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Two methods of radio transmitter attachment and their effects on the behavior and energetics of captive long-tailed ducks (*Clangula hyemalis*) during winter

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Abstract

Background: Attachment of external devices can have negative consequences for the health and fitness of subjects, but these effects are often overlooked. In preparation for a field study with small sea ducks, we investigated the effects of two types of external radio transmitter attachments on activity budgets and energetics of captive long-tailed ducks (*Clangula hyemalis*) during winter.

Methods: We conducted behavioral observations on 15 ducks over 3 months and measured oxygen consumption rates while resting on water and during preening. Ducks were either sham handled ('Control') or had transmitters attached with subcutaneous anchors ('Prongs') or Tesa tape/sutures ('Tesa').

Results: Following transmitter attachment, the activity budgets of Prong and Tesa birds changed significantly, while Controls remained largely unchanged. Prong and Tesa birds reduced locomotor activity (−58 and −54 %, respectively) and the proportion of time spent in water (−48 and −35 %, respectively), while they concomitantly increased time allocated to maintenance behavior (+98 and +151 %, respectively). Tesa birds recovered from these changes over time, at least partially, but Prong birds did not. Also, two of the five Prong birds developed a bacterial infection that spread from the attachment site. Retention time of transmitters was significantly greater for the Prong attachments (4 of 5 tags were retained for the entire 59-day study) than the Tesa technique (26.0 ± 3.2 days). Energy metabolism of ducks resting on water did not change significantly after transmitter attachment. Preening, the primary maintenance behavior, increased oxygen consumption rates by ~70 % over resting. The greater allocation of time to maintenance behavior after transmitter attachment most likely increased daily energy expenditure in these ducks, although the concurrent reduction in locomotor activity might have mitigated this effect. Ducks in our study had food ad libitum and were able to reduce locomotion after transmitter attachment without compromising food intake and, hence, energy balance. In the wild, this strategy might not be viable.

Conclusions: Given the short retention time, the tape-based attachment technique we applied is not suitable if monitoring periods greater than ~2 to 3 weeks are desired. Both methods resulted in significant behavioral changes with energetic consequences that should be considered when planning to attach external transmitters to small sea ducks in the wild.

Keywords: Radio transmitters, Instrumentation effects, Activity budget, Behavior, Energetics, Subcutaneous anchors, Long-tailed ducks, Sea ducks, Respirometry, Tag attachment

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Background

Advances in biotelemetry have led to the development of a multitude of miniaturized transmitting and recording devices that can be attached directly to a growing number of species, enabling the collection of, among other things, vital life history information, often crucial for conservation purposes [1, 2]. These advances are especially promising for the study of species where continuous direct observation is difficult, if not impossible, like many marine vertebrates. In the particular case of sea ducks, telemetry studies have revealed important aspects of their spatial and temporal distribution and led to the discovery of wintering areas and migration corridors for many species of concern (e.g., Steller's eiders *Polysticta stelleri*, spectacled eiders *Somateria fischeri*, and long-tailed ducks *Clangula hyemalis*), which are critical for conservation efforts [3–5].

However, attaching devices to animals might affect their behavior, physiology, and ecology in many ways. Barron and colleagues [6] conducted a meta-analysis of the various effects of transmitters on avian behavior and ecology, which included 84 published studies. They concluded that device attachment to birds had negative effects on most aspects of the birds' behavior and ecology [6]. The most substantial effects were increased energetic costs, a reduced likelihood for nesting, and in extreme cases mortality. Alterations in energy budgets when carrying devices can result from changes in behavior (e.g., time spent foraging, maintenance behavior [7, 8]), increased locomotion costs (e.g., increased mass and/or drag affect flight/diving energetics [9–12]), changes in thermoregulation (e.g., plumage disruption increasing heat loss [7, 13, 14]), and potential changes in metabolism associated with 'stress' [15].

Clearly, wildlife researchers must balance the importance of a research question with the consideration of potential harm that specific techniques may bring to the study subjects, especially when studying threatened and declining wildlife populations. In addition to the ethical concerns, there is also the question of whether acquired data might be biased by instrumentation effects [16].

The potential effects may differ greatly between attachment methods [6]. The choice of attachment technique used will depend on the particular ecology of the animal in question, the size, shape, and weight of the device, and the desired retention time of instruments. Devices have been attached to aquatic birds using a variety of techniques, including a number of external attachment techniques and device implantation [17, 18]. Surgical implantation typically allows for a much longer retention time [19–21] than external attachment techniques, which are often used for short-term studies, ranging from single foraging trips in penguins (using tape [18]) to a few months in ducks and small alcids (using a subcutaneous anchor [22–25]) and up to several months in geese (using a harness [26]). While Barron and colleagues in their meta-analysis found that the type of attachment method had no influence on the strength of detrimental effects, they did report that anchored and implanted transmitters, which usually require anesthesia, were associated with the highest device-induced mortality rates [6]. Another meta-analysis of telemetry effects simplified their comparison to whether the device was externally attached or surgically implanted and found that external devices have a consistent negative effect, whereas implanted devices had no consistent effect, leading the authors to conclude that device implantation is preferable [27]. That recommendation, however, likely only applies to studies where logistics and timing allow for proper invasive surgical technique and with species known to tolerate the anesthesia and implant surgery. For some studies where short handling times are necessitated, or where it is not known how the species might react to the surgical procedure, external attachment methods might be the best choice if the study only requires relatively short monitoring periods.

In preparation for a field study with small sea ducks during winter, our study examined the suitability of two different external attachment techniques, the subcutaneous Prong anchor technique and a tape and suture technique (hereafter, referred to as 'Prong' and 'Tesa' technique, respectively) for attaching a radio transmitter to long-tailed ducks. The Prong technique is currently in use, but its level of invasiveness raises some concerns; so we compared it to the less invasive Tesa technique. We evaluated the potential effects associated with these attachment techniques, by measuring behavioral and energetic parameters in ducks carrying transmitters and in a control group ('Controls'). We investigated the following questions:

1. Which technique (i.e., Prong versus Tesa) is best suited for short-term (1–3 months) radio transmitter attachment to a small sized sea duck, in terms of tolerance by ducks (i.e., behavior and energetic costs) and transmitter retention time?
2. Does transmitter attachment affect the behavior of ducks, i.e., is there a change in the activity budget of ducks?
3. Are there measureable energetic costs associated with transmitter attachment?
4. Do the potential effects on behavior and energetics differ with attachment technique?
5. Do birds acclimate to transmitter attachment, i.e., do any potential behavioral and energetic effects diminish with time?

