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No effect of carrying a leg-loop harness mounted radio transmitter on flight energy expenditure of a small migratory songbird

No hay efecto de llevar un radiotransmisor montado en un arnés de pernera sobre el gasto energético del vuelo de un pequeño pájaro cantor migratorio

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ABSTRACT. Radio transmitters and other miniature electronic devices have greatly enhanced our understanding of avian ecology. However, from both animal welfare and data integrity perspectives, it is crucial to determine if tracking devices adversely affect birds. One important knowledge gap is understanding if carrying tracking devices affects energy costs of flight. We carried out a wind tunnel experiment with a paired design where Yellow-rumped Warblers (*Setophaga coronata*) flew for two hours with and without very high frequency (VHF) radio transmitters mounted with a leg-loop harness (~3% of body mass). We calculated energy expenditure (power; W) by measuring loss of fat and lean mass during flight with quantitative magnetic resonance. There was no effect of VHF radio transmitters on energy expenditure, indicating small songbirds can carry appropriately sized and mounted devices without experiencing increased flight costs. According to aerodynamic theory, smaller birds should have relatively larger power margins compared to larger birds, enabling them to carry relatively greater payloads. Future studies should examine how VHF radio transmitters and other devices of different masses, shapes, and mounting techniques affect flight ability and energy costs across bird species varying in body size and wing morphology.

RESUMEN. Los radiotransmisores y otros dispositivos electrónicos miniatura han mejorado mucho nuestra compresión de la ecología aviar. Sin embargo, desde la perspectiva del bienestar animal y la integridad de los datos es crucial determinar si los dispositivos de rastreo afectan negativamente a las aves. Un importante faltante de información es entender si llevar dispositivos de rastreo afecta los costos energéticos del vuelo. Llevamos a cabo un experimento de túnel de viento con un diseño pareado donde Reinitas Coronadas (*Setophaga coronata*) volaron durante dos horas con y sin radiotransmisores de frecuencia muy alta (VHF) montados con un arnés de pernera (~3% de la masa corporal). Calculamos el gasto energético (potencia; W) midiendo la pérdida de grasa y masa magra durante el vuelo con resonancia magnética cuantitativa. No hubo efecto de los radiotransmisores VHF sobre el gasto energético, lo cual indica que pequeños pájaros cantores puede llevar dispositivos de tamaño y montaje adecuados sin experimentar un aumento en los costos del vuelo. Según la teoría aerodinámica, las aves más pequeñas deberían tener márgenes de potencia relativamente mayores en comparación con las aves más grandes, permitiéndoles transportar relativamente cargas mayores. Estudios futuros deberían examinar cómo los radiotransmisores VHF y otros dispositivos de diferentes masas, formas y técnicas de montaje afectan la capacidad de vuelo y costos energéticos en especies de aves que varían en tamaño corporal y morfología de las alas.

Key Words: *energy expenditure; flight performance; radio transmitter; Setophaga coronata; tag effects; Yellow-rumped Warblers*

INTRODUCTION

Miniature electronic devices, such as very high frequency (VHF) radio transmitters, geolocation loggers, and accelerometers, have revolutionized our understanding of bird behavior, habitat associations, demography, movement, and space use at scales spanning from home ranges to cross-hemispheric migrations (e.g., Evans et al. 2020, González et al. 2020, Fischer et al. 2022). Together, these insights not only improve our basic knowledge of avian biology but also help to inform conservation decisions (e.g., Wilson et al. 2009, Falconer et al. 2016, Howell et al. 2020). Use of VHF telemetry to track birds has increased through time (Geen et al. 2019). This pattern is likely to continue given recent development and expansion of multiple automated VHF tracking arrays (Kays et al. 2011, Řeřucha et al. 2015, Taylor et al. 2017).

VHF radio telemetry is a particularly important tool for tracking small songbirds at local and regional scales. Whereas small songbirds can generally carry either VHF radio transmitters or geolocators for tracking migration movements, they are often too small to carry satellite transmitters (Bridge et al. 2011). Given the importance of VHF radio telemetry for avian research and conservation at multiple spatial scales, it is critical to understand if and how VHF transmitters affect energetics, physiology, behavior, physical well-being, and demography of birds, both for animal welfare and so that potential biases (tag effects) can be accounted for when interpreting results.

Studies investigating effects of VHF radio transmitters and similarly sized geolocators on birds have considered several endpoints, including effects on reproduction, physiology, within season and annual apparent survival, foraging and provisioning behavior, and space use (reviewed by Geen et al. 2019, Brlík et al. 2020, Geldart et al. 2023). To date, no studies have investigated the impacts of VHF radio transmitters on free-living birds during the migration stage of the annual cycle (Geldart et al. 2023). Migration consists of flying and fueling phases (Alerstam 2003,

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McWilliams et al. 2004, Hedenström 2008). Although there has yet to be a study investigating potential impacts of VHF radio transmitters during the fueling phase of migration, presumably, possible effects on fueling birds at stopover sites could be assessed by using methods that have been used during other resident phases of the life cycle, e.g., comparing changes in mass or body composition between tagged and un-tagged individuals (Rae et al. 2009). However, evaluating potential effects of VHF radio transmitters during the flight phase of migration is much more challenging given the need to follow tagged and un-tagged birds during flight (Geldart et al. 2023).

