

## **COMMENTARY**

### **Externally attached bloggers cause compensatory body mass loss in birds**

**Steven J. Portugal<sup>1\*</sup> and Craig R. White<sup>2</sup>**

<sup>1</sup>Department of Biological Sciences, School of Life and Environmental Sciences, Royal Holloway University of London, Egham, TW20 0EX, UK

<sup>2</sup>School of Biological Sciences, Monash University, Clayton, Melbourne, Vic., Australia

10

#### **Correspondence**

\*Steven J. Portugal

Email: Steve.Portugal@rhul.ac.uk

20

## 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 is 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 1,140  
40 kJ of energy lost to the bird, equivalent to 32% 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.

## 50 KEY WORDS

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].

60 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. 2011]. The number of published studies deploying biologging devices now number in the thousands [Bodey et al. 2017; Yoda 2019; Williams et al. 2020;] 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 and White 2010], reptiles [e.g. Gutowsky et al. 2017], fish [e.g. Kawabata et al. 2014] and invertebrates [see Batsleer et al. 2020].

70 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 [Paredes et al. 2005; Bowlin et al. 2010; Vandenabeele et al 2012; McIntyre 2014; Vandenabeele et al. 2015; Tomotani et al. 2018] and meta-analytical approaches [Barron et al. 2010; White et al. 2013; Bodey et al. 2017; Portugal and White, 2018] have 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 [Paredes et al. 2005; Bowlin et al. 2010; Vandenabeele et al. 2014, but see also Authier et al. 2013; Brlík et al. 2019; Lamb et al. 2017]. Empirical studies have demonstrated, for example, that upon the  
80 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; Vandenabeele et al. 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  
90 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 intra- and inter-specific level [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 dictate breeding success [Bryant 1988; Croll et al. 1991], flight performance [Blem 1976; Metcalfe and Ure 1995], over-winter survival [Rogers 1987], and numerous physiological processes [Hiebert 1991; Portugal et al. 2011].  
100 Moreover, mass can determine, or interact with, behavioural components such as dominance [e.g., French 2005; Portugal et al. 2017a], personality [e.g., Bouwhuis et al. 2014; Ost et al. 2015], leadership [e.g., Pettit et al. 2016] and group dynamics [e.g., Funghi et al. 2014; 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 [Johnston 1966; Blem 1976]. Thus, mass is a tightly regulated physiological factor, both at a daily [e.g., Rogers 1987] and annual [e.g., Dittami and 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 biollogger, even when keeping within  
110 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 biolloggers, we studied a captive flock of homing pigeons (*Columba livia*).

## 2| MATERIALS AND METHODS

### *Birds and housing*

A group of 18 homing pigeons (hereonin 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  
120 mass at start of the study,  $590 \pm 75.6$  (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 et al., 2017a; Portugal et al. 2017b 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 m, 1.30 m, 1.60 m), plus two additional single perches (1.30 m).

### *Body mass measurements and artificial mass attachment*

Birds were weighed twice weekly for four 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 five. The artificial devices mimicked the size and mass  
130 of typical logging devices (30 g, 3.7 x 2.4 x 0.8 cm), both those that are generally used for studies with birds and those which have been used previously with homing pigeons [Usherwood et al. 2014; Pettit et al. 2016; Taylor et al. 2019].

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 four-week period. Following the four-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 a further 21 days (Figure 1).

### *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 can found in Supporting Information: Statistical Outputs.

## **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  $560 \pm 76.4$  (*SD*) g,  $5.1 \pm$  % decrease). On day 18 the artificial loggers were removed, and birds were again weighed twice weekly for a four-week period. All birds gained mass during this period, returning to the body mass measured prior to the attachment of the artificial