Methods

Fifteen long-tailed ducks (*Clangula hyemalis*; 8 males and 7 females; between 0.4 and 4.4 years old, mean age ± SEM: 1.8 ± 0.3 years) were obtained from Dry Creek Waterfowl (Port Angeles, WA, USA) and housed communally in a purpose designed outdoor pen at the Alaska SeaLife Center (Seward, AK, USA). The outdoor aviary was 41 m^2 and was constructed of an aluminum frame enclosed with nylon mesh fencing. Opposite a dry resting area, four fiberglass pools (2 × 2 m, 0.6 m deep) were fitted into the frame and continuously supplied with seawater. Ducks were fed a diet of floating Mazuri sea duck pellets (Purina Mills, St. Louis, MO, USA), supplemented with krill (*Euphausia superba*), blue mussels (*Mytilus edulis*), silversides (*Menidia menidia*), and clams (supplements accounted for less than 5 % of their total diet). Pellets were contained in two automatic feeders, placed above water, from which birds could dispense food ad libitum (birds took on average ~80 g per day each). Feeding occurred mainly at the surface; but when pellets fell into the water and eventually sank, birds dived for them and ingested small quantities underwater. Body masses of ducks (M_b; post-absorptive and dry) were obtained before each respirometry trial and on a weekly basis throughout the rest of the study period. Ducks were held for 6 weeks within this setting before experimentation started. All experimental procedures were approved by the Alaska SeaLife Center Institutional Animal Care and Use Committee (Permit #R11-95-05).

Experimental design

Our study took place during the Alaskan winter (Nov. 2011 to Feb. 2012). Before observations started, the 15 ducks were randomly assigned to three different treatment groups, consisting of five ducks each: (1) Prong: transmitters attached using two subcutaneous stainless steel anchors [28], (2) Tesa: transmitters attached using Tesa tape and sutures, and (3) Control: birds that were captured and handled but that did not receive a transmitter. Over the course of 3 months, we conducted behavioral observations and respirometry trials, which were split into distinct treatment periods: (1) the 'pre-attachment period' before any transmitter attachment occurred, which served as a baseline (Nov. 25 to Dec. 08, 2011); (2) the 'attachment-1 period', which was conducted immediately following transmitter attachment (Dec. 10 to Dec. 30, 2011); (3) the 'attachment-2 period', after an acclimation period of 3 weeks (Jan. 02 to Feb. 03, 2012); (4) the 'post-attachment period' after early transmitter loss or removal of remaining transmitters (Feb. 06 to Feb. 20, 2012). Respirometry trials were conducted during the first three periods, while behavioral observations were conducted during all four periods. At the end of the pre-attachment period, all 15 birds were captured and a radio transmitter (mass: 6.4–8.4 g; dimensions: 3.5 cm long × 2 cm wide) with antenna (1.5 mm in diameter, 21 cm in length) was attached to ten of the birds (Prong or Tesa), while the remaining five birds (Controls) underwent the same procedure, without receiving a transmitter. Of the ten birds that received a transmitter, subcutaneous anchors (Prongs) were used in five, while we used the tape-based attachment technique (Tesa) for the remaining five ducks. The design and attachment procedure for the subcutaneous anchors (Prongs) were described in detail by Lewis and Flint [28]. In brief, a 20 × 15 mm, 20-gauge stainless steel anchor was permanently fixed to the anterior base of the transmitter. To the posterior end of the transmitter, a 20-gauge stainless steel wire was fixed and bent into a hollow barrel (2.5 × 2 mm, 4-mm high), which received the posterior anchor. A 16-gauge needle (2.5-cm long) was used to puncture the skin for placement of the anchors. For the tape-based attachment technique, we used two suture anchors (placed transversely through the skin at the anterior and posterior end of the transmitter and secured through holes in the device) and three strips of Tesa tape (Beiersdorf AG, Hamburg, Germany; 6 cm long, 1.5 cm wide), which were applied adhesive side up to groups of feathers and attached to the transmitter in overlaying fashion [18]. In both cases, the transmitter was attached midline, dorsal to the thoracic spine, between the scapulas of a duck (Fig. 1). Transmitter attachment required on average 5 min for the Prong birds (range 3–7 min) and 10 min for the Tesa birds (range 9–13 min).

Behavioral observations

To obtain activity budgets from ducks during the various phases of our study, we conducted behavioral observations of the entire flock of 15 birds. All observations were made from a station overlooking the outside duck aviary behind tinted windows. Each bird was marked with a unique combination of color bands to enable identification. Observations were conducted by a two-person team, one acting as the observer and the other as timer/recorder. During each session, the flock was observed for periods of 30 min. Sessions were scheduled randomly throughout each treatment period and occurred on all days of the week and during all available daylight hours (09:30–15:00 h; i.e., from 30 min after sunrise to 30 min before sunset). Observations were made at least five times a week. During each 30-min observation session, the entire flock was scan sampled once every 2 min, using binoculars, and the behavior and location (land/water) of each individual was recorded [29]. We distinguished between the following behavioral categories: resting (land/water), maintenance (preening, wing flapping,

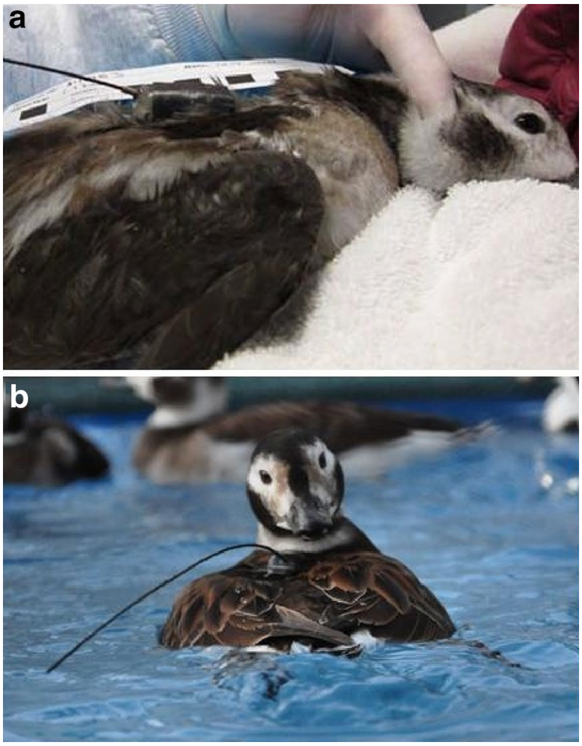
Fig. 1 Attachment of radio transmitters. **a** Transmitters (mass 6.4–8.4 g; dimensions 3.5-cm long × 2-cm wide) with antenna (1.5 mm in diameter, 21 cm in length) were attached midline, dorsal to the thoracic spine, between the scapulas of a duck. **b** Transmitter on the back of a duck floating in the pool. In both cases shown here, the transmitter was attached with Tesa tape

stretching, shaking, bathing), locomotion (walking, running, flying, swimming, diving), foraging (feeding, drinking), and others (alerted and social behaviors). All categories but resting were classified as active behaviors.