The flight phase of migration is energetically demanding and is equivalent to high-intensity endurance exercise that lasts for many hours to days (Jenni-Eiermann and Jenni 1991, Jenni-Eiermann et al. 2002, Guglielmo 2018). Increased flight energy cost owing to added mass, aerodynamic drag, altered behavior, or physiological stress resulting from carrying a VHF radio transmitter or other devices could potentially have negative downstream effects on migration distance, speed, and survival (Caccamise and Hedin 1985, Bowlin et al. 2010, Pennycuick et al. 2012). Aerodynamic analysis indicates that in-flight increases in energy expenditure resulting from carrying tracking devices as a fixed proportion of body weight should be higher for larger versus smaller birds and that the extra aerodynamic drag produced by tracking devices can increase energy expenditure (Caccamise and Hedin 1985, Bowlin et al. 2010, Pennycuick et al. 2012). Although scarce in the literature, an excellent means to directly assess tag effects on the flight phase of migration is to study flight behavior and energetics under controlled conditions with wind tunnel experiments. Previous wind tunnel studies have mainly investigated effects of device shape and mounting position for birds mounted with data logging units, such as geolocators, which typically show that high drag shapes (bluff bodies) mounted high on the back between the wings have the greatest effect on drag, energy expenditure, and ultimately distance flown (Obrecht III et al. 1988, Bowlin et al. 2010, Pennycuick et al. 2012, Mizrahy-Rewald et al. 2023). To our knowledge, no such empirical studies have been conducted on birds wearing VHF radio transmitters that are now commonly used in field research, and which have a much lower vertical profile but often have a much longer and flexible antenna than similar sized data logging units, such as geolocators.

Our objective was to determine if birds flying with VHF radio transmitters mounted using a leg-loop harness experience greater energy expenditure relative to birds without radio transmitters. To do this, we used a paired design, flying migratory Yellow-rumped Warblers (*Setophaga coronata*, ~12 g) with and without VHF radio transmitters in a wind tunnel. To be conservative, we made a directional hypothesis that flight energy expenditure would be greater when birds flew with a VHF radio transmitter.

METHODS

Sixty Yellow-rumped Warblers were captured as part of another study during October 2013 at Long Point Bird Observatory, Long Point, Ontario, Canada (42°34′57.71″ N, 80°23′51.48″ W; Dick and Guglielmo 2019). Birds were banded with standard U.S. Fish and Wildlife Service/Canadian Wildlife Service aluminum leg bands and transported to the Advanced Facility for Avian Research (AFAR) at the University of Western Ontario, London, Ontario, Canada. Birds were then housed in randomly assigned pairs of the same sex in cages (1.2 x 0.7 x 1.8 m) within a single large indoor aviary (3.7 x 4.8 x 3.1 m). Birds were paired together based on sex because previous experience suggested that females lose more mass when housed with males relative to other females, likely owing to competitive exclusion with respect to food and/or water (MD, personal observation). Moreover, we also observed that birds would more readily eat when housed with another bird of the same sex as opposed to being housed alone (MD, personal observation). Room temperature was maintained at 21 °C and birds were exposed to a 12 h light/dark cycle to match the civil twilight day length at the time of capture, i.e., the light cycle experienced during fall migration. A semisynthetic diet (Dick and Guglielmo 2019), mealworms, and water were provided *ad libitum*. From these 60 birds, we selected eight birds for our study that flew in the center of the wind tunnel (described below) for 20 min in duration without interruption during test flights, i.e., they did not fly to the back or front of the wind tunnel and perch.

Experimental flights took place between 22 November and 9 December 2013. Food was removed one h prior to each flight, which began 30 min after lights out. Each bird was flown individually twice for 2 h in a wind tunnel specifically designed for birds at the AFAR (wind speed = 8 m s^{-1}, temperature = 15 ° C, humidity 9 g m^{-3} = 70% RH). Paired flights were either two days apart (n = 6 birds), three days apart (n = 1), or 6 days apart (n = 1). Differences in number of days between flights reflect scheduling constraints with respect to other wind-tunnel experiments occurring concurrently. Prior to the experiment, each bird was randomly assigned to complete their first flight with or without a VHF radio transmitter (Lotek nanotag NTQB2-1, L x W x H = 11 x 5 x 3 mm, antenna length = 15 cm, mass = 0.26 g; Lotek Wireless, Newmarket, Ontario, Canada), where birds flying with a VHF radio transmitter (n = 4) for their first flight, completed their second flight without a transmitter and vice versa. VHF radio transmitters were placed on birds using a figure-eight leg-loop harness (Rappole and Tipton 1991) composed of nylon elastic thread that was affixed to the VHF radio transmitter with a small amount of cyanoacrylate adhesive (Crazy Glue Gel, Toagosei America Inc., Columbus, Ohio, USA). The glue and harness added an additional 0.08 g to the VHF radio transmitter. When VHF radio transmitters were applied, we preened each bird's feathers on the lower back to cover the transmitters, helping minimize potential aerodynamic drag caused by the already small vertical profile of the VHF radio transmitters. VHF radio transmitters were placed on birds 24 h prior to their flight to provide time to adjust to the harness.