160 loggers ( $591 \pm 75.5$  g (*SD*)) (Figure 2). The total amount of body mass the pigeons lost while the artificial bio-logger 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 =  $561.2 \pm 76.6$  g, day 49: mass =  $560.6 \pm 76.4$  g, paired  $t_{17} = 22.6$ ,  $P = 0.43$ ), suggesting the body  
170 mass of the birds had stabilized. By the last day of the first deployment of artificial biologgers on all 18 birds, the pigeons had lost an average of  $29.9 \pm 5.5$  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 per  $\text{g}^{-1}$  (38 kJ  $\text{g}^{-1}$ ), so a 30 g reduction in fat content is the equivalent to losing 1,140 kJ in available energy stores [Blem 1976; Blem 1990]. Based on a metabolic rate of 5 ml/min of oxygen (taken from Rashotte et al. (1995)) for a resting pigeon, we can calculate that this equates to 0.08 ml  $\text{O}_2$  per second, equivalent to 1.675 J/sec, based on a standard conversion of 20.1 J/ml  $\text{O}_2$  [Taylor et al. 1982], thus, 144,720 J/day (144.72 kJ). The total  
180 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 four-week period, with the remaining 8 birds having no devices attached. After 14 days, the 10 selected birds had lost body mass (mean  $555.9 \pm 27.9$  g (*SD*)),  
190 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 ( $\chi^2_1 = 2883.7$ ,  $P < 0.0001$ , Figure 2) and the relationship between body mass and measurement day varied among measurement blocks ( $\chi^2_2 = 331.8$ ,  $P < 0.0001$ ; 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  
200 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 8 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  
210 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  
220 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 three 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].

230

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

**Birds on the borderline:** Portugal and White [2018] detailed how the miniaturization 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 and 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 greater than 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 [Brlík 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 [Philips 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).

**Migratory birds:** Migratory birds undergo intense periods of hyperphagia prior to departure, with many species doubling their body mass during this time [Ramenofsky 1990; Guillemette et al. 2012; Eikenaar 2017]. 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; Scott et al. 1994; Weber and Houston 1997; Goymann et al. 2010]. 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 bilogger will impact both pre-migratory fattening, and migratory range. The initial deployment of loggers 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.

**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 [Guozhen and Hongfa 1986; Portugal et al. 2007; Guillemette 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 and Gavrilov 1979], the reduced foraging time due to the increased risk of being predated upon [Fox and Kahlert 1998],

290 and an adaptive strategy to allow the regaining of flight quicker due to the lower body mass [Geldenhuys, 1983; DuBow, 1985; 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 [Sjöberg, 1986; Hohman et al. 2002]. 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  
300 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.

**‘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 and 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  
310 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% (for example common eider ducks, *Somateria mollissima*) [Guillemette and 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.

**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 [Watanabe & ; Bodey et al. 2017]. 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.

350 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. While this study and associated recommendations focus on birds, it is highly likely similar implications need to be considered  
360 for other flying animals which are studied through the use of biologging technology, such as bats and insects.

## 370 **ETHICS**

All procedures described were conducted in accordance and with approval of the appropriate national regulations and Institutional ethical permissions.

## **CONFLICT OF INTEREST**

We have no competing interests.

## **SUPPLEMENTAL INFORMATION**

Raw data will be available as electronic supplementary file.

## **AUTHORS' CONTRIBUTIONS**

Conceptualization 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.

## 380 **ACKNOWLEDGEMENTS**

This work was supported by a Royal Society Grant to S.J.P. (R10952).

## **ORCID**

Steven J. Portugal <http://orcid.org/0000-0002-2438-2352>

Craig R White <http://orcid.org/0000-0002-0200-2187>

## **REFERENCES**

390 Åkesson S, Karlsson L, Pettersson J. and Wlinder G. (1992). Body composition and migration strategies: a comparison between robins from two stop-over sites in Sweden. *Vogelwarte*. 36, 188-195.

Alexander RM. (2005). Models and scaling of energy costs for locomotion. *J. Exp. Biol.* 208, 1645-1652.

Authier M, Peron C, Mante A, Vidal P. and Gremillet D. (2013). Designing observational biologging studies to assess the causal effect of instrumentation. *Meth. Ecol. Evol.* 4, 802-810.

