

RESEARCH ARTICLE

Carrying a logger reduces escape flight speed in a passerine bird, but relative logger mass may be a misleading measure of this flight performance detriment

Barbara M. Tomotani^{1,2*}  | Wender Bil^{3*} | Henk P. van der Jeugd^{1,3}  |
Remco P. M. Pieters² | Florian T. Muijres² 

¹Department of Animal Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

²Experimental Zoology Group, Wageningen University & Research, Wageningen, The Netherlands

³Vogeltrekstation – Dutch Centre for Avian Migration and Demography, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

Correspondence

Florian T. Muijres
Email: florian.muijres@wur.nl

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Abstract

1. The recent boost in bird migration studies following the development of various tracking devices raised awareness of how detrimental attaching devices can be for animals. Such effects can occur during migration, but also immediately post-release if the device impairs escape flight performance and, consequently, the bird's ability to evade predators.
2. In this study, we investigated the effect of carrying a device on the escape flight speed and aerodynamic force production in a migratory passerine. We recorded upward-directed escape flights of 15 male blackcaps. Each individual was tested without a tag, and when equipped with three different leg-loop dummy tags with masses representing around 3%, 5%, and 7% of their body mass. The experiment was designed such that all individuals passed through all treatments in a randomized order.
3. We found that two factors affected flight speed in roughly equal amounts: first, tagged escape flights had lower flight speeds compared to the control flights, irrespective of tag mass. Second, we found an effect of the total mass, that is, the sum of the masses of the individual bird and of the tag, with heavier birds being slower. In contrast, flight speed was not correlated with relative tag mass in percentage of body mass, the metric commonly used in ethical guidelines for tag attachment. Aerodynamic flight force production also depended on total mass, with heavier birds producing higher forces. But these flight forces did not differ between flights with or without a tag.
4. We conclude that, when tagging birds, it is misleading to choose heavy individuals for tagging in order to minimize the tag mass as a percentage of body mass. This is particularly relevant in species for which body mass is not necessarily related to size, like migratory birds that accumulate large fat reserves. The lower escape speed in “tagged” flights could not be explained by differences in net flight force production, because these did not differ between flights with and without a tag. This suggests that the tag also affected pre-flight take-off dynamics, possibly due to a leg harness-induced reduction in leg push-off performance.

*These authors contributed equally to this work.

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bird flight, Eurasian blackcap, experiment, geolocator, predation, *Sylvia atricapilla*

1 | INTRODUCTION

The study of bird migration has greatly benefitted from the recent development of small and light tracking devices (Bridge et al., 2011). For example, due to their cheap production costs, light-level geolocation archival tracking devices (or shortly “geolocators”) are widely used in animal migration studies. Thanks to their relatively small weight they are suitable for studying even the smallest songbirds (Bridge et al., 2011; Stutchbury et al., 2009). This has allowed researchers to follow individual songbirds throughout their annual cycles, revolutionizing the study of bird migration and boosting the number of investigations looking at several migratory species (Bridge et al., 2011; Stutchbury et al., 2009).

Researchers, however, also started to question how detrimental carrying a device could be. It was expected that attaching a device to a bird would cause a variety of negative effects, not only in terms of survival, but also behavioural changes (Barron, Brawn, & Weatherhead, 2010; Costantini & Møller, 2013), raising both scientific and ethical concerns. For example, individuals may suffer from lowered reproductive output and lowered return rates (e.g., Arlt, Low, & Pärt, 2013); however, not all studies found a significant tag impact on breeding or survival, with many reporting low or no impact (e.g., Atema, Noordwijk, Boonekamp, & Verhulst, 2016; Peterson et al., 2015).

The primary functional mechanism that might cause a reduction in breeding success or survival is arguably the effect of tag attachment on the animal's flight performance. During steady forward flight, tag attachment could affect flight performance in two ways: First, the increase in total bird weight due to the tag requires the animal to produce additional aerodynamic lift (Lind, Jakobsson, & Kullberg, 2010). Second, the tag protrusion changes the shape and size of the bird, and therefore results in an increase in aerodynamic drag on the animal, requiring the animal to produce higher thrust during flight (Bowlin et al., 2010; Pennycuick, Fast, Ballerstädt, & Rattenborg, 2011). Because aerodynamic drag scales with the flight speed squared, the relative effect of weight and aerodynamic drag on flight efficiency varies with bird size, flight speed and streamlining of the tag (Bowlin et al., 2010; Pennycuick et al., 2011). Flight simulations for a range of small-sized to medium-sized birds showed that during migratory flights, where flight speeds are relatively high, aerodynamic drag has a larger detrimental effect on flight range than tag weight (Bowling et al., 2010, but also see Mathjasiak, Rubolini, Romano, & Saino, 2016).

In contrast with studies on migratory flights, the potential impact of tag attachment on birds at the breeding or wintering grounds is not widely discussed. During these annual-cycle stages, many birds tend to fly shorter distances and at lower flight speeds than during migration (but see Norberg, 1981), but they also tend to

perform more rapid flight manoeuvres such as sharp turns and take-off flights. These rapid flight manoeuvres are required for moving through dense vegetation or when capturing prey or escaping predators (Lind et al., 2010). The potential impact of tag attachment on the performance of such flight manoeuvres has not been thoroughly studied and merits further investigation. Because carrying devices may affect the escape performance, and thus, predation avoidance, such investigation is relevant not only to assess tag impacts on survival but also the potential indirect effects on behaviour.

One typical manoeuvre that is particularly important for survival is the rapid upward-directed take-off (Alexander, 2004). It is one of the most power-demanding flight manoeuvres in nature and can, therefore, only be executed by small-sized to medium-sized birds. It is distinct from horizontal steady flight, because during horizontal flight a bird beats its wings to produce forward-directed aerodynamic thrust that is in magnitude equal to the drag of the bird, but during an upward-directed flight manoeuvre, this thrust force needs to equal body drag plus the weight of the bird (Figure 1c,d). Moreover, in order to accelerate upwards, this thrust should even surpass the sum of drag and weight (Alexander, 2004).