Immediately prior to and following each flight, birds were weighed (accuracy = 0.001 g) and wet lean mass and fat mass were measured non-invasively by using quantitative magnetic resonance (QMR; model Echo-MRI-B, Echo-Medical Systems, Houston, Texas, USA; refer to Guglielmo et al. [2011] for further details). For QMR, birds were scanned three times. Each scan was 2 min in duration and resulting measurements were averaged. Average coefficients of variation (± SD) for repeated scans for fat and lean mass prior to flying were 0.06 (± 0.03) and 0.009 (± 0.003), respectively. Average coefficients of variation for repeated scans for fat and lean mass following flight were 0.07 (± 0.04) and 0.006 (± 0.004), respectively. VHF radio transmitters were removed prior to mass measurements or scanning in the QMR and then reapplied. We converted reductions in lean and fat mass to energy expenditure, assuming 39.6 and 5.3 kJ of energy were produced per gram of fat and wet lean mass lost, respectively (Gerson and Guglielmo 2011). We then added these values and converted the sum to power, i.e., the rate of energy expenditure measured in Watts (W; where 1 W = 1 J s^{-1}) by multiplying by 1000 and dividing by the flight duration of 7200 seconds. Research was carried out under permit from the Canadian Wildlife Service (CA-0256) and an animal care protocol approved by the University of Western Ontario Animal Care Committee (protocol #2010-216).

All statistical analyses were done in R 4.1.0 (R Core Team 2021). We analyzed energy expenditure as a function of carrying a VHF radio transmitter or not and initial (wet) mass prior to each flight. We included initial mass to account for differences in cost of transport for heavier versus lighter birds (Caccamise and Hedin 1985). We also included a random effect for individual to control for potential autocorrelation of flight behavior within individuals. Generalized linear mixed models were fit with the glmmtmb package (Magnusson et al. 2017). Model fit was evaluated visually by examining quantile-quantile plots of residuals, residuals versus fitted values, and residuals as a function of each predictor. Data were visualized by using ggplot2 (Wickham et al. 2016). Summary statistics represent means ± SDs. For our mixed-effects model we assessed significance at $\alpha = 0.05$ and all tests were one-sided, where we predicted carrying a VHF radio transmitter would result in increased energy expenditure and heavier birds would have higher energy expenditure.

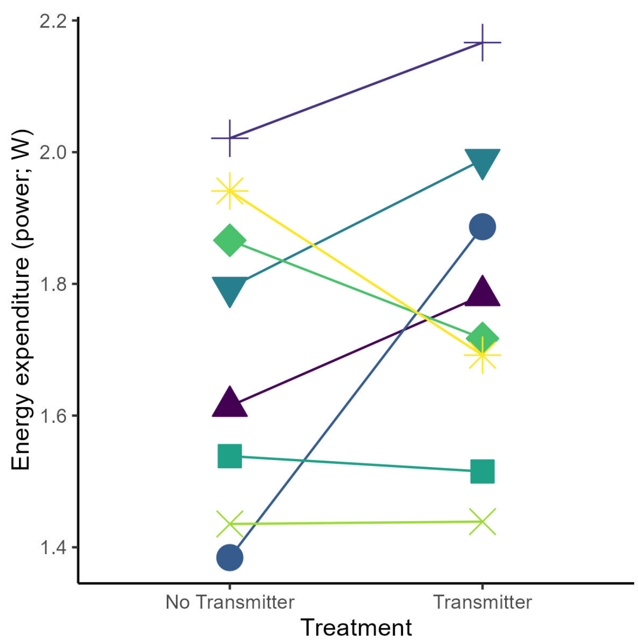
RESULTS

Average body mass of birds with and without VHF radio transmitters on the first flight was 11.52 ± 0.56 g and 12.73 ± 0.54 g, respectively. Average body mass of birds with and without VHF radio transmitters on the second flight was 12.34 ± 0.53 g and 12.53 ± 0.53 g, respectively. Thus, the VHF radio transmitters and harness represented ~3.0% of a bird's body mass for birds flown with a VHF radio transmitter on their first flight and ~2.8% of a bird's body mass for birds flown with a VHF radio transmitter on their second flight.