- Barlein F. (1985). Body weights and fat deposition of Palearctic passerine migrants in the central Sahara. *Oecologia*. 66, 141-146.
- Barron DG, Brawn JD and Weatherheard PJ. (2010). Meta-analysis of transmitter effects on avian behaviour and ecology. *Methods Ecol. Evol.* 1, 180 – 187.
- 400 Bates DM, Mächler B. Bolker, and Walker S. (2015). Fitting linear mixed-effects models using lme4. *J. Statistical Software* 67, 1-48.
- Batsleer F, Bonte D, Dekeukeleire D, Gooseens S, Poelmans W, Van der Cruyssen E, Maes D. and Vandegehuchte ML. (2020). The neglected impacts of tracking devices on terrestrial arthropods. *Methods Ecol. Evol.* 11, 350-361.
- Biebach HB, Friedrich W. and Heine G. (1986). Interaction of body mass, fat, foraging and stopover period in trans-sahara migrating passerine birds. *Oecologia*. 69, 370-379.
- Bishop CM, Spivey RJ, Hawkes LA, Bathbayar N, Chua B, Frappell PB, Milsom WK, Nastagdorj T, Hewman SH, Scott GR, Takekawa JY, Wikelski M. and Butler PJ. (2015). The roller coaster flight strategy of bar-headed geese conserves energy during Himalayan migrations. *Science*. 347, 410 250 – 254.
- Blem CR. (1976). Patterns of Lipid Storage and Utilization in Birds. *Amer. Zool.* 16, 671-684.
- Blem CR. (1990). Avian energy storage. *Curr. Ornithol.* 7, 59–113.
- Block *et al.* (2011). Tracking apex marine predator movements in a dynamic ocean. *Nature*. 475, 86 – 90.
- Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, Votier SC, and Bearhop S. (2017). A phylogenetically controlled meta-analysis of biologging device effects on birds: Deleterious effects and a call for more standardized reporting of study data. *Meth. Ecol. Evol.* 9, 946–955.
- Bowlin MS, Henningson P, Muirjes FT, Vleugel RHE, Liechti F. and Hedenstrom A. (2010). The effects of geolocator drag and weight on the flight ranges of small migrants. *Meth. Ecol. Evol.* 1, 420 398-402.
- Bouwhuis S, Quinn JL, Sheldon BC. and Verhulst S. (2013). Personality and basal metabolic rate in a wild population. *Oikos*. 123, 56-62.
- Brlik V. et al. (2020). Weak effects of geolocators on small birds: a meta-analysis controlled for phylogeny and publication bias. *J. Anim. Ecol.* 89, 207-220.
- Bryant DM. (1988). Energy expenditure and body mass changes as measures of reproductive costs in birds. *Funct. Ecol.* 2, 23-34.
- Croll DA, Gaston AJ and Noble DG. (1991). Loss of mass in thick-billed murre. *Condor*. 93, 496-502.



