

ABDOMINALLY IMPLANTED TRANSMITTERS WITH PERCUTANEOUS ANTENNAS AFFECT THE DIVE PERFORMANCE OF COMMON EIDERS

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Abstract. Implanted transmitters have become an important tool for studying the ecology of sea ducks, but their effects remain largely undocumented. To address this, we assessed how abdominally implanted transmitters with percutaneous antennas affect the vertical dive speeds, stroke frequencies, bottom time, and dive duration of captive Common Eiders (*Somateria mollissima*). To establish baselines, we recorded video of six birds diving 4.9 m prior to surgery, implanted them with 38- to 47-g platform transmitter terminals, and then recorded their diving for 3.5 months after surgery to determine effects. Descent speeds were 16–25% slower and ascent speeds were 17–44% slower after surgery, and both remained below baseline at the end of the study. Dive durations were longer than baseline until day 22. On most days between 15 and 107 days after surgery, foot-stroke frequencies of birds foraging on the bottom were slower. Foot- and wing-stroke frequencies during descent and bottom time did not differ across the time series. If birds that rely on benthic invertebrates for sustenance dive slower and stay submerged longer after being implanted with a satellite transmitter, their foraging energetics may be affected. Researchers considering use of implanted transmitters with percutaneous antennas should be mindful of these effects and the possibility of concomitant alterations in diving behavior, foraging success, and migratory behavior compared to those of unmarked conspecifics.

Key words: Common Eider, dive performance, PTT, radio telemetry, sea duck, *Somateria mollissima*, transmitter effect.

Transmisores Implantados en el Abdomen con Antenas Percutáneas Afectan el Desempeño de Buceo en *Somateria mollissima*

Resumen. Los transmisores implantados se han tornado una herramienta importante para el estudio de la ecología de aves marinas, sin embargo sus efectos permanecen escasamente documentados. Con el fin de abordar este problema, determinamos como los transmisores implantados en la región abdominal con antenas percutáneas afectan la velocidad de buceo vertical, la frecuencia de impulsos de nado, el tiempo de permanencia en el fondo y la duración del buceo en individuos de *Somateria mollissima* en cautiverio. Antes de la cirugía, grabamos videos de seis aves que se encontraban buceando a 4.9 m para establecer una línea base. Luego, implantamos en las aves los transmisores que pesaron de 38 a 47 g, y grabamos el buceo por 3.5 meses posteriores a la cirugía para determinar sus efectos. Las velocidades de descenso fueron un 16 a 25 % más lentas y las velocidades de ascensión fueron un 17 a 44% más lentas después de la cirugía, y ambas permanecieron por debajo de la línea base hasta el final del estudio. Los buceos fueron más largos hasta el día 22. En la mayoría de los días, de 15 a 107 días después de la cirugía, la frecuencia de los impulsos con las patas de las aves que se encontraban forrajeando en el fondo fue menor. Las frecuencias de los impulsos de nado con las patas y las alas durante los descensos y el tiempo de permanencia en el fondo no cambiaron con el tiempo. Si las aves que dependen de invertebrados bentónicos para subsistir bucean a una velocidad más lenta y permanecen inmersas por más tiempo después de ser implantadas con un transmisor satelital, entonces sus energéticas de forrajeo podrían verse afectadas. Las investigaciones con transmisores implantados con antenas percutáneas deberían considerar estos efectos y la posibilidad de alteraciones concomitantes en el comportamiento de buceo, el éxito de forrajeo y el comportamiento migratorio.

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INTRODUCTION

Implanted satellite transmitters (platform transmitter terminals; PTTs) have revolutionized scientists' ability to determine the movement patterns of sea ducks. The use of PTTs has led to the discovery of migration corridors and wintering areas and has allowed researchers to better understand migration timing and habitat use (e.g., Petersen et al. 1995, Brodeur et al. 2002, Petersen et al. 2003, 2006, Phillips et al. 2006). Despite these advances, concerns remain about health effects and the validity of information provided by these devices. Assessing transmitters' effects on sea ducks is made more challenging because of the often harsh and remote environments these birds inhabit. To fill this gap, researchers have generally relied on ecological and physiological metrics to determine whether manipulation and transmitter implantation have detrimental effects. Although diving is central to sea duck ecology, and external devices have been reported to affect the dive behavior of other marine birds, no studies have addressed whether implanted transmitters with percutaneous antennas affect sea ducks' dive performance.