Tags increase both the weight and drag of a bird, and therefore during ascending flight, tag attachment can be particularly detrimental to flight performance (Alexander, 2004; Barron et al., 2010). In contrast, flight speeds during vertical take-off manoeuvres are relatively low, and thus tag drag, which scales with velocity squared, might also be relatively low compared to that during high-speed migration flights. Therefore, we hypothesize that, opposed to the tag effect on migration flight, tag weight has a relatively high detrimental effect on upward-directed escape performance, whereas aerodynamic drag has a negligible effect.

We tested this hypothesis by filming the upward-directed flight performance of a migratory songbird, the Eurasian Blackcap (*Sylvia atricapilla*), carrying tags with variable weight but constant size and shape, and tested how each device type impacted their flight speed and net aerodynamic force production throughout the flight manoeuvre. We used especially designed dummy tags of three different weights, equalling circa 3%, 5%, and 7% of an average blackcap body mass. This tag mass range was chosen because, in order to reduce actual (or potential) impacts of tagging birds, a commonly observed principle is to use devices that do not weigh more than 5% of the body mass of the individual. This threshold rule is based on a suggestion first made by Brander and Cochran (1969), although there is no empirical basis for this rule in birds. The threshold rule was tested in bats (Aldridge & Brigham, 1988), showing that manoeuvrability decreased as load mass increased, but the authors also argued that the 5% rule might not always apply, particularly for relatively heavy individuals. Here, we argue that this 5% is, at most, an arbitrary value that does not necessarily apply to every species, and therefore in

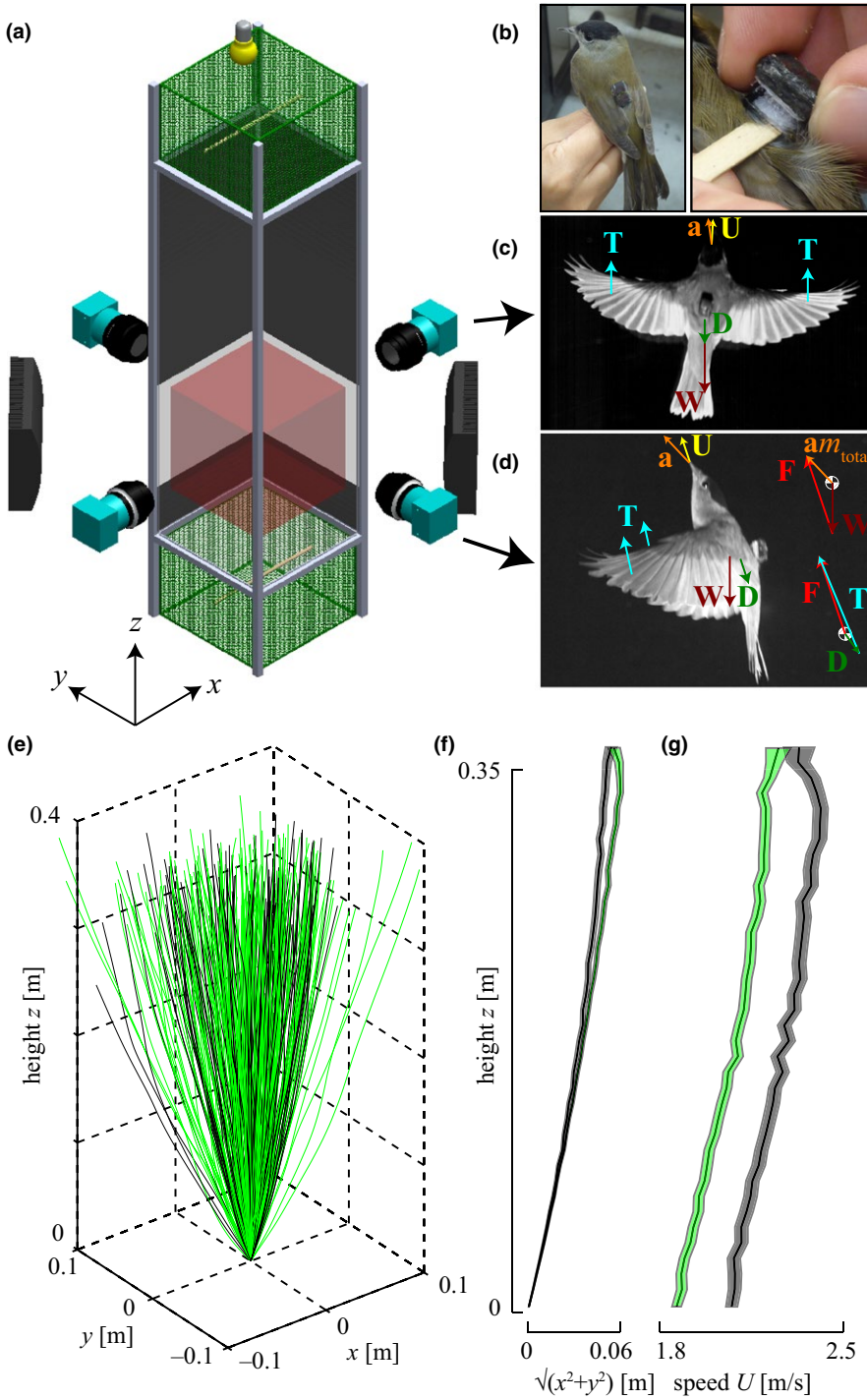


FIGURE 1 (a) Schematic representation of the experimental setup, with the focal area of the stereoscopic camera system highlighted in red; (b) design of the dummy tag and harness used on the birds; (c, d) Rear view image (c) and side view image (d) of a tagged flight, recorded using the high-speed cameras. The images include schematics of the velocity vector \mathbf{U} , acceleration vector \mathbf{a} , and primary forces acting on the flying animal: the thrust force produced by the beating wings \mathbf{T} , the weight of the animal \mathbf{W} , and the aerodynamic drag on the animal \mathbf{D} . (d) The net aerodynamic force \mathbf{F} equals the vector sum of thrust and drag, as well as the vector sum of weight and $\mathbf{am}_{\text{total}}$, where m_{total} is the total mass of bird and tag ($m_{\text{total}} = m_{\text{body}} + m_{\text{tag}}$). Relative vector sizes are not to scale; (e) three-dimensional trajectories of all measured flights, whereby trajectories of control flights are in black and tagged in green. The start of each track was aligned to $x = y = z = 0$ m; (f) horizontal vs. vertical movement of all control flights (black) and tagged flights (green); (g) flight speed vs. vertical movement of control flights (black) and tagged flights (green). In panel (e) and (f), results are shown as binned averages with binned standard errors

this study we also tested how valid this threshold rule is. Note that because there is a trade-off between device size/weight and battery life/quality of data, devices used for songbirds may be at or very close to this 5% limit, and thus testing the 5% threshold rule is particularly relevant for these animals.