- 430 Curtin NA, Bartlam-Brooks HLA, Hubel TY, Lowe JC, Gardner-Medwin AR, Bennett E., Amos SJ, Lorenc M, West TG. And Wilson AM. (2018). Remarkable muscles, remarkable locomotion in desert-dwelling wildebeest. *Nature*. 563, 393-396.
- Dittami JP and Gwinner E. (1985). Annual cycles in the African stonechat and their relationship to environmental factors. *J. Zool.* 207, 357-370.
- Dolnik, R. D. and Gavrilov, V. M. (1979). Bioenergetics of molt in the chaffinch (*Fringilla coelebs*). *Auk* 96, 253-264.
- DuBowy PJ. (1985). Molt and plumages and testicular regression of postbreeding male Blue-winged Teal (*Anas discors*) and Northern Shovelers (*Anas clypeata*). *J. Zool.* 207, 459-466
- Eikenaar C. (2017). Endocrine regulation of fueling by hyperphagia in migratory birds. *J. Comp. Physiol. A.* 203, 439-445.
- 440 French AR. 2005 Importance of body size in determining dominance hierarchies among diverse tropical frugivores. *Biotropica* 37, 96–101.
- Fox AD, Kahlert J, Walsh AJ, Stroud DA, Mitchell C, Kristiansen JN. and Hansen EB. (1998). Patterns of body mass change during moult in three different goose populations. *Wildfowl* 49, 45-56.
- Fox AD. and Kahlert J. (1999). Adjustments to nitrogen metabolism during wing moult in Greylag Geese *Anser anser*. *Funct. Ecol.* 13, 661-669.
- Funghi C, Leitao AV, Ferreiea AC, Mota PG and Cardoso GC. (2015). Social dominance in a gregarious bird is related to body size but not to standard personality assays. *Ethology*. 121, 84-93.
- Geldenhuis JN. (1983). Morphological variation in wing-moulting South African Shelduck. 450 *Ostrich* 54, 19-25.
- Goymann W, Spina F, Ferri A, and Fusani L. (2010). Body fat influences departure stopover sites in migratory birds: evidence from whole-island telemetry. *Biol. Lett.* 6, 478-481.
- Guillemette M. and Ouellet JF. (2005). Temporary flightlessness as a potential cost of reproduction in pre-laying common eiders. *Ibis* 147, 301–306.
- Guillemette M, Pelletier D, Grandbois J.-M. and Butler PJ. (2007). Flightlessness and the energetic cost of wing moult in a large sea duck. *Ecol.* 88, 2936–2945.
- Guillemette M, Richman SE, Portugal SJ. And Butler PJ. (2012). Behavioural compensation reduces energy expenditure during migration hyperphagia in a large bird. *Funct. Ecol.* 26, 876-883.
- Guozhen Q. and Hongfa X. (1986). Molt and resting metabolic rate in the common teal *Anas crecca* 460 and the shoveller *Anas clypeata*. *Acta Zool. Sin.* 32, 73-84.
- Gutowsky LFG, Stoot LJ, Cairns NA, Thiem JD, Brownscombe JW, Danylchuk AJ, Blouin-Demers G and Cooke SJ. (2016). Biologgers reveal post-release behavioural impairments of freshwater turtles following interactions with fishing nets. *Anim. Con.* 20, 350-359.

- Halsey LG, White CR (2010). Measuring Energetics and Behaviour Using Accelerometry in Cane Toads *Bufo marinus*. *PLoS ONE* 5, e10170.
- Handrich Y, Bevan RM, Charrassin JB, Butler PJ, Ptz K, Woakes AJ, Lage J. and Le Maho Y. (1997). Hypothermia in foraging king penguins. *Nature*. 388, 64 – 67.
- Hiebert SM. (1991). Differences in the response of rufous hummingbirds to food restriction: body mass and the use of torpor. *Condor*. 93, 526-537.
- 470 Hohman WL, Ankney CD. and Gordon DH. (1992). Ecology and management of postbreeding waterfowl. In *Ecology and Management of Breeding Waterfowl* (ed. BDJ. Batt, AD. Afton, MG. Anderson, CD. Ankney, DH. Johnson, JA. Kadlec and GL. Krapu), pp. 128-189. Minneapolis: University of Minnesota.
- Johnston DW. (1966). A review of the vernal fat deposition picture in overland migrant birds. *Bird-Banding*. 37, 172-183.
- Jonsson KI. (1997). Capital and income breeding as alternative tactics of resource use in reproduction. *Oikos*. 78, 57-66.
- Kawabata Y, Noda T, Nakashima Y, Nanami A, Sato T, Takebe T, Mitamura H, Arai N, Yamaguchi T. and Soyano K. (2014). Use of a gyroscope/accelerometer data logger to identify  
480 alternative feeding behaviours in fish. *J. Exp. Biol.* 217, 3204-3208.
- Kay WP, Nausmann DS, Bowen HJ, Withers SJ, Evans BJ, Wilson RP, Stringell TB, Bull JC, Hopkins PW. and Borger L. (2019). *Meth. Ecol. Evol.* 10, 1222-1233.
- Kenwood, R.E. (2001). A manual for wildlife radio tracking. 2 Edn. Academic Press. San Diego, USA.
- Klaassen RHG, Alerstam T, Carlsson P, Fox JW, Lindstrom A. (2011). Great flights by great snipes: long and fast non-stop migration over benign habitats. *Biol. Lett.* 7, 833-835.
- Kuznetsova AP, Brockhoff B. and Christensen RHB. (2016). lmerTest: Tests in Linear Mixed Effects Models. R package version 2.0-33.
- Lamb JS, Satge YG, Fiorello CV. and Jodice PGR. (2017). Behavioural and reproductive  
490 effects of bird-borne data logger attachment on brown pelicans on three temporal scales. *J. Ornithol.* 158, 617-627.
- McIntyre, T. (2014). Trends in tagging of marine mammals: a review of marine mammal biologging studies, *Afr. J. Marine Sci.* 36, 409-422.
- Meijer T. and Drent R. (1999). Re-examination of the capital and income dichotomy in breeding birds. *Ibis*. 141, 399-414.
- Metcalf NB. and Ure SE. (1995). Diurnal variation in flight performance and hence potential predation risk in small birds. *Proc. Roy. Soc. B.* 261, 395-400.
- Newton I. (2006). Can conditions experienced during migration limit the population levels of