Respirometry system

We used an open-circuit respirometry system to measure the oxygen consumption rates ($\dot{V}O_2$) of ducks floating calmly on water. Resting on water was chosen as the behavioral category to investigate any potential energetic costs that might be associated with transmitter attachment, since it contributes strongly to the activity budget of ducks in the wild, especially during winter [30], but we also determined the cost of preening. Our setup consisted of (1) a clear plexiglass chamber in the shape of a dome (39 cm in diameter, 22-cm high; volume: ~30 l), serving as the respirometer, (2) a primary flow control unit ('Flowkit 100', Sable Systems International, Las Vegas, NV, USA), and (3) an integrated gas analyzer unit ('FMS', Field Metabolic System, Sable Systems). The plexiglass dome was positioned upright in the middle of a holding tank (1 × 1 m, 1-m deep), which had seawater flowing through it at a low rate. This seawater was supplied from the SeaLife Center's non-recirculating supply, pumped from the ocean, so the temperature of the water varied with the ambient seawater temperature in the ocean adjacent to the Center. The open bottom end of the plexiglass dome was slightly submerged within the seawater tank to provide a seal. Four small holes, evenly spaced, were drilled into the side walls of the dome near its bottom, just a few centimeters above the waterline, which allowed ambient air to enter the dome. During a trial, the primary flow control unit pulled air through the chamber at a rate of 9 l min^{-1} (automatically corrected to STP, 273 K and 101.3 kPa). A subsample (200 ml min^{-1}) was passed through a humidity meter (RH-300), a CO_2 analyzer, and a fuel cell oxygen analyzer (i.e., the FMS unit). Oxygen and CO_2 concentrations within the chamber, main flow rate through the chamber, humidity of the gas sample, and barometric pressure were recorded every second onto a laptop computer using ExpeData (Sable Systems). All connections between the various components of the respirometry system were made using gas-impermeable tubing. The O_2 analyzer was calibrated before each trial using ambient air scrubbed of water vapor and CO_2 (set to 20.95 % O_2; the zero point was fixed and not subjected to drift). The CO_2 analyzer was calibrated daily using 99.995 % pure N_2 and 1.01 % CO_2 (Air Liquide, America Specialty Gases LLC, Longmont, CO, USA). The humidity meter was calibrated weekly according to recommendations of the manufacturer. We used wet and dried (using magnesium perchlorate) ambient air to set the span and zero water vapor pressure reading (kPa), respectively. We regularly tested our system using N_2 dilution [31] and by burning known amounts of 100 % ethanol using a clean burning lamp [32].

The respirometry system was set up in a well-ventilated indoor area, adjacent to the outside duck holding pen. We chose this location because weather conditions were often severe during the study period and air temperatures outside fluctuated strongly between −14 and 3 °C. By contrast, inside air temperatures remained stable at 13 °C.

Respirometry trials

All respirometry measurements were conducted during the hours of daylight (9:30–15:00 h) with post-absorptive birds (birds were fasted overnight for at least 16 h). Before a trial, a bird was captured in its holding pen, weighed, and left in a transportation cage indoors for a period of at least 30 min to acclimate to inside conditions. It was then placed into the respirometry dome. After initial disturbance, birds typically calmed down quickly and floated calmly inside the dome for the remainder of the trial. To reduce any disturbance (visually and acoustically) from the experimenter, the seawater tank, containing dome and bird, was placed behind a wall, constructed from insulated wooden boards, and lighting was kept very low, comparable to the end of civil twilight. To enable observation of the bird during a trial, a low-light video camera was positioned on top of the dome and connected to a video monitor, sitting beside the respirometry equipment. Water temperature (T_w) was recorded for each trial using an NIST traceable thermometer.

Ducks behaved differently following transmitter attachment. While some birds continued to rest and float calmly during trials, others were more agitated, often pecking at the transmitter and/or engaging in preening. To obtain a representative resting measurement, trials continued up to 2 h (mean trial duration: 1.5 h). In cases where birds were not resting, trials were repeated on subsequent days to obtain a qualifying 'resting' measurement. Only trials during which birds appeared calm and the corresponding oxygen consumption trace remained stable for at least 10 min were included in the analysis of resting metabolic rate.

Data analysis and statistics

Behavioral data were compiled and for each behavioral category its proportional occurrence was calculated for each bird by dividing the number of times a certain behavior was observed in an individual by the total number of observations for that individual. The reported 'proportion of time' that birds engaged in a particular behavior assumed that the recorded behavior remained unchanged for the duration of each scan (2 min). Grand means were calculated for each category from bird means. In our statistical analysis, we first compiled the proportions for all behavioral categories during the pre-attachment period for all treatment groups and tested for significant differences between treatment groups. This served as our baseline to which all other observations were compared. In the following analysis, we investigated how proportions for the various behavioral categories changed over the course of the treatment period within each treatment group and between treatment groups. Comparisons were made within a treatment group (across treatment periods) or within a treatment period (across treatment groups), rather than across multiple treatment group/period interactions. Tesa birds started to lose their transmitters within 16 days of attachment and all transmitters in that group were lost before the end of the attachment-2 period. If a bird lost its transmitter, all subsequent behavioral observations after transmitter loss for this individual were only included in the post-attachment period category and observations continued until the end of the study.

Respirometry data were analyzed using ExpeData. During analysis, gas analyzer drift and lag time of the respirometry system were corrected for. Main flow rate was corrected to STP dry (STPD) using Eq. 8.6 in Lighton [32]. Similarly, we did not scrub water vapor before gas analysis, but corrected for this dilution effect during data analysis using Eq. 15.3 in Lighton [32]. Oxygen consumption rate ($\dot{V}O_2$) and CO_2 production rate ($\dot{V}CO_2$) were calculated using Eqs. 11.7 and 11.8 in Lighton [32], respectively.

From each respirometry trial, a stable 10-min segment of oxygen consumption rate data ($\dot{V}O_2$) was selected when birds floated calmly inside the respirometry dome without preening, to represent the resting metabolic rate of the bird for that trial [33]. For each distinct treatment period, we aimed to obtain two independent measurements of $\dot{V}O_2$ per bird. After transmitter attachment, ducks more frequently engaged in preening behavior during respirometry trials. To obtain an estimate of the energetic costs associated with preening, a 10-min period during which preening behavior had been observed was selected from the recorded trace and an average $\dot{V}O_2$ was calculated. Oxygen consumption rate values are presented mass specifically as $s\dot{V}O_2$ (ml min^{-1} kg^{-1}).