Understanding the ways in which a device may affect the performance of rapid upward-directed flights and, consequently, predation avoidance is crucial for the success of studies that depend on tracking devices, not only for maximizing survival and return rates, but also to minimize the effect of tagging on the natural

behaviour of the studied individuals. Because the development of guidelines of tag use depends on experimental research, the present study aimed to assess how tag deployment may hinder the escape flight ability of a bird, with a focus on the impact at primarily the breeding and wintering grounds of migratory passerine birds. For this, we focused on the effect of tag attachment on the performance of upward-directed take-off manoeuvres as a proxy for predator escape performance, as tag-induced impaired take-off ability during a predator attack might determine survival probability to a great extent (Lind et al., 2010).

2 | MATERIALS AND METHODS

2.1 | Study species and experimental design

We used the Eurasian Blackcap as the model species for this work. We captured 15 male Blackcaps during autumn migration (between 18th and 20th of September) in the Netherlands around Utrecht (52.0907° N, 5.1214° E) and Wageningen (51.9692° N, 5.6654° E). Birds were immediately taken to the Netherlands Institute of Ecology where the flight tests took place. They were housed in individual 90 × 50 × 40 cm cages with ad libitum supply of water and food (live mealworms, crickets, and berries). Each individual was acclimatized to the captive conditions for exactly 1 week before being tested in the flight setup for the first time. After approximately 17 days in captivity, when experiments were finished, individuals were released further south along their migratory route (52.1260° N, 4.3386° E) to increase their survival probability.

We tested each individual bird in five different days (henceforth “flight day”), varying the treatment between days and with 1-day interval between each “flight day.” The first and last “flight days” always consisted of a control “flight day” (without a tag). The second, third, and fourth “flight days” consisted in the actual experimental “flight days” in which the bird was equipped with a dummy tag of either 0.49, 0.76, or 1.17 g. These masses roughly represent 2–3%, 4–5%, and 6–7% of an average blackcap body mass, and we will call them the “light tag,” “medium tag,” and “heavy tag,” respectively. We applied all treatments to each individual bird once and with the order of treatments randomly allocated to each individual. However, we also designed it in a blocked fashion, that is, all six possible combinations of treatment orders were used, with 2–3 individuals having the same combination, but planned in a way that we had exactly five “heavy tag,” “medium tag,” and “light tag” treatments in each experimental “flight day” (Table S1). It is important to clarify that a “flight day” is relative to the day that the bird arrived in the Institute. Thus, the first “flight day” is always the eighth day in captivity for that bird, but the corresponding calendar dates differ between individuals as they were caught within a 3-day interval.

Our dummy tags were fabricated using lead kernels inside a uniformly shaped and sized foam shell in order to minimize differences in aerodynamic drag between the treatments (Figure 1b). This was crucial to separate the effect of tag weight and drag on flight performance. In order to prevent any variation in tag manufacturing, we constructed a single “light tag,” a single “medium tag,” and a single “heavy tag,” each with dimensions of 13 × 8 × 8 mm (length × width × height). Birds may undergo physiological changes after tag attachment (Atema et al., 2016); to prevent this, we minimized tag exposure by fitting the tags to the birds immediately before each test and removed them as soon as the test was finished. To do that, 2 days before the second “flight day” (the first experimental “flight day”), we fitted a leg-loop harness with a piece of Velcro to the bird, which allowed us to easily attach the dummy tag before each “flight day” and remove it afterwards with minimal handling time

and stress for the bird (Figure 1b). Harnesses had an average weight of 0.15 g, which was included in the above-reported tag mass. We removed this harness after the last experimental “flight day,” and thus all control flights were done without any additional weight or harness.

In total, we recorded and digitized 118 manoeuvres of birds without a tag (control flights at the first and last “flight day”) and 178 manoeuvres of tagged birds (including all tag weights) (Figure 1e; Movies S1 and S2, respectively), distributed over 75 experimental blocks (Table S1).

2.2 | Flight setup and procedure

We collected flight performance data using an experimental setup consisting of a vertical flight chamber of 50 × 50 × 210 cm (width × depth × height), comprising a release box on the bottom, a collection box on top and in between a flight space of approximately 150 cm in length (Figure 1a, also see Tomotani, Muijres, Koelman, Casagrande, & Visser, 2018).

We filmed birds flying upward across a section of approximately 40 × 40 × 40 cm within the bottom half of the setup using a stereoscopic videography system, consisting of four synchronized high-speed cameras (Mikrotron EoSens MC1362). Each camera recorded at 400 frames per second, with a resolution of 1,020 × 1,020 pixels, and an exposure time of 1 millisecond (Movies S1 and S2). We used infrared lights (Bosch Aegis SuperLed 850nm) to illuminate the recording area, whereas a visible light source (40 W incandescent light bulb) illuminated the collection box (Figure 1a). The room where the experimental setup was placed was otherwise kept completely dark during all experiments.

At the start of each experimental day, we calibrated the stereoscopic camera system by placing a calibration grid in the setup. The calibration grid consisted of a randomly distributed array of lead beads on strings, covering the complete filming volume. We manually tracked the position of all beads in each camera view, and based on these we calibrated the camera system using a DLT calibration routine (Hatze, 1988).