- birds? *J. Ornithol.* 147, 146-166.
- 500 Ost M, Seltmann MW. and Jaatinen K. (2015). Personality, body condition and breeding experience drive sociality in a facultatively social bird. *Anim. Behav.* 100, 166-173.
- Paredes R, Jones IL. and Boness DJ. (2005). Reduced parental care, compensatory behaviour and reproductive costs of thick-billed murres equipped with data loggers. *Anim. Behav.* 69, 197-208.
- Pennycuik CJ. (1975). Mechanics of flight. In *Avian Biology*, vol. V (ed. Farner, D. S. and King, J. R.), pp. 1–75. New York: Academic Press.
- Pennycuik CJ, Fast PLF, Ballerstadt N. and Rattenborg N. (2012). The effect of an external transmitter on the drag coefficient of a bird's body, and hence on migration range, and energy reserves after migration. *J. Ornithol.* 153, 633-644.
- 510 Pettit B, Akos Z, Vicsek T, Biro D. (2016). Speed determines leadership and leadership determines learning during pigeon flocking. *Curr. Biol.* 25, 3132– 3137.
- Phillips RA, Silk JRD, Croxall JP, Afanasyev V, & Briggs DR. (2004). Accuracy of geolocation estimates for flying seabirds. *Marine Ecol. Progress Ser.* 266, 265–272.
- Piersma T. (2002). Energetic bottlenecks and other design constraints in avian annual cycles. *Integ. Comp. Biol.* 42, 51-67.
- Portugal SJ. and White, CR. (2018). Miniaturisation of biologgers is not alleviating the 5% rule. *Methods in Ecology and Evolution.* 9, 1662-1666.
- Portugal SJ, Sivess L, Butler PJ, Martin GR. and White CR. (2017a). Perch height predicts dominance rank in birds. *Ibis.* 159, 456-462.
- 520 Portugal SJ, Ricketts R, Chappell J, White CR, Shepard EL. and Biro D. (2017b). Boldness traits, not dominance, predicts exploratory flight range and homing behaviour in homing pigeons. *Phil. Tran. Roy. Soc. B.* 372, 20160234.
- Portugal, S.J., Hubel, T.Y, Fritz, J, Heese, S., Trobe, D., Voelkl, B., Hailes, S., Wilson, A.M. and Usherwood, J.R. (2014). Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. *Nature.* 505, 399 – 402.
- Portugal SJ, Green JA, Piersma T, Eichhorn G. and Butler PJ. (2011). Energy stores enable flightless moulting geese to maintain cryptic behaviour. *Ibis.* 153, 868-874.
- Portugal SJ, Green JA. and Butler PJ. (2007). Annual changes in body mass and resting metabolism in captive barnacle geese: the importance of wing moult. *J. Exp. Biol.* 210, 1391-1397.
- 530 R Core Team. 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