Statistical summaries and analyses for all behavioral data were conducted in R [34], while all other statistical analyses were conducted using JMP (v. Pro 9.0.2, SAS Institute Inc.). For the behavioral data, we compared the proportional occurrence of all behavioral categories for both sexes and between treatment periods and treatment groups using a two-sided Pearson's Chi-squared test to determine inequality in the proportions. The same test was used to test if weather conditions (temperature, precipitation, and wind) differed between treatment groups over the course of the study, which could have affected bird behavior. This was particularly important after Tesa birds dropped their transmitters before the scheduled date of removal, which resulted in different calendar dates for the post-attachment period of Tesa birds compared with the other treatment groups (Prong/Control). For the respirometry data, the effects of treatment and treatment period on $s\dot{V}O_2$ of ducks resting on water were tested using a linear mixed-effects model (LME; standard least squares regression fitted by restricted maximum likelihood). Similarly, LME analysis was also used to test for differences in $s\dot{V}O_2$ of ducks resting on water or preening and for the effect of T_w on duck $s\dot{V}O_2$. Where appropriate, interaction terms were included in the respective model. Treatment (Prong, Tesa, Control), treatment period (pre-attachment, attachment-1, attachment-2), T_w, and behavior (resting vs. preening) were included as fixed effects, while bird ID was included as a random effect. For example, we used the following mixed linear effects model to test whether treatment and/or treatment period affected duck resting $s\dot{V}O_2$: $s\dot{V}O_2 =$ treatment group + treatment period + treatment group × treatment period + bird ID [random]. To test for differences in duck body masses between treatment groups and treatment periods, and to test for differences in transmitter retention times, we also used LME analysis. Significance for all statistical tests was accepted at $p < 0.05$. All mean values are presented with standard error (SEM).

Results

Efficacy of transmitter attachment methods and bird health status

The retention time of transmitters was significantly greater for the Prong attachment technique than the Tesa technique ($F = 82.23$, $p < 0.0001$, $df = 1$). The mean retention time for the Tesa attachment technique was 26.0 ± 3.2 days (range 16–34 days), while the Prong attachment in four out of five birds lasted for the entire pre-determined attachment period (i.e., 59 days). Body mass of birds averaged 666 ± 23 g (range 511–818 g) during the pre-attachment period and 657 ± 21 g (range 505–808 g) upon study completion and did not differ between treatment groups at any point of the study ($F = 0.29$, $p = 0.75$, $df = 2$). However, the model returned a significant body mass change across treatment periods ($F = 10.28$, $p = 0.0002$, $df = 2$) and a significant interaction between treatment group and treatment period ($F = 3.02$, $p = 0.03$, $df = 4$). Further tests showed that this was explained by Tesa birds, which lost on average ~4 % of their mass (from pre-attachment to post-attachment period; $F = 7.05$, $p = 0.006$, $df = 3$), while body mass in the other treatment groups remained stable over the course of the study (Control: $F = 0.45$, $p = 0.72$, $df = 3$; Prong: $F = 3.14$, $p = 0.08$, $df = 3$). Two out of five Prong birds encountered health problems after transmitter attachment. One Prong bird was found dead on the morning of the 2nd day after transmitter attachment. It had not been handled since attachment and appeared outwardly normal up to that point, but it died of bacterial septicemia that originated at the prong insertion site. A second Prong bird also developed an increased white blood cell count due to an infection at the implant site, but it was treated with antibiotics and showed no other symptoms. Apart from this, regular health checks revealed no differences in overall health status of birds, regardless of treatment.

Behavioral observations

Over the course of the study, 25,500 individual behavioral observations from 15 long-tailed ducks were recorded. In our study design, we attempted to acquire a comparable number of observations across sexes (14,460 male vs. 11,040 female observations), treatment groups (9225 Control vs. 7425 Prong, and 8850 Tesa observations), and treatment periods (4050 pre-attachment vs. 13,515 attachment, and 7935 post-attachment observations). We found no significant differences between males and females in the proportion of time birds engaged in resting (0.21 for both sexes; $\chi^2 = 2.93$, $df = 1$, $p = 0.087$) or active behaviors (0.79 for both sexes; $\chi^2 = 3.0$, $df = 1$, $p = 0.083$), regardless of treatment group and treatment period. During the pre-attachment period, Control birds were somewhat more active than Prong and Tesa birds and rested less often than the other two groups (Table 1). This was mostly accounted for by the

Table 1 Proportion of time spent in various behavioral categories during the different treatment periods for all treatment groups

Treatment	Period	Resting	Active	Active behaviors			
				Maintenance	Locomotion	Foraging	Others
Control	Pre-attachment	0.20 ± 0.01	0.80 ± 0.01	0.14 ± 0.01	0.43 ± 0.01	0.13 ± 0.01	0.10 ± 0.01
Control	Attachment-1	0.23 ± 0.01	0.77 ± 0.01	0.16 ± 0.01	0.31 ± 0.01	0.23 ± 0.01	0.07 ± 0.01
Control	Attachment-2	0.16 ± 0.01	0.84 ± 0.01	0.16 ± 0.01	0.40 ± 0.01	0.18 ± 0.01	0.10 ± 0.00
Control	Post-attachment	0.20 ± 0.01	0.80 ± 0.01	0.15 ± 0.01	0.37 ± 0.01	0.15 ± 0.01	0.13 ± 0.01
Prong	Pre-attachment	0.24 ± 0.01	0.76 ± 0.01	0.14 ± 0.01	0.38 ± 0.01	0.16 ± 0.01	0.08 ± 0.01
Prong	Attachment-1	0.29 ± 0.01	0.71 ± 0.01	0.27 ± 0.01	0.16 ± 0.01	0.22 ± 0.01	0.06 ± 0.01
Prong	Attachment-2	0.20 ± 0.01	0.80 ± 0.01	0.31 ± 0.01	0.20 ± 0.01	0.20 ± 0.01	0.09 ± 0.01
Prong	Post-attachment	0.24 ± 0.01	0.76 ± 0.01	0.22 ± 0.01	0.27 ± 0.01	0.13 ± 0.01	0.14 ± 0.01
Tesa	Pre-attachment	0.26 ± 0.01	0.74 ± 0.01	0.14 ± 0.01	0.37 ± 0.01	0.13 ± 0.01	0.10 ± 0.01
Tesa	Attachment-1	0.24 ± 0.01	0.76 ± 0.01	0.34 ± 0.01	0.17 ± 0.01	0.20 ± 0.01	0.05 ± 0.00
Tesa	Attachment-2	0.22 ± 0.02	0.78 ± 0.02	0.21 ± 0.01	0.26 ± 0.02	0.26 ± 0.02	0.05 ± 0.01
Tesa	Post-attachment	0.17 ± 0.01	0.83 ± 0.01	0.22 ± 0.01	0.36 ± 0.01	0.14 ± 0.01	0.11 ± 0.00

Values shown are grand means (±SEM), which were established from individual bird means ($N = 5$ birds per treatment group). Values from the pre-attachment period served as baseline for comparisons. For a first comparison, the proportions for resting and active behavior are shown. Active behavior is then divided into its constituents: maintenance (preening, wing flapping, stretching, shaking, and bathing), locomotion (walking, running, flying, swimming, and diving), foraging (feeding and drinking), and others (alerted and social behaviors) frequency that they engaged in locomotive behavior, especially swimming and diving (Table 1; Fig. 2). By contrast, the observed proportion of time spent in foraging behavior and maintenance (i.e., preening) did not differ between the treatment groups during the pre-attachment period ($\chi^2 = 3.32$, $df = 2$, $p = 0.19$ and $\chi^2 = 0.24$, $df = 2$, $p = 0.88$, respectively; Table 1; Fig. 2c).