At the start of an experiment, a single bird was weighed and placed on the perch of the release box at the bottom of the flight chamber. We elicited upward-directed flights by quickly opening the sliding door of the release box. This caused the bird to quickly fly upward towards the brightly illuminated collection box, and land on its perch. After perching inside the collection box, we closed the sliding door of the collection box and swapped the collection and release box, after which the experimental procedure could be repeated. In a few instances, birds would change direction mid-flight and land back on the bottom perch, or try to escape sideways. Therefore, for each day and bird combination, we recorded 5–8 consecutive flight sequences until we had a minimum of three straight fully completed upward-directed flight manoeuvres.

Throughout each flight sequence, we manually tracked the beak of the bird in each camera view (Hedrick, 2008), and used this as a proxy for the movement of the centre of mass of the bird. We

used the beak position because this point was easy to identify in each camera view, and because the beak oscillated relatively little as a result of the flapping wingbeat movements (Movies S1 and S2). Using the camera calibration, we converted the stereoscopic camera tracks into a three-dimensional flight path $\mathbf{X}(t)$, which was then Kalman filtered to remove tracking noise and estimate flight velocity and body acceleration throughout the flight trajectory ($\mathbf{U}(t)$ and $\mathbf{a}(t)$, respectively).

From the filtered flight velocities, we estimated the trajectory-mean total flight speed U , vertical flight speed U_z , and ascent angle γ . From the acceleration data, we estimated the net aerodynamic force produced by the bird throughout the flight manoeuvre as:

$$\mathbf{F}(t) = \mathbf{a}(t) m_{\text{total}} + \mathbf{g} m_{\text{total}}, \quad (1)$$

where m_{total} is the total mass of the bird body and tag combined ($m_{\text{total}} = m_{\text{body}} + m_{\text{tag}}$) in kg, and \mathbf{g} is the downward-directed gravitational acceleration vector ($\mathbf{g} = [0, 0, -9.81]$ m/s²). This net aerodynamic force also equals the sum of all aerodynamic thrust and drag forces produced by the animal (Figure 1d), and thus the animal should maximize this force to maximize escape performance. From the $\mathbf{F}(t)$ distribution throughout each flight track, we estimated the trajectory-mean total net flight force F and vertical net flight force F_z . Finally, because flight control might also be affected by carrying a device, we also estimated the tortuosity defined as:

$$\tau = \frac{\sum_{n=2}^N |\mathbf{X}_n - \mathbf{X}_{n-1}|}{|\mathbf{X}_N - \mathbf{X}_1|}, \quad (2)$$

where \mathbf{X}_n is the beak location at video frame n , and N is the last video frame tracked in that sequence.

2.3 | Statistical analyses

We tested the effect of treatment ("control," "light tag," "medium tag," and "heavy tag"), "total mass" (combined mass of bird and tag) and "flight day" (as a proxy for a learning effect) on the total flight speed, the vertical flight speed, ascent angle, net flight force production, vertical net flight force production, and tortuosity. We also tested for the relation between ascent angle and flight speed.

A post hoc analysis showed that birds did not differ in flight speed when carrying distinct tag types, thus, we also lumped all treatments into a single component ("tagged") and tested the effect of carrying a tag or not independently of the tag type on flight speeds and flight forces. Finally, we calculated for each individual the percentage of body mass that each tag represented and used this "percentage of body mass" instead of treatment and "total mass" as an explanatory variable for flight speed.

All analyses were performed in R version 3.4.3 (R Core Team, 2017), using the R packages "LME4" (Bates, Mächler, Bolker, & Walker, 2015) and "PBKRTTEST" (Halekoh & Højsgaard, 2014). To define the minimal model, we used backward model selection, dropping nonsignificant terms in each step. We used mixed-effect models with treatment (either all tag types or just "tagged" vs. "control"), "total mass", "flight

day", and the interaction between treatment and mass as fixed effects. In the case of the model with the "percentage of body mass" as an explanatory variable, we also included the "flight day" and a squared percentage of body mass because we expected a nonlinear relation between flight velocity and percentage of body mass, as suggested by the literature (Aldridge & Brigham, 1988). In all cases, we also included individual nested within a group variable that represented the order that each individual passed through the treatments (6 levels) as random effects to account for the fact that individuals were tested multiple times and with different orders of treatments across flight days.

3 | RESULTS

On average, the mass of birds in "control" flights did not differ from those in tagged flights (body mass excluding tag): "control": $m_{\text{body}} = 17.51 \pm 0.10$ g (mean \pm SE, $n = 30$); "tagged": $m_{\text{body}} = 17.54 \pm 0.08$ g ($n = 45$). However, between the treatment groups, the body masses of the birds were significantly different: "light tag": $m_{\text{body}} = 17.32 \pm 0.13$ g ($n = 15$), "medium tag": $m_{\text{body}} = 17.76 \pm 0.14$ g ($n = 15$), and "heavy tag": $m_{\text{body}} = 17.52 \pm 0.16$ g ($n = 15$). The average speed of the "control" flights was $U = 2.31 \pm 0.03$ m/s ($U_z = 2.27 \pm 0.03$ m/s, $n = 118$ flights), whereas for the tagged flights the average speed was $U = 2.13 \pm 0.03$ m/s ($U_z = 2.09 \pm 0.03$ m/s, $n = 178$ flights) (Figure 1g). The average ascent angles for the "control" and "tagged" flights were $\gamma = 81.4^\circ \pm 0.4^\circ$ and $\gamma = 80.4^\circ \pm 0.4^\circ$, respectively (Figure 1f). The average net aerodynamic force production in the "control" flight was $F = 0.227 \pm 0.003$ N ($F_z = 0.211 \pm 0.003$ N, $n = 118$ flights), and in the "tagged" flights force production was $F = 0.234 \pm 0.002$ N ($F_z = 0.217 \pm 0.002$ N, $n = 178$ flights). The flight paths tortuosity throughout the "control" and "tagged" flights were $\tau = 1.0039 \pm 0.0002$ and $\tau = 1.0042 \pm 0.0002$, respectively. See below and supplementary Tables S2–S6 for the full statistical analysis.