- Ramenofsky M. (1990). Fat storage and fat metabolism in relation to migration. *Bird Mig.*, 214-213. In: Gwinner E. (eds) *Bird Migration*. Springer, Berlin, Heidelberg. [https://doi.org/10.1007/978-3-642-74542-3\\_15](https://doi.org/10.1007/978-3-642-74542-3_15).
- Rashotte ME, Basco PS. and Henderson RP. (1996). Daily cycles in body temperature, metabolic rate and substrate utilization in pigeons: influence of amount and timing of food consumption. *Physiol. and Behav.* 57, 731-746.
- Rogers CM. (1987). Predation risk and fasting capacity: do wintering birds maintain optimal body mass? *Ecology.* 68, 1051-1061.
- 540 Sankey DWE. and Portugal SJ. (2019). When flocking is costly: reduced cluster-flock density over long-duration flight in pigeons. *Sci. of Nat.* 106, 47.
- Sankey DWE, Shepard ELC, Biro D. and Portugal SJ. (2019). Speed consensus and the “Goldilocks principle” in flocking birds (*Columba livia*). *Anim. Beh.* 157, 105-119.
- Sankey DWE, Storms RF, Musters RJ, Russell TW, Hemelrijk CK. and Portugal SJ. (2021). Absence of “selfish-herd” dynamics in bird flocks under threat. *Curr. Biol.* 31, 1-7.
- Sargisson RJ, McLean IG, Brown GS, White, KG. (2007). Seasonal variation in pigeon body weight and delayed matching-to-sample performance. *J. Exp. Anal. Behav.* 88, 395–404.
- Scott IS, Mitchell I. and Evans PR. (1994). Seasonal changes in body mass, body composition and food requirements in wild migratory birds. *Proc. Nut. Soc.* 53, 521-531.
- 550 Sims *et al.* (2008). Scaling laws of marine predator search behaviour. *Nature.* 451, 1098 – 1102.
- Schmidt-Wellenburg CA, Engel S. and Visser GH. (2008). Energy expenditure during flight in relation to body mass: effects of natural increases in mass and artificial load in Rose Coloured Starlings. *J. Comp. Physiol. B.* 178, 767-777.
- Sjöberg K. (1986). The flightless period of free-living male Teal *Anas crecca* in northern Sweden. *Ibis* 130, 164-171.
- Stanback M, Millican D, Visser P. and Marker L. (2018). The simultaneous moult of female hornbills is not triggered by the darkness of their nest cavity. *Ostrich.* 89, 373-375.
- Taylor CR, Heglund NC. and Maloiy GM. (1982). Energetics and mechanics of terrestrial locomotion. I. Metabolic energy consumption as a function of speed and body size in birds and mammals. *J. Exp. Biol.* 97, 1-21.
- 560 Taylor LA, Taylor GK, Biro D, Lambert B, Walker JA. and Portugal SJ. (2019). Birds invest wingbeats to keep a steady head and reap the ultimate benefits of flying together. *PLOS Biology.* 17, e3000299.
- Tobalske BW, Hedrick TL, Dial KP. and Biewener AA. (2003). Comparative power curves in bird flight. *Nature.* 421, 364-366.
- Tomotani *et al.* (2019). Carrying a logger reduces escape flight speed in a passerine bird, but