After transmitter attachment, we did not observe any substantial changes in the overall ratio between resting and active behaviors, which remained relatively constant (apart from small and variable changes) over the course of the study, regardless of treatment (Table 1). However, within the active behavior category, the relative contribution of particular behaviors changed considerably in ducks that received a transmitter. Three major behavioral differences between Controls and Prong/Tesa birds occurred after transmitter attachment. (1) Prong and Tesa birds reduced the proportion of time spent in water, especially during the period immediately following transmitter attachment (a reduction of 48 % for Prong birds and 35 % for Tesa birds; $\chi^2 = 193.11$, $df = 1$, $p < 0.0001$, and $\chi^2 = 148.31$, $df = 1$, $p < 0.0001$, respectively; Fig. 2a). While Tesa birds recovered appreciably with time ($\chi^2 = 0.26$, $df = 1$, $p = 0.60$ for post-attachment), this was not the case for Prong birds, where changes persisted even after transmitter removal ($\chi^2 = 75.09$, $df = 1$, $p < 0.0001$; Fig. 2a). (2) There was also a reduction in locomotor activity (especially, swimming and diving) in Prong and Tesa birds immediately following transmitter attachment ($\chi^2 = 159.66$, $df = 1$, $p < 0.0001$, and $\chi^2 = 136.09$,

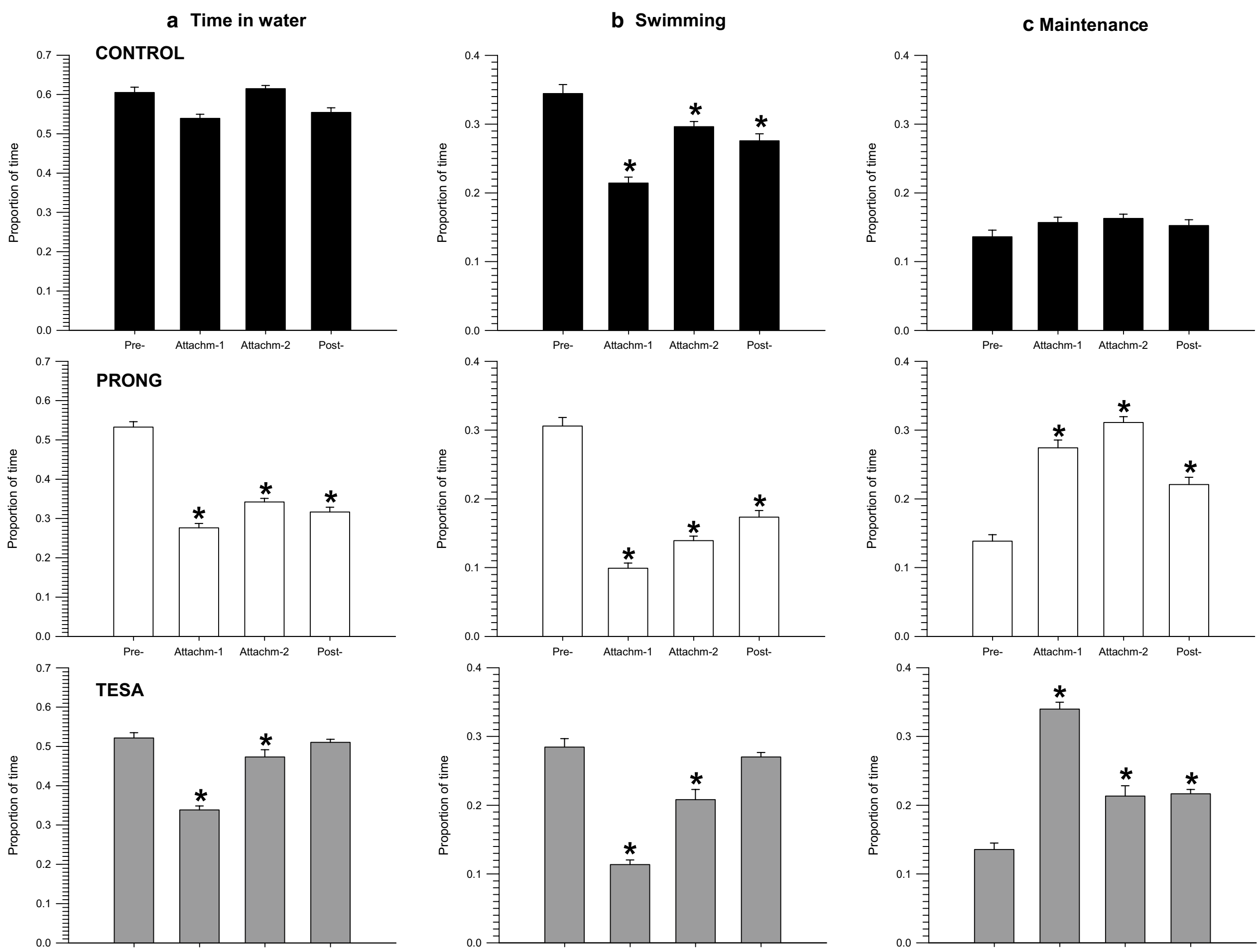

Fig. 2 Behavioral changes observed in the different treatment groups over the course of the study. Values are grand means (±SEM), established from individual bird means ($N = 5$ birds per treatment group). *Asterisks* indicate a significant difference from the pre-attachment period. **a** Proportion of time ducks spent in water (resting, maintenance, locomotion, foraging, others). **b** Proportion of time birds engaged in swimming behavior. **c** Proportion of time ducks spent in maintenance behavior. The activity budget remained stable in Control birds, but changed significantly after transmitter attachment in Prong and Tesa birds. While Tesa birds recovered from these changes over time, at least partially, this was not the case for Prong birds