Most research on how transmitters and other devices affect dive performance has been performed on penguins to which the device was attached externally. These studies found numerous effects including increased cost of transport, longer foraging trips, lower foraging success, and altered swim speeds (Wilson et al. 1986, Croll et al. 1991, Culik and Wilson 1991). In some cases, effects were attributed to increased drag (Wilson et al. 1986, Croll et al. 1996). For diving waterfowl, abnormal behavior and reduced foraging have been reported when transmitters were attached externally (Woakes and Butler 1975, Perry 1981, Robert et al. 2006).

In an attempt to reduce the effects of external mounts, Korschgen et al. (1984, 1996) developed a technique to implant the transmitter into the abdominal cavity of waterfowl. This technique has since been used with most sea duck species (e.g., Petersen et al. 1995, 2006, Phillips et al. 2006). Although implantation should reduce the complications of an external mount, detrimental effects of surgery and of carrying the device internally are still possible.

Only a few studies have investigated how implanted devices affect diving in marine birds. In the Macaroni Penguin (*Eudyptes chrysolophus*), 21-g data loggers implanted into the abdominal cavity to monitor heart rate had no effect on foraging-trip duration (Green et al. 2004). Adélie Penguins (*Pygoscelis adeliae*) abdominally implanted with 20-g telemetric heart-rate transmitters swam slower but more efficiently than controls, although the sample size was small ($n = 2$) and implanted birds may have been habituated (Culik and Wilson 1991).

Although no studies have measured how abdominally implanted devices affect diving in sea ducks, other metrics have been assessed. For example, Guillemette et al. (2002) detected no change in return rates or measures of reproduction

of Common Eiders (*Somateria mollissima*) implanted with 17-g data loggers. Presumed or known short-term (~2 weeks) mortality ranged from relatively low [3% for Harlequin Ducks (*Histrionicus histrionicus*) implanted with 15- to 18-g radio transmitters with percutaneous antennas after modifications of the anesthetic technique; Mulcahy and Esler 1999] to relatively high (39% for scoters implanted with 36- to 52-g PTTs with percutaneous antennas; Rosenberg and Petrula 2000). Esler et al. (2000) found that Harlequin Ducks implanted with 15- to 18-g radio transmitters with percutaneous antennas lost more mass than banded controls in the first few weeks after implantation but not ~1 yr after implantation.

Although the optimal method to determine whether implanted transmitters affect derived information would be to follow marked and control birds in the wild throughout the year, such a study would not be possible for many sea duck species. Additionally, merely catching and handling control birds may cause muscle damage (Dabbert and Powell 1993), which could bias results. If dive performance changes after PTT implantation both a bird's health and the parameters scientists use PTTs to measure could be affected. To assess changes in dive performance we recorded video of six Common Eiders diving before surgery to establish baselines, implanted birds with PTTs with percutaneous antennas, and then recorded additional video at intervals for 3.5 months.

We chose the Common Eider as our study species because it has been implanted with similar PTTs in field studies (Petersen and Flint 2002), the ratio of transmitter mass to body mass is within the recommended range (Kenward 2001), and depths of foraging in the wild (Guillemette et al. 2004) are consistent with the depth of the dive column in our aquarium. Additionally, the Common Eider's ecology is broadly similar to that of threatened species for which an understanding of the effects of transmitters is a management goal (K. Laing, U.S. Fish and Wildlife Service, pers. comm.). Common Eiders feed on a variety of benthic prey including mussels, clams, urchins, and crabs (reviewed by Goudie et al. 2000, Leopold et al. 2001). Their diving is constrained by factors such as available oxygen stores, buoyancy, and drag (Stephenson et al. 1989a, Lovvorn and Jones 1991a, Lovvorn et al. 1991, Hawkins et al. 2000, Lovvorn et al. 2001). Common Eiders dive by using coordinated foot and wing strokes for propulsion during descent and swim by using foot strokes only while foraging on the bottom (Heath et al. 2006). From the depth of a typical dive, ascent is passive, the bird relying on positive buoyancy to return it to the surface (Lovvorn and Jones 1991b, Heath et al. 2007).

To assess the transmitter's effect, we tested the null hypothesis that manipulation, surgery, and carrying an implanted PTT do not affect the Common Eider's dive performance. We tested changes between pre- and post-surgery descent rate, ascent rate, foot/wing-stroke frequency during descent, foot-stroke frequency while the bird was foraging on the bottom, bottom time, and dive duration.