The vertical flight speed and force were both highly correlated with total speed and force, respectively (Figure S1; speeds: correlation coefficient: 0.99; $R^2 = 0.99$; slope: 0.97; $p < 0.01$, forces: correlation coefficient: 0.91; $R^2 = 0.83$; slope: 0.90; $p < 0.01$). Therefore, we will only present here the results related to the total flight speed and force (vertical component results are given in Tables S3 and S4).

For the total flight speed test with multiple tag types, the minimal model retained the "total mass" ($F_{1,209.32} = 7.76$; $p = 0.01$; slope = -0.08 ± 0.03), "tag type" ($F_{3,282.56} = 4.32$; $p = 0.01$; estimates: "control": $U = 3.30 \pm 0.49$ m/s; "light tag": $U = 3.26 \pm 0.50$ m/s; "medium tag": $U = 3.14 \pm 0.52$ m/s; "heavy tag": $U = 3.22 \pm 0.52$ m/s); and "flight day" ($F_{1,287.56} = 97.83$; $p < 0.01$; slope = 0.11 ± 0.01) terms, while the interaction "total mass" and treatment was not significant ($F_{3,276.23} = 0.56$, $p = 0.64$). Thus, flight speed increased in later days, indicating a learning effect, and heavier birds flew significantly slower than lighter ones. Tag type also had an effect on flight speed, but it did not follow the expected direction of heavier tags having the

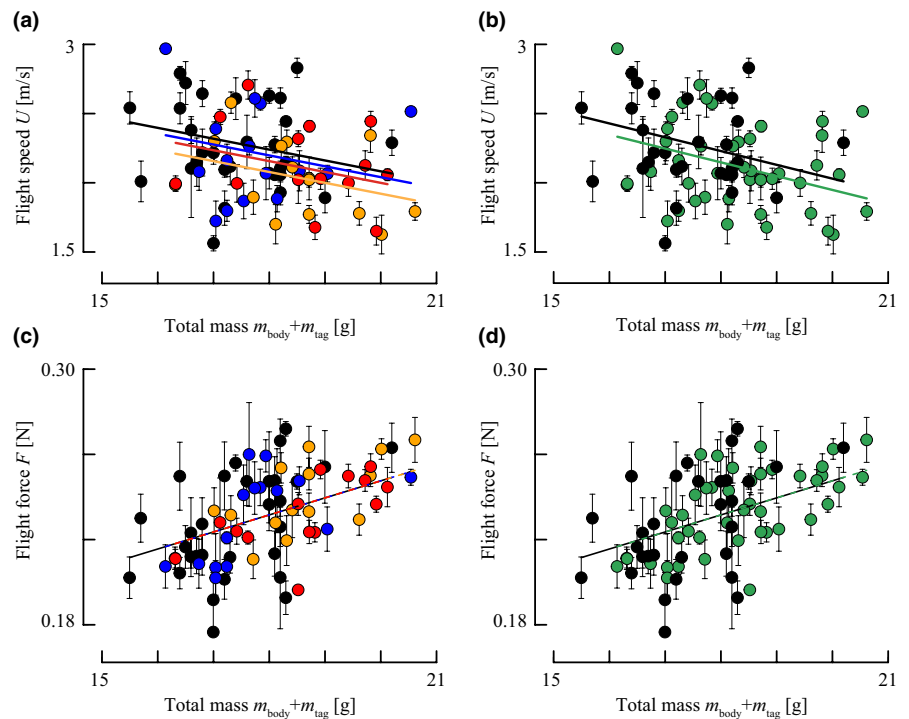


FIGURE 2 (a, b) Relationship between flight speed and total mass of bird and tag combined; (c, d) Relationship between the net aerodynamic flight force and total mass of bird and tag combined. Each data point represents the average and standard errors of all flights of a single individual on a specific “flight day.” Lines represent the model predictions. (a, c) All treatments separately (black=“control”; blue=“light tag”; orange=“medium tag”; red=“heavy tag”). (b, d) Treatments lumped into the single component “tag” flights (green) compared with “control” flights (black)

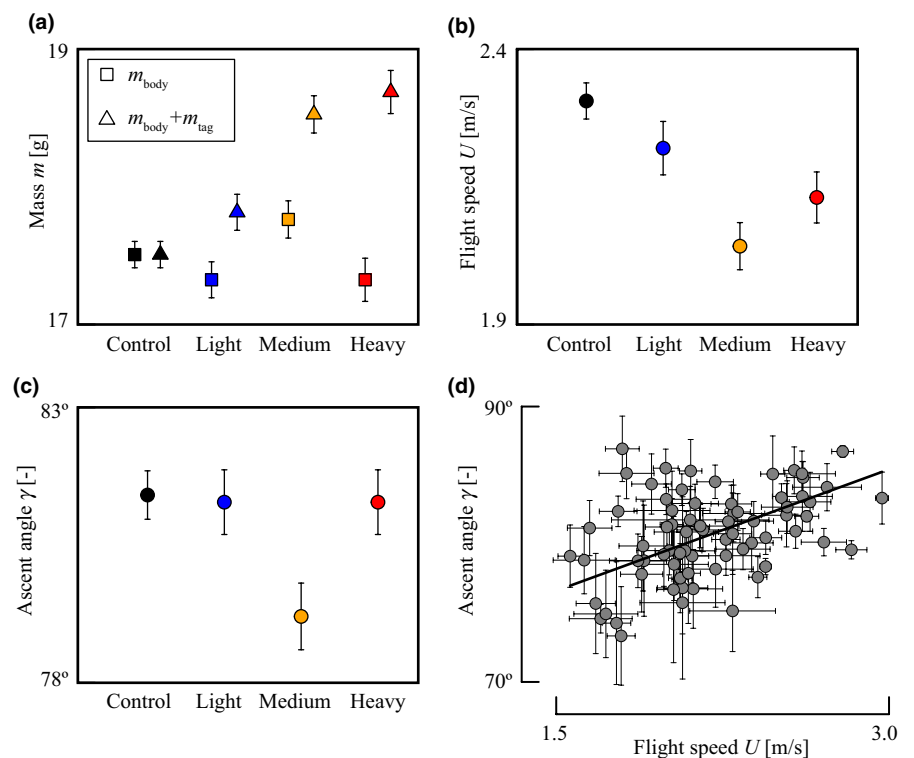


FIGURE 3 Average and standard error per treatment group of mass (a), flight speed (b), and ascent angle (c), whereby colours indicate treatment (black=“control”; blue=“light tag”; orange=“medium tag”; red=“heavy tag”). For average masses (a), we show both body mass without tag (squares) and total mass comprising of body mass and tag mass (triangles). (d) Relationship between ascent angle and flight speed, whereby each point represents the average and standard error of ascent angle and flight speed across all flights of an individual at a given “flight day”

strongest effect on performance (Figures 2a and 3b). A post hoc analysis showed that only control flights and “medium tag” flights had significantly different flight speeds, while the difference was borderline significant between flights with light and medium tags. Finally, there was no difference between the other treatment combinations.