- relative logger mass may be a misleading of this flight performance detriment. *Meth. Ecol. Evol.* 10, 70-79.
- Usherwood JR, Stavrou M, Lowe J C, Roskilly K. and Wilson AM. (2011) Flying in a flock comes at a cost in pigeons. *Nature* 474, 494–497.
- 570 van der Jeugd HP, Gurtovaya E, Eichhorn G, Litvin KY, Minneev OY. and van Eerden M. (2003). Breeding Barnacle Geese in Kolokova Bay: number of breeding pairs, reproductive success and morphology. *Polar Biol.* 26, 700– 706.
- Vandenabeele SP, Shepard EL, Grogan A, & Wilson RP. (2012). When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Marine Biol.* 159, 1–14.
- Vandenabeele SP, Grundy E, Friswell MI, Grogan A, Votier SC, et al. (2014). Excess Baggage for Birds: Inappropriate Placement of Tags on Gannets Changes Flight Patterns. *PLoS ONE* 9, e92657
- 580 Vandenabeele SP, Shepard ELC, Gremillet D, Butler PJ, Martin GR. and Wilson RP. (2015). *Marine Eco. Prog. Ser.* 519, 239: 249.
- Vandenabeele SP, Shepard ELC, Grogan A. and Wilson RP. (2012). When three per cent may not be three per cent; device-equipped seabirds experience variable flight constraints. *Mar. Biol.* 159, 1-14.
- Voelkl B, Portugal SJ, Unsold M, Usherwood JR, Wilson AM, and Fritz J. (2015). Matching times of leading and following suggest cooperation through direct reciprocity during V-formation flight of Northern bald ibis. *PNAS (Proceedings of the National Academy of Sciences of the United States)*. 112, 2115-2120.
- 590 Watanabe YY. & Nathan R. (2016). Flight mode affects allometry of migration range in birds. *Ecol. Lett.* 19, 907-914.
- Weber TP. And Houston AI. (1997). Flight costs, flight range and the stopover ecology of migrating birds. *J. Anim. Ecol.* 66, 297-306.
- Wilmers, CC, Nickel B, Byrce CM, Smith JA, Wheat RE, Yovovich. (2015). The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. *Ecology.* 96, 1741–1753.
- White CR, Cassey P, Schimpf N, Green JA, Halsey LG and Portugal SJ. (2013). Implantation reduces the negative effects of bio-logging devices on birds. *J. Exp. Biol.* 216, 537-542.
- 600 Williams HJ. et al. (2020). Optimizing the use of biologgers for movement ecology research *J. Anim. Ecol.* 89, 186-206.
- Yoda K. (2019). Advances in bio-logging techniques and their application to study navigation

in wild seabirds. *Ad. Robotics*. 33, 108-117.

Yohannes E, Biebach H, Nikolaus G. and Pearson DJ. (2009). Passerine migration strategies and body mass variation along geographic sections across East Africa, the Middle East and the Arabian Peninsula. *J. Ornithol.* 150, 369-381.

## FIGURE LEGENDS

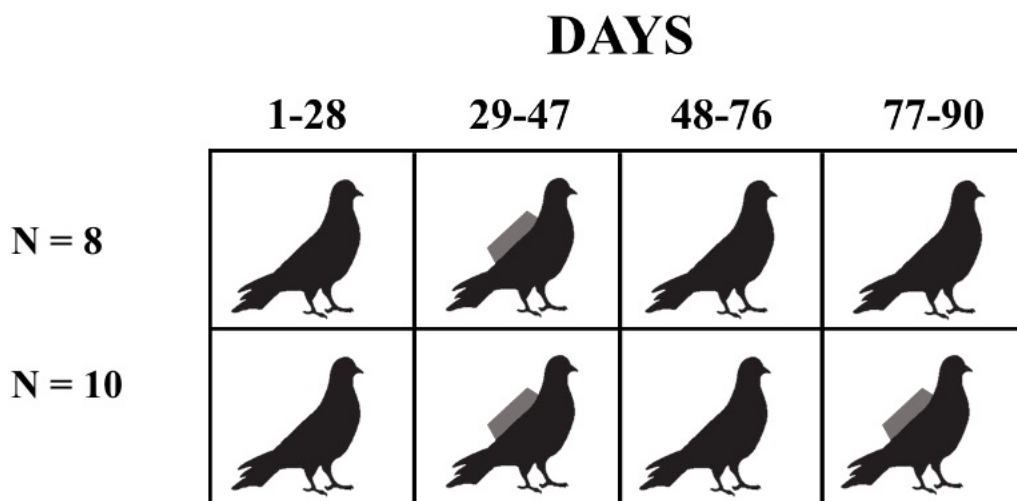
### FIGURE 1. Experimental design

610 18 homing pigeons were used to determine the effects of artificial mass attachment (see Methods). 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.

### 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 ( $\pm SEM$ ) of the data in (B). In all panels, birds with artificial weights added are shown in orange.