$df = 1$, $p < 0.0001$, respectively; Table 1; Fig. 2b). During this period, locomotor activity was reduced to ~1/3 that of the pre-attachment period in both of these groups. Again, Tesa birds slowly recovered from this ($\chi^2 = 0.27$, $df = 1$, $p = 0.59$ for post-attachment), but locomotion proportions never fully reached pre-attachment values in Prong birds and remained decreased by ~1/3 during the post-attachment period ($\chi^2 = 39.11$, $df = 1$, $p < 0.0001$; Table 1; Fig. 2b). Diving activity was especially affected and declined strongly in Prong and Tesa birds following transmitter attachment (to ~15 % and ~25 % of the pre-attachment value in Prong and Tesa birds, respectively). Diving activity remained at this low level in Prong birds, while Tesa birds recovered during the post-attachment period. (3) Lastly, the proportion of time spent in maintenance behavior (preening) greatly increased in Prong and Tesa birds after transmitter attachment ($\chi^2 = 68.67$, $df = 1$, $p < 0.0001$, and $\chi^2 = 146.62$, $df = 1$, $p < 0.0001$, respectively; Table 1; Fig. 2c). In Prong birds, the proportion of time engaged in maintenance behavior remained elevated throughout the remainder of the study ($\chi^2 = 111.06$, $df = 1$, $p < 0.0001$, and $\chi^2 = 29.62$, $df = 1$, $p < 0.0001$ for the attachment-2 phase and the post-attachment period, respectively), while it decreased appreciably in Tesa birds during the attachment-2 phase (but remained significantly elevated, $\chi^2 = 23.92$, $df = 1$, $p < 0.0001$). By contrast, in Control birds the proportional time spent in water ($\chi^2 = 5.12$, $df = 3$, $p = 0.16$) and maintenance behavior ($\chi^2 = 5.42$, $df = 3$, $p = 0.14$) remained stable throughout the entire study (Table 1; Fig. 2a, c, respectively). Locomotor activity (especially swimming) also declined in Control birds, particularly during the attachment-1 phase ($\chi^2 = 44.66$, $df = 1$, $p < 0.0001$). However, the scope of this decline was significantly less (~half) than that of Prong/Tesa birds ($\chi^2 = 34.37$, $df = 1$, $p < 0.0001$) and locomotor activity returned to near pre-attachment values thereafter in Control birds (Table 1; Fig. 2b). Finally, the proportion of observed foraging behavior (feeding and drinking) changed in all groups throughout the study, following a similar pattern (Table 1). This was most likely caused by changes in weather conditions (most importantly air temperatures) over the course of our study, so that birds spent a greater proportion of time feeding in response to colder temperatures.

Energy expenditure

Oxygen consumption rates of long-tailed ducks resting on water did not differ between treatment groups during the pre-attachment period ($F = 1.70$, $p = 0.22$, $df = 2$ Table 2; Fig. 3) and averaged 28.53 ± 0.93 ml min^{-1} kg^{-1}. Following transmitter attachment, resting $s\dot{V}O_2$ did not change significantly between treatment groups, despite a tendency to increase in Prong/Tesa birds (Table 2; Fig. 3). Hence, we did not observe a significant effect of treatment on duck resting $s\dot{V}O_2$ ($F = 1.70$, $p = 0.23$, $df = 2$; $N = 15$ birds, $n = 78$ observations). However, there was a significant effect of treatment period on duck resting $s\dot{V}O_2$ ($F = 5.32$, $p = 0.008$, $df = 2$). Resting $s\dot{V}O_2$ was significantly increased during the attachment-2 period (i.e., 2–4 weeks after transmitter attachment; $t = 3.07$, $p = 0.0033$, $df = 2$; Table 2; Fig. 3), mainly due to the increased $s\dot{V}O_2$ values of Prong and Tesa birds. There was no interaction between treatment group and treatment period ($F = 1.06$, $p = 0.39$, $df = 4$).

Water temperature decreased significantly over the course of the study ($F = 79.80$, $p < 0.0001$, $df = 2$), from 6.7 ± 0.1 °C during pre-attachment to 5.4 ± 0.1 °C during the attachment-2 period. However, the effect of T_w per se on duck resting $s\dot{V}O_2$ over the course of the study was not significant ($F = 2.23$, $p = 0.14$, $df = 1$).

After transmitter attachment, Prong and Tesa birds often engaged in preening behavior during respirometry trials. During these preening periods, $s\dot{V}O_2$ of ducks was significantly increased over resting by ~70 % ($F = 282.09$, $p < 0.0001$, $df = 1$; Table 2) and averaged 46.66 ± 2.01 ml min^{-1} kg^{-1}.

Discussion

Prong versus Tesa attachment technique: retention time and bird health status

Our results indicate that a tape-based attachment technique, while causing no observed health issues, is not suited for a study of long-tailed ducks requiring monitoring periods greater than ~2 to 3 weeks. The retention time in our study was short within the Tesa group, where the first transmitter was lost less than 2.5 weeks after attachment and all five transmitters were lost within 5 weeks. The Prong technique provided a much greater retention time, and four out of five transmitters were still attached to a duck at the end of our pre-determined attachment period of 2 months. However, given the invasive nature of the Prong technique, the potential for infections is a problem. Within 2 days of transmitter attachment, one of our Prong birds died due to a bacterial infection, while a second Prong bird required antibiotic treatment. Accordingly, when using this technique, the possibility for bacterial infections should be considered, especially in areas with potential microbial contamination of the environment.

Energy expenditure during the pre-attachment period

The oxygen consumption rates we measured in our ducks when they floated calmly on water (pre-attachment period) were comparable to values reported by Jenssen and Ekker [35] for winter-acclimatized long-tailed ducks of smaller body mass, measured under similar conditions

Table 2 Oxygen consumption rates ($s\dot{V}O_2$) (ml min^{-1} kg^{-1}) of long-tailed ducks during respirometry trials

Bird	Sex/age (years)	Treatment	M_b (g)	Resting $s\dot{V}O_2$ (ml min^{-1} kg^{-1})			Preening	
				Pre-attachment	Attachment-1	Attachment-2	$s\dot{V}O_2$ (ml min^{-1} kg^{-1})	Factorial increase
019	f/1.4	*Control*	644 ± 6	34.40 ± 2.66	30.29 ± 0.05	31.23 ± 1.18		
1082 J	m/2.4	Control	691 ± 4	27.01 ± 0.31	26.49 ± 0.27	27.10 ± 0.22		
1084 J	m/2.4	Control	760 ± 12	29.28 ± 1.66	31.26 ± 1.03	31.77 ± 0.70		
7269 J	f/0.4	Control	578 ± 4	31.83 ± 0.17	32.68 ± 1.72	30.59 ± 1.91		
773 J	f/3.4	Control	588 ± 4	28.73 ± 1.17	30.10	32.99 ± 0.46		
Grand mean			*652 ± 34*	*30.25 ± 1.29*	*30.17 ± 1.03*	*30.73 ± 0.99*		
1083 J	m/2.4	*Prong*	684 ± 6	23.65 ± 0.25	26.20 ± 0.70	25.96 ± 0.48	48.32	2.04
4584 J	f/1.4	Prong	590 ± 21	28.62 ± 1.95	32.23		54.21 ± 1.27	1.89
4585 J	m/1.4	Prong	675 ± 13	23.03 ± 0.11	23.49 ± 0.33	32.75 ± 0.85	43.53 ± 4.79	1.89
7230 J	m/2.4	Prong	687 ± 7	25.61 ± 1.41	26.16 ± 0.72	28.46 ± 0.80	39.28 ± 5.99	1.53
7268 J	f/0.4	Prong	561 ± 2	30.71 ± 3.18				
Grand mean			*639 ± 27*	*26.32 ± 1.47*	*27.02 ± 1.85*	*29.06 ± 1.98*	*46.33 ± 3.21*	*1.84 ± 0.11*
002	m/1.4	*Tesa*	775 ± 9	26.84 ± 2.07	26.45 ± 2.30	29.26 ± 0.58	39.88	1.49
003	m/1.4	Tesa	787 ± 11	27.51	28.49	31.30 ± 0.68	44.56 ± 2.31	1.62
016	m/1.4	Tesa	729 ± 12	31.97 ± 2.11	34.53 ± 0.81	30.82 ± 2.33	51.21 ± 1.91	1.60
14198 J	f/0.4	Tesa	514 ± 4	34.41	34.31	34.28 ± 2.42	52.31	1.52
586 J	f/4.4	Tesa	586 ± 3	24.41	30.81 ± 0.11	36.27 ± 2.60		
Grand mean			*678 ± 54*	*29.03 ± 1.82*	*30.92 ± 1.59*	*32.39 ± 1.27*	*46.99 ± 2.92*	*1.56 ± 0.03*