Lean mass loss during first flights for birds with and without VHF radio transmitters was 0.29 ± 0.31 g and 0.22 ± 0.10 g, respectively. Fat mass loss during first flights for birds with and without VHF radio transmitters was 0.28 ± 0.06 g and 0.29 ± 0.02 g, respectively. Lean mass loss during second flights for birds with and without VHF radio transmitters was 0.25 ± 0.07 g and 0.31 ± 0.07 g, respectively. Fat mass loss during second flights for birds with and without VHF radio transmitters was 0.29 ± 0.02 g and 0.27 ± 0.05 g, respectively.

Average energy expenditure for birds that flew with and without VHF radio transmitters was 1.77 ± 0.24 W and 1.70 ± 0.24 W, respectively. We did not find any evidence for an effect of carrying a VHF radio transmitter on energy expenditure ($\beta = 0.07$, SE = 0.09, $z = 0.8$, $p = 0.20$; Fig. 1). We also did not find an effect of body mass on energy expenditure ($\beta = -0.01$, SE = 0.11, $z = -0.1$, $p = 0.47$). Variance associated with intercepts and residual variance for the random effect for individual were 0.4 and 0.3, respectively. The intercept for the main effects was $\beta = 1.77$ (SE = 1.28, $z = 1.4$).

Fig. 1. Energy expenditure (power; W) of Yellow-rumped Warblers (*Setophaga coronata*) flown with and without VHF radio transmitters for two-hour flights in a wind tunnel at the Advanced Facility for Avian Research, University of Western Ontario, London, Ontario, Canada. Lines of the same color and symbols of the same shape connect flights completed by the same bird. Energy expenditure ranged from 1.4 to 2.0 W for birds flown without VHF radio transmitters and 1.4 to 2.2 W for birds flown with VHF radio transmitters. Mean energy expenditure was 1.77 W (± 0.24) and 1.70 W (± 0.24) for birds flown with and without VHF radio transmitters, respectively.



DICUSSION

Although it is feasible that carrying a VHF radio transmitter might impact flight energy expenditure through multiple pathways, e.g., increased mass, aerodynamic drag, physiological stress, or altered behavior during flight (e.g., Obrecht III et al. 1988, Suedkamp Wells et al. 2003, Woolnough et al. 2004, Irvine et al. 2007), we did not find an effect of carrying VHF radio transmitters weighing ~3% of a bird's body mass mounted with a leg loop harness on energy expenditure during flight. This is important, because migration is very energetically demanding (Jenni-Eiermann and Jenni 1991, Jenni-Eiermann et al. 2002, Guglielmo 2018), and it is not only important to make sure we are not impacting our study subjects from an animal welfare perspective (Geen et al. 2019), but also that migration behavior, e.g., flight distance or speed, is unbiased (e.g., Irvine et al. 2007).

It is perhaps not surprising that a small bird carrying a VHF radio transmitter weighing ~3% of its body mass did not experience negative effects on in-flight energy expenditure given wide fluctuations in body mass observed in the field for passerines during the migratory period. For example, it is common for migratory passerines to have departure fuel loads equivalent to

20–30% of lean mass, and some species of similar size to Yellow-rumped Warblers, such as Blackpoll Warblers (*Setophaga striata*) and many trans-Saharan migrant passerines, can nearly double their mass when preparing to make multi-day nonstop flights (Odum 1960, Nisbet et al. 1963, Bairlein 2002, Holberton et al. 2005). Migratory birds also show flexibility of flight muscle size that is adjusted to match body mass changes (Lindström et al. 2000). Thus, typical songbirds likely have spare power capacity and phenotypic flexibility to adjust to extra mass and a certain amount of aerodynamic drag.

Whereas small songbirds may have spare power capacity and phenotypic flexibility to carry small VHF radio transmitters as observed in this study, we caution against extrapolating these results to larger species. This is because small birds have greater power margins relative to large birds, meaning they can carry proportionally greater loads relative to their lean body mass (Caccamise and Hedin 1985, Hedenström and Alerstam 1992, Klaassen 1996). This further suggests that smaller birds may be able to accommodate heavier tracking devices in terms of percent body mass relative to larger birds (Caccamise and Hedin 1985). For example, using aerodynamic theory, Caccamise and Hedin (1985) estimated a 20 g bird carrying a radio transmitter weighing 5% of its mass would experience a reduction in its power surplus (difference between available power needed to fly at a birds maximum range velocity and power available) of ~1.5% compared with a 200 g bird carrying a transmitter weighing 5% of its body mass, which would experience a reduction in power surplus of ~5%. Last, we caution against extrapolating our results to other tracking devices having higher profiles when mounted on a bird (e.g., geolocators). This is because higher profiles increase the frontal area of the tracking device, resulting in increased drag and an associated increase in energy expenditure as well as reductions in potential flight ranges (Obrecht III et al. 1988, Bowlin et al. 2010, Pennycuick et al. 2012).