The test on total flight speed with only “control or tagged” as treatments gave similar results as the test with multiple tag types (Figure 2b). The minimal model, again, retained the “total mass” ($F_{1,252.80} = 16.69$; $p < 0.01$; slope = -0.10 ± 0.02), “treatment” (control or tagged) ($F_{1,288.64} = 5.72$; $p = 0.02$; estimates: “control”: $U = 3.69 \pm 0.43$ m/s, “tagged”: $U = 3.60 \pm 0.45$ m/s), and “flight

day" ($F_{1,287.40} = 93.39$; $p < 0.01$; slope = 0.11 ± 0.01) terms, while the interaction "total mass" and "treatment" was not significant ($F_{1,281.91} = 0.64$, $p = 0.42$). Once more, flight speed was higher for later days and "control" flights.

Finally, the test of total flight speed with the tag mass in percentage of body mass as explanatory variable (Figure 4), showed that the quadratic term of the percentage of body mass was significant ($F_{1,162.58} = 7.13$; $p = 0.01$) but at the opposite direction as expected (quadratic estimate = 0.03 ± 0.01 , linear estimate = 0.31 ± 0.11). Thus, flight speed is lower for flights with tags of intermediate percentages of body mass in comparison to low and high percentages. Again, "flight day" was significant, with birds flying faster in later dates ($F_{1,161.12} = 66.71$; $p < 0.01$; slope = 0.19 ± 0.02).

We repeated the tests with all tag types and with "control or tagged" as treatments for the metric "net flight force" (Figure 2c,d). Striking in both tests was that, unlike for total flight speed, there was no effect of treatment (tag attachment) on force production (all tag types: $F_{3,274.06} = 1.59$; $p = 0.19$, Figure 2c; control or tagged: $F_{1,283.50} = 0.002$; $p = 0.97$, Figure 2d). Both tests also show that bird mass had a significant effect on the force production, with birds with a higher total mass producing higher forces (both tests: $F_{1,147.29} = 19.33$; $p < 0.01$; slope = 0.82 ± 0.17), suggesting that the birds respond to an increase in total body mass by working harder. "Flight day" was once more significant, with birds producing higher forces in later dates (both tests: $F_{1,290.38} = 7.05$; $p = 0.01$; slope = 0.27 ± 0.10), which is again indicative of learning.

The other two components, ascent angle and tortuosity were not related to the "total mass". Ascent angle was only explained by treatment ($F_{3,280.24} = 3.50$; $p = 0.02$), with flights in which birds carried a medium tag having a shallower angle than the others (estimates: "control": $\gamma = 81.25^\circ \pm 0.56^\circ$; "light tag": $\gamma = 81.25^\circ \pm 0.69^\circ$; "medium tag": $\gamma = 79.13^\circ \pm 0.67^\circ$; "heavy tag": $\gamma = 80.65^\circ \pm 0.72^\circ$; Figure 3c). A post hoc analysis revealed a similar pattern as the flight speed with only "control" flights and "medium tag" flights with significantly different ascent angles, borderline significant between light and

medium tags, and no difference among the other treatment combinations. Ascent angle was also significantly related to flight speed ($F_{1,216.12} = 41.06$; $p < 0.01$), with faster birds flying at a steeper angle (slope = 5.88 ± 0.89 ; Figure 3d). In this analysis, the flight number was also significant ($F_{1,288.06} = 4.38$; $p = 0.04$), with birds flying at shallower angles over time (slope = -0.45 ± 0.21). Tortuosity was only explained by "flight day" ($F_{1,282.43} = 7.60$; $p = 0.04$) with birds flying less straight in later days (slope = -0.0004 ± 0.0001).

Finally, when we tested differences in mass of the birds across treatments, we observed that birds not only differed significantly in their mass with tag as expected, but also in their body mass without tag (Figure 4a). This was partly due to the fact that, over time, birds first increased and then decreased their body masses. The post hoc analysis showed that when individuals were tagged with lighter tags they were also lighter themselves than when they were subjected to the other treatments. Moreover, when birds were equipped with "medium" and "heavy" tags they did not significantly differ in their "total mass" (mass with tag).

4 | DISCUSSION

The results of our experiment indicate that a reduction in flight performance measured as flight speed during rapid ascending flight is primarily caused by how heavy the bird is after deployment (Figure 2a,b), rather than how heavy the device is in relation to the animal's own mass (Figure 4). In addition, there is always a consistent extra effect of carrying a tag, irrespective of tag mass (Figure 2b).

The effect of absolute, overall mass is particularly evident in the results that looked at the effect of the percentage of body mass, where we obtained a reversed relation compared to what was expected (Figure 4), with the intermediate percentage of body masses having the lowest performances, while lower performances would be expected in higher relative percentages. Due to variation in body mass throughout the experiment, individual birds with medium tags were as heavy as when deployed with heavy tags in terms of "total mass" (body mass + tag mass). Consequently, when equipped with medium tags, birds showed a flight speed reduction comparable to that of carrying heavy tags, despite the relatively lower tag mass (Figure 3b). Therefore, our results suggest that, in a field situation, if one chooses birds to be tagged only based on their body mass, by tagging the heaviest individual with the lowest relative tag mass, one may, counterintuitively, end up choosing the birds that will have the poorest immediate post-deployment performance. The main result of our study can be readily seen when comparing panels a, b, and c in Figure 3: average flight speed (Figure 3b) and ascent angle (Figure 3c) associated with the three treatments mirror the associated bird weights (Figure 3a), albeit at a consistently lower level due to the added effect of carrying a tag.