620

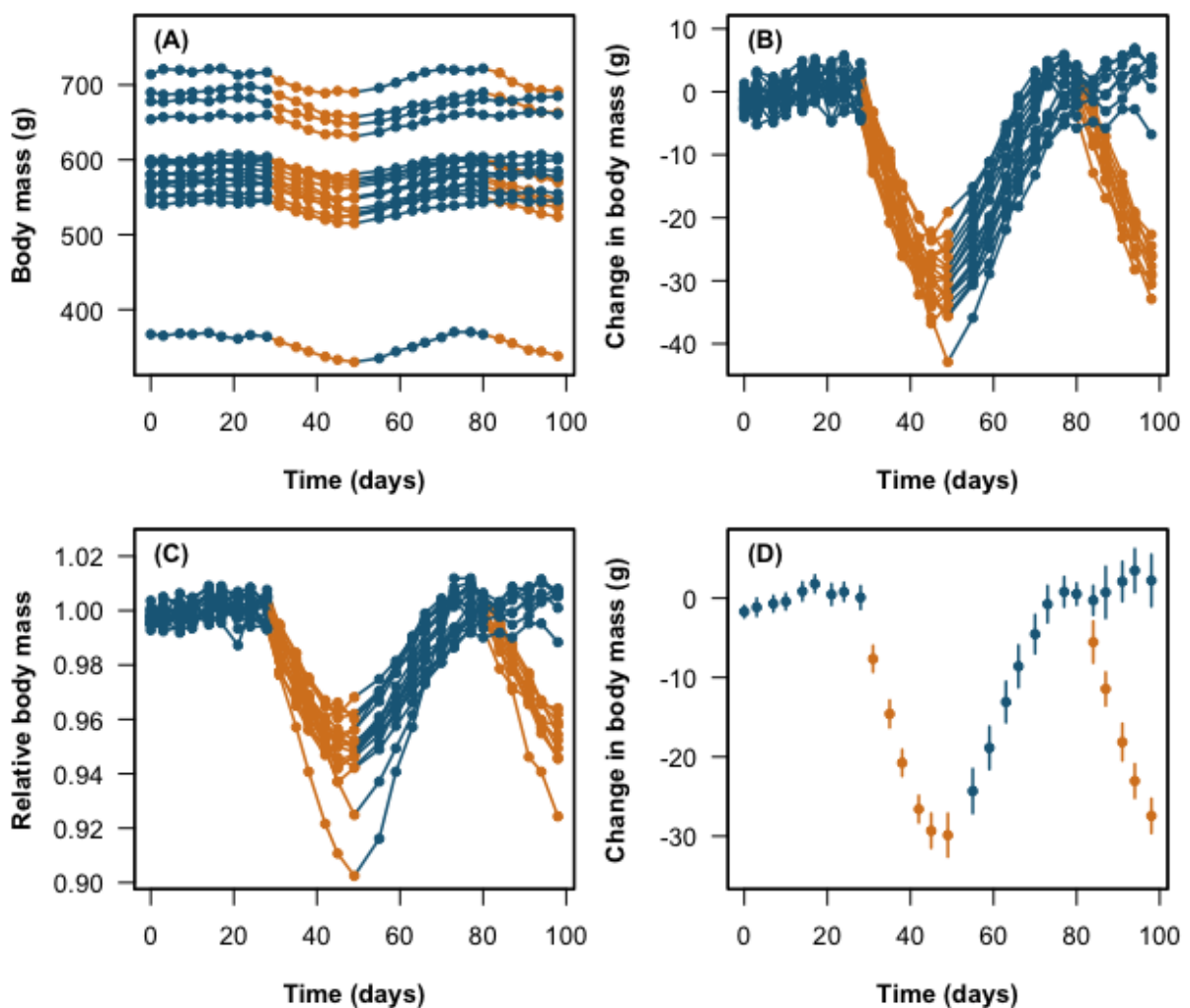




**FIGURE 1** Experimental design.

18 homing pigeons were used to determine the effects of artificial mass attachment (see Methods). 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.

630



**FIGURE 2** 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 ( $\pm SEM$ ) of the data in (B). In all panels, birds with artificial weights added are shown in orange.

640