Values are means ± SEM which, in case of resting $s\dot{V}O_2$, were averaged from two trials conducted per bird during each treatment period. M_b values were averaged from measurements taken before each trial over the course of the study period. Grand means were established from individual bird means. The different treatment groups and treatment periods are indicated. Shown also are the $s\dot{V}O_2$ values for ducks when preening during trials, which occurred in all but one duck after transmitter attachment (Prong and Tesa birds only). The factorial increase indicates how much $s\dot{V}O_2$ during preening was increased over the resting situation before transmitter attachment (pre-attachment)

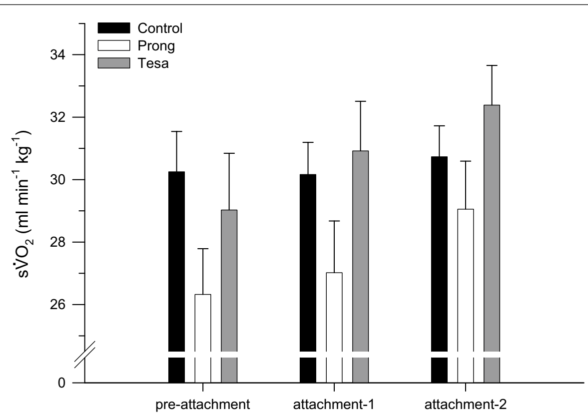

Fig. 3 Oxygen consumption rates (ml min^{-1} kg^{-1}) of long-tailed ducks resting on water ($N = 15$ birds, $n = 78$ observations). Values shown are means (±SEM) established from five birds per treatment group and two respirometry trials per bird and treatment period. Oxygen consumption rates did not differ significantly between treatment groups during the pre-attachment period and after transmitter attachment

(mean M_b was 666 g in the current study vs. 490 g in Jenssen and Ekker [35]). Mean $s\dot{V}O_2$ when our ducks rested on water at 6.7 °C was 28.53 ± 0.93 ml min^{-1} kg^{-1}, which was ~10 % higher than the corresponding value predicted from the regression equation in Jenssen and Ekker [35]. Jenssen and Ekker [35] reported a lower critical temperature of 12 °C for their ducks in water. Water temperature during our trials was below this lower critical temperature, so that ducks had to thermoregulate, elevating their metabolism well above the basal metabolic rate (BMR) of 17.0 ml min^{-1} kg^{-1} reported by Jenssen and Ekker [35].

Behavioral and energetic changes associated with transmitter attachment

The proportion of time Control ducks engaged in the various behavioral categories (apart from a temporary, less substantial, decline in locomotion behavior) and their oxygen consumption rate while resting on water remained stable throughout the treatment period (Tables 1, 2; Fig. 2a–c). This suggests that any behavioral/energetic changes observed in the Prong/Tesa groups are genuinely associated with transmitter attachment. Transmitter attachment significantly altered the behavior of long-tailed ducks, regardless of attachment technique. Most noticeably, immediately after transmitter attachment, Prong and Tesa birds significantly reduced the proportion of time spent in water, as they reduced locomotor activity (especially swimming) to ~1/3 its pre-attachment value (Table 1; Fig. 2a, b). In parallel, these birds increased the proportion of time spent in maintenance behavior (preening) by 98–151 % (Table 1; Fig. 2c). There is some indication that Tesa birds acclimated to transmitter attachment over time, as most behavioral changes returned toward baseline (but remained significantly different from the pre-attachment period) over the course of the study (notably during the attachment-2 period; Table 1; Fig. 2). By contrast, behavioral changes in Prong birds persisted even into the post-attachment period. All Tesa birds lost their transmitters before the planned date of removal, so that all behavioral observations after transmitter loss for these birds were placed into the post-attachment phase and were continued until the end of the study. This resulted in a longer post-attachment phase and a greater number of observations during this phase for Tesa birds, when compared with Prong birds. Accordingly, Tesa birds had a longer period to recover from the effects of transmitter attachment during the post-attachment phase than Prong birds. However, a clear reversal in the behavioral changes associated with transmitter attachment in Tesa birds had already occurred before the post-attachment phase (i.e., during the attachment-2 phase), suggesting at least a partial recovery. This was clearly not the case in Prong birds. Furthermore, Tesa birds that dropped their transmitter early might have experienced environmental conditions at the beginning of their post-attachment phase that differed from those of Prong and Control birds that entered the post-attachment phase at a later date, with potential consequences for their recovery. However, weather conditions (temperature, precipitation, and wind) during the post-attachment period did not differ significantly between treatment groups, regardless of date.

Similar behavioral changes in response to external transmitter attachment have been reported for a number of avian species (see [6] and references therein). An extreme case, for example, was reported by Perry [7], when wild canvasbacks (*Aythya valisineria*) equipped with radio transmitters greatly increased maintenance behavior, so that some birds spent about three-fourths of the daylight hours on shore pulling on the transmitter. Such abnormal behavior was observed for up to 2 weeks after transmitter attachment [7]. In a similar study on captive mallards (*Anas platyrhynchos*) and blue-winged teal (*Anas discors*) equipped with back-mounted radio packs, birds increased preening behavior, while the number of birds engaging in swimming and diving behavior decreased [36]. In a more recent study, female breeding Barrow's goldeneyes (*Bucephala islandica*) were found to decrease feeding time and increase maintenance activities in the wild in response to the external attachment of radio transmitters [8].

Clearly, changes in behavior after external device attachment seem to be common and are well documented in the literature. However, to understand how these behavioral changes might impact on the fitness or even survival of animals, it is important to consider the potential energetic costs associated with device attachment [14]. In parallel with our behavioral observations, we therefore conducted respirometry trials to investigate potential changes in energy metabolism after transmitter attachment. Ideally, we should have measured energy expenditure during a number of behaviors, especially costly behaviors, like diving, or better yet, over full days. Transmitter attachment will increase hydrodynamic drag during diving [11], thereby potentially causing changes in dive behavior [12] and energy expenditure [10]. Including a number of behavioral categories in this energetics investigation might have enabled us to establish a detailed time–energy budget for our ducks [37] and, consequently, assess how transmitter attachment might have affected it. However, we decided to investigate the energy metabolism of long-tailed ducks when floating/resting on water because, apart from foraging, this behavior contributes most strongly to the activity budget of sea ducks in the wild, especially during winter [30]. Many sea ducks, and particularly long-tailed ducks, are considered to be diurnal feeders [38], which will mostly float/rest during the hours of darkness. Hence, the metabolic costs associated with resting on water should contribute substantially to the energy budget of sea ducks.