We used changes in lean and fat mass, derived from QMR, to calculate in-flight energy expenditure (power) based on Gerson and Guglielmo (2011). The derivation of flight energy expenditure from changes in lean and fat mass has been used in numerous other studies and has been validated by using ^{13}C -labelled sodium bicarbonate and doubly-labelled water (Hedh et al. 2020, Elowe et al. 2023). Energy expenditure in our study was very similar to several previous studies for Yellow-rumped Warblers (Hedh et al. 2020, Elowe et al. 2023, Groom et al. 2023), highlighting the accuracy of our estimates. Overall, we suggest that quick and non-invasive QMR scanning combined with wind tunnel flights provides a powerful experimental system to evaluate potential energetic costs of carrying tracking devices for birds.

We acknowledge our experimental flights were relatively short in duration compared to migratory flights that can last overnight or even longer. We chose two-hour flights because flights of this length were sufficient to detect effects of experimental challenges on energy expenditure in our other studies (Maggini et al. 2017, Ma et al. 2018, Yap et al. 2018). However, because birds lose lean and fat mass during flight, tag effects could be both negated and exacerbated during longer flights. On one hand, reductions in lean and fat mass during longer flights will reduce total power needed to stay aloft (Pennycuick 1969, Lindström et al. 2000), possibly freeing up additional capacity to carry the extra load resulting from a VHF radio transmitter. Alternatively, if part of lean mass loss includes catabolism of flight muscles (Dick and Guglielmo 2019), then we might expect flight performance to diminish with flight duration. However, we suggest the latter effect is unlikely to occur given observations that reductions in flight muscle size during flight appear adaptive in relation to concurrent losses in other components of body mass, e.g., fat (Lindström et al. 2000). Despite the latter observation, we still encourage future assessments of impacts of tracking devices using wind tunnels to explore potential effects over longer flight durations. We also encourage using particle image velocimetry to assess aerodynamic effects of devices in relation to changes in mechanical power output (Hedh et al. 2020).

An important caveat to our study is that we had a sample size of eight transmitter flights and eight control flights ($n = 16$ flights in total), potentially limiting statistical power. However, we suggest our results are unlikely to change with larger sample sizes for two main reasons. First, average energy expenditure and variability in individual energy expenditure for Yellow-rumped Warblers with VHF radio transmitters in our study are very similar to those values measured from Yellow-rumped Warblers without VHF radio transmitters in other studies (Gerson et al. 2020, Hedh et al. 2020, Elowe et al. 2023), indicating minimal effects of carrying VHF radio transmitters. Second, the lower 95% CI bound for our one-sided test is −0.07 W, which is well below zero and unlikely to change substantially with increased sample sizes. With a growing body of literature measuring energy expenditure in flight, we recommend future studies carry out *a priori* power analyses to estimate optimal sample sizes and estimate expected increases in energy expenditure using aerodynamic theory (e.g., Caccamise and Hedin 1985, Kelling et al. 2024).

In conclusion, use of VHF radio transmitters and other tracking devices to study birds has increased through time (Geen et al. 2019), and it can be reasonably assumed their use will continue to increase given the expansion of automated tracking arrays (e.g., Kays et al. 2011, Řeřucha et al. 2015, Taylor et al. 2017) and continued improvements in tracking technology. We agree with Geldart et al. (2023) that wind tunnel studies provide a unique opportunity to explore potential in-flight tagging effects, an area of research that represents a significant knowledge gap. It is likely one size does not fit all in terms of a general rule for tracking devices as a percentage of body mass (i.e., isometric scaling) with respect to animal welfare and data quality. Based on aerodynamic considerations, effects are more likely to scale allometrically (Caccamise and Hedin 1985). In addition, other factors such as wing shape could also be important (Norberg 1995). Lastly, migratory birds are vulnerable to predation, where large fuel loads may impair their ability to take flight and evade predators (Alerstam and Lindström 1990). Thus, tracking devices could potentially affect predator avoidance at takeoff and maneuverability in the air. Further, it is reasonable to assume that at some percentage of body weight extrinsic devices will negatively affect birds. What is unclear is where the boundary between no effect and detriment lies, and how it may change with bird size, wing shapes, and different fat loads. Is a safe limit 3%, 5%, or even 8% depending on the size of the bird, and how does device size, shape, and mounting position affect energy expenditure? We suggest that systematic wind tunnel and take-off performance studies using a variety of bird species varying in body size and wing shape are urgently needed to resolve conditions under which devices are safe.

Author Contributions:

C.G.G, G.W.M., and M.F.D conceived the study. G.W.M., M.F.D., and A.M. flew the birds. G.W.M. and C.G.G. wrote the manuscript. C.G.G., M.F.D., and G.W.M all provided edits during writing.

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Data Availability:

The data/code that support the findings of this study are openly available in the Open Science Framework at https://www.doi.org/10.17605/OSF.IO/83QKA. Ethical approval for this research study was granted by the Canadian Wildlife Service (CA-0256) and by the University of Western Ontario Animal Care Committee (protocol #2010-216).