To further highlight the effect of variation in body weight on escape flight performance, we modelled this effect based on the relation found between "total mass" (body mass + tag mass) and escape speed. Using only the lumped treatments as "tagged"

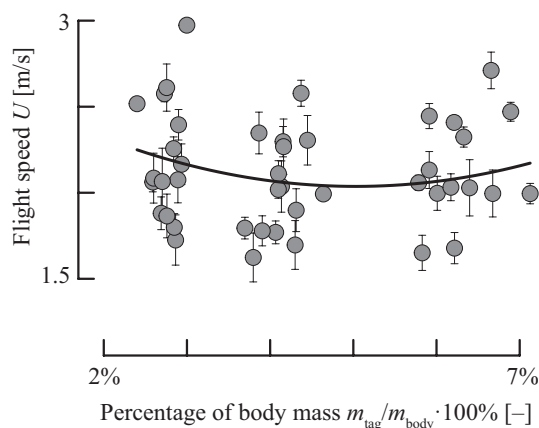


FIGURE 4 Relationship between flight speed and tag mass as percentage of body mass. Each data point represents the average and standard error of all flights of a single individual on a specific "flight day." The line represents the model prediction

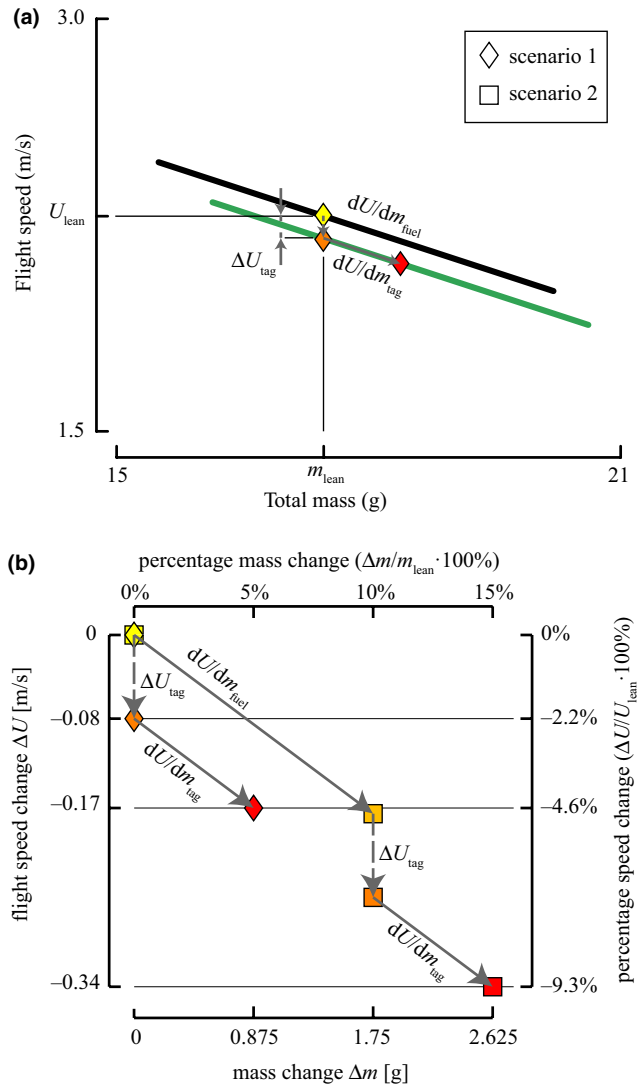


FIGURE 5 Simulations based on the predictions of the model that test for the effect of tag attachment on upward-directed escape flight speed (Figure 2b). (a) Scenario 1: A bird with a lean mass (m_{lean}) equal to the average of all “control” flights (17.5 g) receives a tag with a mass equal to 5% body weight ($m_{tag} = 0.05 m_{lean}$). (b) Scenario 1 (diamonds) vs. scenario 2 (squares): a lean bird and a bird fattened up for migration (fat mass equals 10% of lean body mass: $m_{fuel} = 0.1 m_{lean}$) both receive a tag equal to 5% lean body weight ($m_{tag} = 0.05 m_{lean}$). Results are provided as absolute changes in mass and flight speed, and as percentage of lean mass and speed of the lean bird

(Figure 2b). As suggested by our results, flight speed is affected by both the “total mass” and the fact that the animal is carrying a device. Thus, we assumed that adding a tag to a bird has two effects on upward-directed escape speed: First, there is an effect of tag attachment on flight speed that is independent of tag mass, and, second, there is an effect of total weight on flight speed. This weight effect corresponds to the “base” mass of the individual and any subsequent increase in mass, either due to external devices such as the tag, or a weight increase due to food or water intake (carried in the stomach) or from fattening up. Given these

assumptions, the reduction in upward-directed escape flight speed can be modelled as (Figure 5):

$$\Delta U = \Delta U_{tag} + \frac{dU}{dm} \cdot \Delta m, \quad (3)$$

where ΔU is the change in flight speed, ΔU_{tag} ($= -0.08$ m/s) is the effect of tag attachment on flight speed independent of tag weight, $\frac{dU}{dm}$ ($= -0.10$ m s $^{-1}$ g $^{-1}$) is the linear relation between flight speed and mass change, and Δm is mass change, for example, from tag attachment and/or increase in body weight after food/water intake.

Using equation 2, we can simulate two scenarios (Figure 5): Scenario 1: a blackcap with a lean body mass equal to the mass of all “control” flights in our dataset ($m_{lean} = 17.5$ gram) receives a tag with a mass equal to 5% of its own body mass ($m_{tag} = 0.05 m_{lean}$). Scenario 2: a blackcap with the same lean mass has fattened up for migration, which has resulted in an increase in body mass of 10% (fat fuel mass $m_{fuel} = 0.1 m_{lean}$). This bird receives a tag with the same mass as in scenario 1 (5% of m_{lean}).