METHODS

Common Eider eggs salvaged from the Yukon–Kuskokwim delta, Alaska, were hatched at the Alaska SeaLife Center (ASLC) in Seward, Alaska, in 2003. Three males and three females (pre-surgery mass 1800–2040 g) were housed in an outdoor aviary with shallow pools (<1 m deep) and fed Mazuri sea duck pellets (Purina Mills, St. Louis, MO), blue mussels (*Mytilus edulis*), and krill (*Euphausia suberba*) prior to the experiment.

We conducted our study at the ASLC in an outdoor seawater aquarium, in which we constructed a dive column (1.5 × 1.5 m wide and 4.9 m deep) with an attached terrestrial haul-out. We enclosed the aviary with nylon netting and the dive column with plastic mesh and Plexiglas. We covered the aviary floor with Nomad matting (Safety-Walk 1500, 3M, St. Paul, MN) to minimize the birds' risk of injury. Prior to beginning the experiment, we trained the birds to dive to the bottom of the dive column. Training consisted of providing food in a metal tray on the side of the dive column at progressively lower depths and was necessary because birds had not previously foraged at depths >1 m. Once birds were diving to the bottom, we passed Mazuri sinking waterfowl pellets and blue mussels through a PVC pipe onto an acrylic feeding tray on the floor of the dive column four to five times daily, thus allowing only benthic foraging.

We collected baseline data and implanted transmitters in November 2005. Before establishing baselines we allowed ~50 days for the birds to acclimate to the deeper dive depth. This was essential because waterfowl diving to deeper depths acclimate to increased demands (Stephenson et al. 1989b). Veterinarians deemed birds were in good physiological health prior to the study. This study was approved by the ASLC Institutional Animal Care and Use Committee (05-005).

One male (hereafter referred to as bird A) developed necrosis of a toe and surrounding webbing after the transmitter was implanted. Histopathology showed severe granulomatous necrotizing pododermatitis consistent with bacterial embolization and subsequent osteomyelitis. Because the etiology of this condition was uncertain and we could not rule out a surgical link, we included this bird in our primary tests but also performed separate analyses excluding it.

SATELLITE TRANSMITTERS

Birds were implanted when they were 29 months old with either a PTT 100 (Microwave Telemetry, Columbia, MD) or a 5130 PTT (HABIT Research, Victoria, British Columbia, Canada) by procedures similar to those of Korschgen et al. (1984, 1996). The transmitters were approximately 38–47 g, 70 × 35 × 15 mm, and 22.5 mL in volume with an antenna 200 mm long and 1.7 mm in diameter. Surgery was conducted at the ASLC under sterile conditions by veterinary surgeons experienced in the technique. Briefly, the surgeons anesthetized birds with propofol and a local anesthetic block (Machin and Caulkett 2000) and, in one case due to complications in maintaining the

intravenous catheter, isoflurane. To maximize plumage integrity after the operation, feathers were not plucked. Incision sites were prepared by application of a sterile gel (facilitator) to part the feathers. Sterile disposable drapes were used, and exposed skin was swabbed with povidone iodine solution. A transmitter was placed into the right abdominal air sac through a ventral midline incision, with the antenna exiting the body dorsally near the synsacrum and extending from the bird caudally. Two individual internal sutures were used to anchor a mesh housing (surrounding the transmitter) to the body wall. One suture was used at the antenna's dorsal exit site to secure the skin and muscle to a mesh collar attached to the base of the antenna inside the body wall. The abdominal incision was closed with two layers of monofilament absorbable suture.

VIDEO RECORDING AND ANALYSIS

We examined over 850 dives by using five to seven color digital video-recording devices: three on horizontal planes, one recording foraging on the bottom, and one to three capturing surface activities (Fig. 1). We captured footage at 29.97 frames sec⁻¹ in long-play format on mini-DV tapes. We transferred video from tapes to computer files in uncompressed Audio Video Interleave format and analyzed data in Adobe Premiere Pro 2.0 (Adobe Systems, San Jose, CA). We recorded approximately