LITERATURE CITED

Alerstam, T. 2003. Bird migration speed. Pages 253-267 in P. Berthold, E. Gwinner, and E. Sonnenschein, editors. Avian migration. Springer, Berlin, Germany. https://doi.org/10.1007/978-3-662-05957-9_17

Alerstam, T., and Å. Lindström. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pages 331-351 in E. Gwinner, editor. Bird migration. Springer, Berlin, Germany. https://doi.org/10.1007/978-3-642-74542-3_22

Bairlein, F. 2002. How to get fat: nutritional mechanisms of seasonal fat accumulation in migratory songbirds. Naturwissenschaften 89:1-10. https://doi.org/10.1007/s00114-001-0279-6

Bowlin, M. S., P. Henningsson, F. T. Muijres, R. H. E. Vleugels, F. Liechti, and A. Hedenström. 2010. The effects of geolocator drag and weight on the flight ranges of small migrants. Methods in Ecology and Evolution 1(4):398-402. https://doi.org/10.1111/j.2041-210X.2010.00043.x

Bridge, E. S., K. Thorup, M. S. Bowlin, P. B. Chilson, R. H. Diehl, R. W. Fléron, P. Hartl, R. Kays, J. F. Kelly, W. D. Robinson, and M. Wikelski. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. Bioscience 61(9):689-698. https://doi.org/10.1525/bio.2011.61.9.7

Brlík, V., J. Koleček, M. Burgess, S. Hahn, D. Humple, M. Krist, J. Ouwehand, E. L. Weiser, P. Adamík, J. A. Alves, et al. 2020. Weak effects of geolocators on small birds: a meta-analysis controlled for phylogeny and publication bias. Journal of Animal Ecology 89(1):207-220. https://doi.org/10.1111/1365-2656.12962

Caccamise, D. F., and R. S. Hedin. 1985. An aerodynamic basis for selecting transmitter loads in birds. Wilson Bulletin 97 (3):306-318.

Dick, M. F., and C. G. Guglielmo. 2019. Flight muscle protein damage during endurance flight is related to energy expenditure but not dietary polyunsaturated fatty acids in a migratory bird. Journal of Experimental Biology 222(5):jeb187708. https://doi.org/10.1242/jeb.187708

Elowe, C. R., D. J. Groom, J. Slezacek, and A. R. Gerson. 2023. Long-duration wind tunnel flights reveal exponential declines in protein catabolism over time in short-and long-distance migratory warblers. Proceedings of the National Academy of Sciences 120(17):e2216016120. https://doi.org/10.1073/pnas.2216016120

Evans, D. R., K. A. Hobson, J. W. Kusack, M. D. Cadman, C. M. Falconer, and G. W. Mitchell. 2020. Individual condition, but not fledging phenology, carries over to affect post-fledging survival in a Neotropical migratory songbird. Ibis 162(2):331-344. https://doi.org/10.1111/ibi.12727

Falconer, C. M., G. W. Mitchell, P. D. Taylor, and D. C. Tozer. 2016. Prevalence of disjunct roosting in nesting Bank Swallows (Riparia riparia). Wilson Journal of Ornithology 128(2):429-434. https://doi.org/10.1676/1559-4491-128.2.429

Fischer, S. E., K. Granillo, and H. M. Streby. 2022. Post-fledging survival, movements, and habitat associations of Gray Vireos in New Mexico. Avian Conservation and Ecology 17(1):13. https://doi.org/10.5751/ACE-02053-170113

Geen, G. R., R. A. Robinson, and S. R. Baillie. 2019. Effects of tracking devices on individual birds-a review of the evidence. Journal of Avian Biology 50(2):e01823. https://doi.org/10.1111/jav.01823

Geldart, E. A., L.-A. Howes, H. Wheeler, S. A. Mackenzie. 2023. A review of impacts of tracking devices on birds. North American Bird Bander 47(4):201-212.

Gerson, A. R., J. G. DeSimone, E. C. Black, M. F. Dick, and D. J. Groom. 2020. Metabolic reduction after long-duration flight is not related to fat-free mass loss or flight duration in a migratory passerine. Journal of Experimental Biology 223(19):jeb215384. https://doi.org/10.1242/jeb.215384

Gerson, A. R., and C. G. Guglielmo. 2011. Flight at low ambient humidity increases protein catabolism in migratory birds. Science 333(6048):1434-1436. https://doi.org/10.1126/science.1210449

González, A. M., N. J. Bayly, and K. A. Hobson. 2020. Earlier and slower or later and faster: spring migration pace linked to departure time in a Neotropical migrant songbird. Journal of Animal Ecology 89(12):2840-2851. https://doi.org/10.1111/1365--2656.13359