In scenario 1, tag attachment alone reduces flight speed by 0.08 m/s in relation to a non-tagged individual (2.2% of U_{lean}), and the tag mass effect reduces flight speed by an additional 0.10 m/s per unit of mass increase (in grams). Therefore, the reduction in total flight speed caused by carrying a device is 0.17 m/s, which is a 4.6% reduction in flight speed (relative to U_{lean}). In scenario 2, the effect of the tag is the same as in scenario 1, but the bird’s fat load reduces the flight speed by an additional 0.17 m/s. Thus, in scenario 2, the total flight speed is reduced by 9.3% relative to U_{lean} .

At the moment of tagging, the relative tag mass was lower for scenario 2 (4.6%) than for scenario 1 (5%) but counterintuitively, the bird with the 5% tag (scenario 1) has a 0.17 m/s higher escape speed than the bird with the 4.6% tag (scenario 2) (Figure 5). These results are less counterintuitive when taking physics of flight into consideration (Alexander, 2004). According to Newton’s first law of motion, during ascending flight at a constant speed, the net upward-directed aerodynamic thrust force produced by the animal balances weight and aerodynamic drag of the animal (Figure 1d). These thrust forces are produced by the flapping wings and are powered by the flight muscles. Thus, flight performance should scale with wing morphology and flight muscle mass, and not body mass. This is particularly relevant for migratory birds such as the blackcap, because these birds can strongly vary in body mass when fattening up before migration (Kaiser, 1992; Langslow, 1976). Flight muscle mass in these birds will most likely not increase in an equal amount, and they will certainly not have larger wings. Therefore, the increase in fat mass can be expected to cause a reduction in escape flight performance. Adding a logger with a mass of 5% body mass to a heavily fattened-up bird might thus be particularly detrimental, as the combination of fat mass and tag mass might push the escape flight performance to critically low values.

The remaining question is: what caused the weight-independent detrimental effect of tag attachment on flight speed (Figure 5, $\Delta U_{\text{tag}} = -0.08$ m/s in Equation 2)? Arguably, the two most likely explanations for this weight-independent tag-induced reduction in flight speed are: (a) the tag might increase the aerodynamic drag on the bird, resulting in a reduction in net flight force production (Figure 1d) and consequently a decreased upward acceleration during flight, (b) the leg-loop harness might affect the freedom of leg movement during the push-off phase of the take-off. During the initial phase of an escape take-off, birds rely for a large part on leg-based push-off forces (Earls, 2000; Provini, Tobalske, Crandell, & Abourachid, 2012), and thus a leg-loop harness that restrains leg movement would significantly affect force production during this push-off phase, but not during the flight phase.

We tested which one of the two explanations is most likely using the net flight force results (Figure 2d). These results show that, unlike flight speed, flight force did not differ between the tagged and control flights, showing that tag attachment did not negatively affect net in-flight force production. This suggests that the weight-independent tag-induced reduction in flight speed might originate from the take-off dynamics prior to the time-window of our measurements. This notion is further supported by the mean flight speed tracks of all control and tagged flights (Figure 1g), which shows that the increase in flight speed throughout the flight track is similar between control and tagged flights, but tagged flights have a lower initial flight speed, resulting in an almost constant speed offset between control and tagged flights. These combined results are thus in support of the second explanation that the leg-loop harness might reduce the freedom of leg movement during the push-off phase of the take-off, prior to our measurement window.

In addition, the combined results support of our hypothesis that, relative to tag weight, aerodynamic drag caused by tag attachment has a negligible effect on upward-directed escape speed. Note that we do not expect that our tags do not generate any aerodynamic drag, but simply that—during upward-directed escape manoeuvres—tag-induced drag is most likely not responsible for the measured mass-independent reduction in flight speed. The negligible effect of tag-induced drag on escape speed could be due to motivation differences (tagged birds might compensate for increased drag by producing extra thrust), or because at the relatively low flight speeds of escape manoeuvres, tag drag is negligible relative to the thrust required for the bird to carry its own weight and accelerate upwards (Figure 1d). A future study, focusing specifically on the effect of differently shaped and sized loggers on escape performance, could answer this question (Bowlin et al., 2010; Pennycuik et al., 2011).

In summary, for an average blackcap, the mass-independent and mass-dependent tag effects on escape flight speed are roughly similar in magnitude (Figure 5), suggesting that both the harness attachment and the weight of a tag significantly reduce escape performance. We suggest to explicitly test and quantify the harness attachment effect on escape performance using experiments focussing on the push-off phase, rather than the flight

phase, of an escape take-off. Such future study would allow the comparison of different attachment methods, in order to optimize harness design.

The tag mass effect on escape performance depends on the total mass of bird and tag combined, and thus not on the commonly used metric of tag-to-body mass ratio. Hence, our results suggest that in order to maximize the chance of a bird to survive the post-release period, it is important to base the allowed tag mass for a bird species on the average lean mass of that species, and not, for example, on body mass at the onset of migration. Moreover, we also propose that when tagging individual birds, it is important to avoid tagging the heaviest birds captured in order to minimize relative tag mass, but instead to preferably tag the larger birds.

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AUTHORS' CONTRIBUTIONS

H.P.vdJ. and F.T.M. conceived the ideas for the study; B.M.T., H.P.vdJ., and F.T.M. developed the experimental procedure; B.M.T., R.P.M.P., and F.T.M. designed the experimental setup; R.P.M.P. built the setup; B.M.T. and W.B. performed the experiments; F.T.M. developed the analysis tools; B.M.T. and W.B. tracked the videography data; B.M.T. and F.T.M. analysed the data; B.M.T. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Flight performance metrics, treatment information, and flight tracks of all analysed upward-directed escape flight manoeuvres of blackcaps with and without tags are available in the Dryad Digital Repository with the Digital Object Identifier <https://doi.org/10.5061/dryad.961nn65> (Tomotani, Bil, van der Jeugd, Pieters, & Muijres, 2018).

ORCID

Barbara M. Tomotani  <http://orcid.org/0000-0002-8855-4803>

Henk P. van der Jeugd  <http://orcid.org/0000-0002-5332-9526>

Florian T. Muijres  <http://orcid.org/0000-0002-5668-0653>

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