to breed (Jonsson, 1997). While the precise definition of capital breeding has been refined and modified through time (Meijer & Drent, 1999), overall it is agreed that such a breeding approach involves the accumulation of fat stores and then the subsequent use of them to produce eggs and, for some, provision the young. Often the acquisition of the fat stores is undertaken in a different locality to the reproductive event, such as in many Arctic breeding species of Anatidae. Many species of the Anatidae use late-winter and spring stop-over sites to deposit fat reserves which are then used for the production of the eggs upon arrival at the breeding grounds, often when available food is limited due to the snow not yet retreating. Such fat stores are fine-tuned to trade off future reproductive effort against the energy required for maintaining the fat stores and the associated locomotory cost of transporting this increased mass (e.g. Alexander, 2005). The reliance on acquired fat stores for breeding can be as much as 100% (e.g. common eider ducks, *Somateria mollissima*; Guillemette & Ouellet, 2005), and substantial body mass gains are observed during the pre-reproductive fattening period ahead of incubation (Guillemette et al., 2012). These finely tuned temporal body mass dynamics are similar to those experienced by species that undergo a simultaneous flight feather moult (see above), and suggests that capital breeding birds should not have externally attached loggers deployed during the pre-reproductive fattening period, or at spring stop-over sites for those species that are migratory.

3.5 | Caveats

The present study was conducted on a domesticated species which exhibit natural cyclic changes in body mass throughout the year (Sargisson et al., 2007; see discussion below). Different species will vary in the extent of their natural changes in body mass throughout the year, and their propensity for losing mass at all. Thus, we are not suggesting that our study should present a new arbitrary rule by which biologging devices should adhere to prior to deployment, but rather, another factor to be taken into consideration when designing biologging experiments. Indeed, an ideal scenario would be to move away from arbitrary percentage rules and to adopt a more nuanced holistic approach to the ethics surrounding biologger deployment.

Any deleterious effects of biologgers are likely to be linked to specific life-history traits of a species. Moving forward, a rubric design to determine the appropriate biologger mass would be a more appropriate, species specific, approach. Such a rubric can take into account life-history factors which are known to influence the extent to which biologgers impact a species. For example, Bodey et al. (2017) highlighted migration distance and flight style as life-history traits which, together with the duration of deployment, determined the degree of negative effects a logger can produce. For example, survival and reproduction were negatively affected to a greater extent by logger attachment in birds which exhibit greater flapping flight, than soaring or flightless species (Bodey et al., 2017; Watanabe & Nathan, 2016). Thus, a rubric approach could integrate other facets to be considered include hunting or foraging style, reliance on rapid acceleration, longevity and typical lifetime recruitment, and general activity levels. One issue being, however, that often the purpose of the logger deployment itself is to determine and investigate these traits.

Given the extent to which body mass can change throughout an annual cycle in many bird species, it is feasible that the response, or the degree of response, in body mass to the attachment of a logger may be season dependent (e.g. Hiebert, 1991). The current study was conducted from January through to April, a period of the year typically associated with stable body mass in captive homing pigeons (Sargisson et al., 2007), meaning that this is a period within the year where the birds are not typically experiencing changes in body mass. Therefore, a sudden increase in mass above what had plateaued and could be potentially thought of as optimal on an individual basis may be responsible for the observed compensation in body mass, through loss of mass. Further study is required in a greater range of species encompassing a mix of life-history traits (e.g. short- and long-distance migrants, sedentary species) to ascertain if compensatory body mass loss is ubiquitous in bird species. In particular, more studies should utilise captive birds under tightly controlled experimental conditions to further understand the mechanisms behind any body mass adjustments in response to externally attached devices, and most importantly, how context-dependent and species-dependent changes are. While this study and associated recommendations focus on birds, it is highly likely similar implications need to be considered for other flying animals which are studied through the use of biologging technology, such as bats and insects.

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CONFLICT OF INTEREST

We have no competing interests.

AUTHORS' CONTRIBUTIONS

Conceptualisation and methodology, S.J.P. and C.R.W.; data collection, S.J.P.; formal analysis, C.R.W.; resources, S.J.P. and C.R.W.; writing, S.J.P. with input from C.R.W.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All data are available visa Dryad Digital Repository https://doi.org/10.5061/dryad.6q573n606 (Portugal & White, 2021).

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