Groom, D. J. E., B. Black, J. E. Deakin, J. G. DeSimone, M. C. Lauzau, B. P. Pedro, C. R. Straight, K. P. Unger, M. S. Miller, and A. R. Gerson. 2023. Flight muscle size reductions and functional changes following long-distance flight under variable humidity conditions in a migratory warbler. Physiological Reports 11(20): e15842. https://doi.org/10.14814/phy2.15842

Guglielmo, C. G. 2018. Obese super athletes: fat-fueled migration in birds and bats. Journal of Experimental Biology 221(Suppl_1): jeb165753. https://doi.org/10.1242/jeb.165753

Guglielmo, C. G., L. P. McGuire, A. R. Gerson, and C. L. Seewagen. 2011. Simple, rapid, and non-invasive measurement of fat, lean, and total water masses of live birds using quantitative magnetic resonance. Journal of Ornithology 152:75-85. https://doi.org/10.1007/s10336-011-0724-z

Hedenström, A. 2008. Adaptations to migration in birds: behavioural strategies, morphology and scaling effects. Philosophical Transactions of the Royal Society B: Biological Sciences 363(1490):287-299. https://doi.org/10.1098/rstb.2007.2140

Hedenström, A., and T. Alerstam. 1992. Climbing performance of migrating birds as a basis for estimating limits for fuel-carrying capacity and muscle work. Journal of Experimental Biology 164 (1):19-38. https://doi.org/10.1242/jeb.164.1.19

Hedh, L., C. G. Guglielmo, L. C. Johansson, J. E. Deakin, C. C. Voigt, and A. Hedenström. 2020. Measuring power input, power output and energy conversion efficiency in un-instrumented flying birds. Journal of Experimental Biology 223(18):jeb223545. https://doi.org/10.1242/jeb.223545

Holberton, R. L., A. M. Dufty Jr, R. Greenberg, and P. Marra. 2005. Hormones and variation in life history strategies of migratory and nonmigratory birds. Pages 290-302 in R. Greenberg and P. P. Marra, editors. Birds of two worlds: the ecology and evolution of migration. John Hopkins University Press, Baltimore, Maryland, USA.

Howell, J. E., A. E. McKellar, R. H. Espie, and C. A. Morrissey. 2020. Predictable shorebird departure patterns from a staging site can inform collision risks and mitigation of wind energy developments. Ibis 162(2):535-547. https://doi.org/10.1111/ibi.12771

Irvine, R. J., F. Leckie, and S. M. Redpath. 2007. Cost of carrying radio transmitters: a test with racing pigeons Columba livia. Wildlife Biology 13(3):238-243. https://doi.org/10.2981/0909-6396(2007)13[238:COCRTA]2.0.CO;2

Jenni-Eiermann, S., and L. Jenni. 1991. Metabolic responses to flight and fasting in night-migrating passerines. Journal of Comparative Physiology B 161:465-474. https://doi.org/10.1007/BF00257901

Jenni-Eiermann, S., L. Jenni, A. Kvist, A. Lindström, T. Piersma, and G. H. Visser. 2002. Fuel use and metabolic response to endurance exercise: a wind tunnel study of a long-distance migrant shorebird. Journal of Experimental Biology 205 (16):2453-2460. https://doi.org/10.1242/jeb.205.16.2453

Kays, R., S. Tilak, M. Crofoot, T. Fountain, D. Obando, A. Ortega, F. Kuemmeth, J. Mandel, G. Swenson, T. Lambert, et al. 2011. Tracking animal location and activity with an automated radio telemetry system in a tropical rainforest. Computer Journal 54(12):1931-1948. https://doi.org/10.1093/comjnl/bxr072

Kelling, M., S. E. Currie, S. A. Troxell, C. Reusch, M. Roeleke, U. Hoffmeister, T. Teige, and C. C. Voigt. 2024. Effects of tag mass on the physiology and behaviour of common noctule bats. Movement Ecology 12(1):38. https://doi.org/10.1186/s40462-024-00477-7

Klaassen, M. 1996. Metabolic constraints on long-distance migration in birds. Journal of Experimental Biology 199(1):57-64. https://doi.org/10.1242/jeb.199.1.57

Lindström, Å., A. Kvist, T. Piersma, A. Dekinga, and M. W. Dietz. 2000. Avian pectoral muscle size rapidly tracks body mass changes during flight, fasting and fuelling. Journal of Experimental Biology 203(5):913-919. https://doi.org/10.1242/jeb.203.5.913

Ma, Y., C. R. Perez, B. A. Branfireun, and C. G. Guglielmo. 2018. Dietary exposure to methylmercury affects flight endurance in a migratory songbird. Environmental Pollution 234:894-901. https://doi.org/10.1016/j.envpol.2017.12.011

Maggini, I., L. V. Kennedy, A. Macmillan, K. H. Elliott, K. Dean, and C. G. Guglielmo. 2017. Light oiling of feathers increases flight energy expenditure in a migratory shorebird. Journal of Experimental Biology 220(13):2372-2379. https://doi.org/10.1242/jeb.158220

Magnusson, A., H. Skaug, A. Nielsen, C. Berg, K. Kristensen, M. Maechler, K. van Bentham, B. Bolker, M. Brooks, and M. M. Brooks. 2017. Package "glmmtmb." R Package Version 0.2.0.