We expected that oxygen consumption rate ($s\dot{V}O_2$) of long-tailed ducks resting on water after transmitter attachment would be increased based on the following considerations: (1) Birds might be 'stressed' by carrying a transmitter and/or by the attachment procedure. Birds are known to secrete corticosterone in response to variable 'stressors' on a short-term basis [39], but also over longer time periods [40]. Since corticosterone has a marked influence on metabolism [41], it might have affected the $s\dot{V}O_2$ of ducks. (2) Transmitter attachment might disrupt the plumage of ducks, which would leave them more prone to heat loss, especially when on water, elevating thermoregulatory costs. Increased heat loss around externally anchored transmitters due to feather (down) disruption has been indicated in a study on mallard ducklings, albeit without apparent effect on energy metabolism [13]. Increased thermoregulatory costs were also seen as the main factor contributing to the greater daily energy expenditure (DEE) of free-living flightless Takahe (*Porphyrio mantelli*) when carrying radio transmitters [14]. Contrary to our expectations, the oxygen consumption rate ($s\dot{V}O_2$) of ducks resting on water was not significantly elevated after transmitter attachment (Table 2; Fig. 3). Such elevation might have been concealed by the observed inter- and intra-individual variability in $\dot{V}O_2$ measurements (Table 2), as ducks probably were not always equally calm during trials.

However, after transmitter attachment, both Prong and Tesa birds often engaged in maintenance behavior (preening) during the respirometry trials. Oxygen consumption rate during these periods was significantly increased, on average by ~70 %, when compared with resting behavior (Table 2). Accordingly, if birds increase the proportion of time they engage in maintenance/preening behavior, this carries some energetic consequences. If birds substitute resting with preening time, this will increase their DEE, requiring more food and, consequently, a greater foraging effort. However, our captive birds concomitantly reduced the proportion of time they engaged in energetically costly activities (i.e., locomotion) and also reduced the time spent in water. While this might indicate some discomfort associated with the attachment procedure and/or some plumage issues (i.e., feather disruption causing increased heat loss), reducing locomotor costs must have to some degree offset the elevations in DEE associated with increased maintenance activity. It is unclear how representative the behavioral responses we observed in our captive ducks might be for long-tailed ducks in the wild.

Relevance to sea ducks wintering at high latitude

When compared with other waterfowl, sea ducks spend substantial amounts of their time feeding, which is probably a consequence of their diet, typically low in caloric density [30]. Long-tailed ducks have been observed to spend ~80 % of the daylight hours during winter foraging [38, 42]. These ducks forage predominantly on motile prey (e.g., crustaceans and fish [43, 44]), which might require sufficient light conditions for successful capture and prevent night foraging. Foraging activity in long-tailed ducks was also shown to change with temperature, so that foraging time was greatest during the coldest months [38, 42]. Accordingly, Goudie and Ankney [42] suggested that these small sea ducks have little buffering capacity to adjust their foraging behavior to changes in environmental conditions. Building on that, Systad and colleagues suggested that the high diving rate they observed in their birds during midwinter (long-tailed ducks spent 53 % of daylight hours underwater) might be close to the maximum rate possible for this species [45]. The long-tailed duck is also one of the smallest sea duck species, so that energetic constraints might be considerable when wintering at high latitude. Small body size, their foraging mode (diving in cold water to potentially great depth [46]), and the cold/windy weather they encounter during winter will all make them especially vulnerable to heat loss, so that DEE might be high. It might be difficult for these ducks, even under undisturbed conditions, to balance their energy budget during a time when foraging is restricted by short day length and when prey availability might be unfavorable.

The findings from our captive study indicate that external transmitter attachment could significantly alter the time–activity budget of long-tailed ducks in the wild, with potentially adverse effects. If wild ducks will react in a similar way to transmitter attachment as our captive ducks, then the greater amount of time spent in maintenance behavior might limit the time available for foraging. If foraging conditions are unfavorable (i.e., reduced daylight hours during winter, severe weather conditions), this might affect their food intake and, consequently, their energy balance. Our captive ducks had access to food ad libitum during daylight hours, so they were likely not energetically challenged, even during severe weather. It is unclear to what extent the increased maintenance time observed in Prong/Tesa birds was required to maintain plumage integrity or if part of this might have been related to disturbance caused by carrying the transmitter (i.e., causing pecking of the transmitter/pulling of the antenna). It could be that long-tailed ducks in the wild will react less strongly, as they have to deal with time and energetic constraints, especially during winter. However, numerous field studies found similarly altered activity patterns in wild birds after transmitter attachment [6–8 and references therein]. In our study, Prong and Tesa birds engaged less frequently in locomotion immediately following transmitter attachment (especially, swimming and diving) and also reduced the time spent in water. Because they partially recovered from this (especially, Tesa birds), we suggest that this response might be related to some temporary discomfort caused by the transmitter and/or the attachment procedure. In the context of overwintering wild long-tailed ducks, however, it is unclear to what degree birds might be able to afford to reduce locomotion (i.e., reduce foraging), when they already might be pushed for foraging time to balance their energetic needs. Furthermore, if the potential discomfort associated with carrying a transmitter and/or the attachment procedure affects their vigilance, it might also leave ducks more vulnerable to predation, especially during the period immediately following attachment.

Conclusions

We found important changes in the activity budget of long-tailed ducks after transmitter attachment. By contrast, the energetic costs associated with resting on water did not change significantly. However, after transmitter attachment, birds spent significantly more time on maintenance behavior (especially, preening), and preening metabolism was ~70 % above resting metabolism. While ducks concomitantly reduced the time spent in water and in locomotion in general, potentially mitigating increased maintenance costs, ducks in our study had access to food ad libitum. In the wild, however, ducks will have to search for food (i.e., fly and dive) to satisfy their energetic needs and, hence, might not be able to reduce locomotor activity substantially, if at all. Our study suggests that the observed behavioral changes associated with transmitter attachment in captive long-tailed ducks (Prong and Tesa method) may significantly alter the energy budget of this small sea duck in the wild, with potentially adverse effects that should be considered when planning a study with external transmitters.

Abbreviations

$\dot{V}O_2$: oxygen consumption rate; $s\dot{V}O_2$: mass-specific oxygen consumption rate; T_w: water temperature; DEE: daily energy expenditure; Mb: body mass.

Authors' contributions

MRE participated in the study design, collected and analyzed the respirometry data, and drafted the manuscript. TEH and RDA conceived and designed the study, assisted in data collection and analysis, and contributed to the manuscript. JF participated in study design, collected behavioral data, and contributed to the manuscript. CF participated in study design, performed the statistical analysis of the behavioral data, and helped to draft the manuscript. All authors read and approved the final manuscript.

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Compliance with ethical guidelines

Competing interests

The authors declare that they have no competing interests.

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