McWilliams, S. R., C. G. Guglielmo, B. Pierce, and M. Klaassen. 2004. Flying, fasting, and feeding in birds during migration: a nutritional and physiological ecology perspective. Journal of Avian Biology 35(5):377-393. https://doi.org/10.1111/j.0908-8857.2004.03378.x

Mizrahy-Rewald, O., N. Winkler, F. Amann, K. Neugebauer, B. Voelkl, H. A. Grogger, T. Ruf, and J. Fritz. 2023. The impact of shape and attachment position of biologging devices in Northern Balk Ibises. Animal Biotelemetry 11:8. https://doi.org/10.1186/s40317-023-00322-5

Nisbet, I. C. T., W. H. Drury Jr, and J. Baird. 1963. Weight-loss during migration part I: deposition and consumption of fat by the Blackpoll Warbler Dendroica striata. Bird-Banding 34 (3):107-138.

Norberg, U. M. 1995. How a long tail and changes in mass and wing shape affect the cost for flight in animals. Functional Ecology 9(1):48-54. https://doi.org/10.2307/2390089

Obrecht III, H. H., C. J. Pennycuick, and M. R. Fuller. 1988. Wind tunnel experiments to assess the effect of back-mounted radio transmitters on bird body drag. Journal of Experimental Biology 135(1):265-273. https://doi.org/10.1242/jeb.135.1.265

Odum, E. P. 1960. Premigratory hyperphagia in birds. American Journal of Clinical Nutrition 8(5):621-629. https://doi.org/10.1093/ajcn/8.5.621

Pennycuick, C. J. 1969. The mechanics of bird migration. Ibis 111 (4):525-556. https://doi.org/10.1111/j.1474-919X.1969.tb02566.x

Pennycuick, C. J., P. L. F. Fast, N. Ballerstädt, and N. Rattenborg. 2012. The effect of an external transmitter on the drag coefficient of a bird's body, and hence on migration range, and energy reserves for migration. Journal of Ornithology 153:633-644. https://doi.org/10.1007/s10336-011-0781-3

Rae, L. F., G. W. Mitchell, R. A. Mauck, C. G. Guglielmo, and D. R. Norris. 2009. Radio transmitters do not affect the body condition of Savannah Sparrows during the fall premigratory period. Journal of Field Ornithology 80(4):419-426. https://doi.org/10.1111/j.1557-9263.2009.00249.x

Rappole, J. H., and A. R. Tipton. 1991. New harness design for attachment of radio transmitters to small passerines. Journal of Field Ornithology 62(3):335-337.

R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Řeřucha, Š., T. Bartonička, P. Jedlička, M. Čížek, O. Hlouša, R. Lučan, and I Horáček. 2015. The BAARA (Biological AutomAted RAdiotracking) system: a new approach in ecological field studies. PLoS ONE 10(2):e0116785. https://doi.org/10.1371/journal.pone.0116785

Suedkamp Wells, K. M., B. E. Washburn, J. J. Millspaugh, M. R. Ryan, and M. W. Hubbard. 2003. Effects of radio-transmitters on fecal glucocorticoid levels in captive Dickcissels. The Condor 105(4):805-810. https://doi.org/10.1093/condor/105.4.805

Taylor, P., T. Crewe, S. Mackenzie, D. Lepage, Y. Aubry, Z. Crysler, G. Finney, C. Francis, C. G. Guglielmo, D. Hamilton, et al. 2017. The Motus Wildlife Tracking System: a collaborative research network to enhance the understanding of wildlife movement. Avian Conservation and Ecology 12(1):8. https://doi.org/10.5751/ACE-00953-120108

Wickham, H., W. Chang, and M. H. Wickham. 2016. Package "ggplot2." Create elegant data visualisations using the grammar of graphics. Version 2(1):1-189.

Wilson, L. J., C. A. McSorley, C. M. Gray, B. J. Dean, T. E. Dunn, A. Webb, and J. B. Reid. 2009. Radio-telemetry as a tool to define protected areas for seabirds in the marine environment. Biological Conservation 142(8):1808-1817. https://doi.org/10.1016/j.biocon.2009.03.019

Woolnough, A. P., W. E. Kirkpatrick, T. J. Lowe, and K. Rose. 2004. Comparison of three techniques for the attachment of radio transmitters to European Starlings. Journal of Field Ornithology 75(4):330-336. https://doi.org/10.1648/0273-8570-75.4.330

Yap, K. N., M. F. Dick, C. G. Guglielmo, and T. D. Williams. 2018. Effects of experimental manipulation of hematocrit on avian flight performance in high-and low-altitude conditions. Journal of Experimental Biology 221(22):jeb191056. https://doi.org/10.1242/jeb.191056