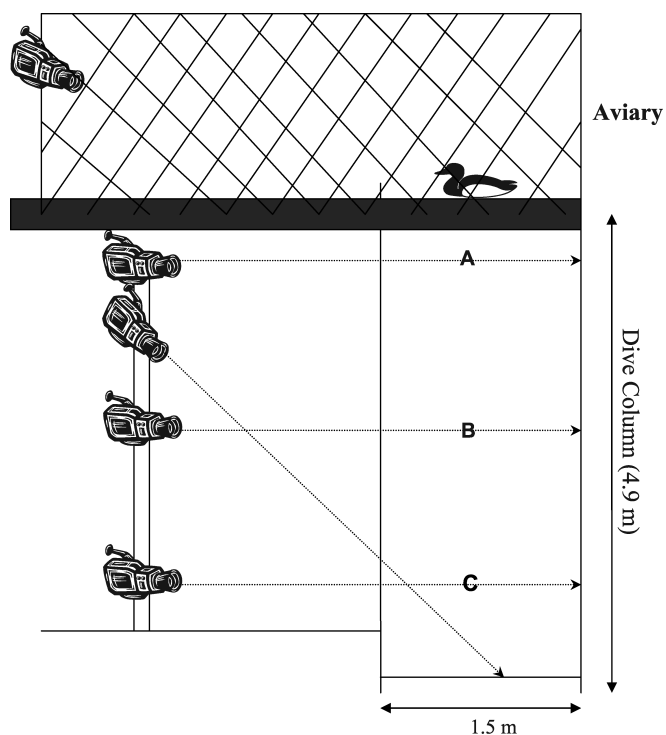


FIGURE 1. Dive column and surrounding aviary in which experiments on six Common Eiders took place. Three cameras recorded video of the birds while diving, one camera recorded video of their behavior and foot strokes on the bottom, and one to three cameras recorded video of their activity on the surface.

10 hr of baseline video 2–4 days prior to surgery and 5–6 hr of video on days 1, 2, 3, 4, 9, 15, 22, 29, 58, and 107 after implantation. Because some birds dove very few times in the days directly after surgery, and all birds did not begin diving the same day, we combined days 1–4 in analyses. Additionally, because of camera failure during a recording session, we used footage from day 14 to augment footage from day 15.

We measured dive speeds and descent foot/wing-stroke frequency at depths between ~1.5 and 3.5 m. We began counts with the first frame a bird passed a marker on a horizontal plane with the camera (Fig. 1; marker A) and continued until the bird passed a similar marker for the next camera (Fig. 1; marker B). We calculated foot strokes on the bottom and bottom time by starting with the frame a bird began pecking for food on the bottom and ending when foot strokes ceased and the bird began passively rising from the bottom. Foot strokes on the bottom and foot/wing strokes during descent were divided by time to obtain frequencies. For dive duration, we considered a dive to start when a bird's bill first entered the water and to end when any part of the bird arose from the water. We report dive speeds only for the middle of the dive column because most interactions between birds occurred at the top and bottom of the dive column.

Coordinated strokes of the foot and wing were the only mode of descent Heath et al. (2006) described for wild Common Eiders. The birds we studied, however, sometimes used mixed foot and foot/wing propulsion or, on a few occasions, used only foot propulsion during descent. Thus, we present two speeds of descent: (1) "overall descent rate," generated from all forms of propulsion, and (2) "coordinated descent rate," generated from dives containing only coordinated foot/wing strokes.

We analyzed dives only when food was present and we saw birds feeding. Over the entire time series, an individual's daily median for overall descent rate, coordinated descent rate, ascent rate, foot/wing-stroke frequency during descent, foot-stroke frequency while foraging on the bottom, bottom time, and dive duration were generated from 6–36, 6–27, 4–28, 4–26, 2–24, 7–36, and 8–38 dives, respectively. This large range was due to variance in individual behavior. We excluded descent rates and foot/wing-stroke frequencies if the bird interacted with another, searched for food, or paused during descent. Interactions occurred because birds often dove together; during most feedings, more than one bird dove at a time, and during some feedings, all birds were submerged at the same time. We excluded ascent rates if the bird searched for food, handled food items, or interacted with other birds during ascent. We excluded dive durations if birds interacted with other birds during the dive. We examined foot-stroke frequency on the bottom only when three or fewer birds were present because as the number of birds foraging increased, discerning an individual's foot strokes became more difficult and interactions among birds became more common. Also, we excluded sequences for foot-stroke frequency on the bottom and bottom time if the bird rose >1 m from the bottom while foraging or interacted with other birds while on the bottom.

We calculated the change in buoyant force associated with implantation of the transmitter as

$$\text{change in buoyant force } (\Delta B) = B_t - B_d$$

with

$$B_t \text{ (buoyant force of transmitter)} = (V_d - M_t)g$$

$$B_d \text{ (buoyant force of displaced air at water surface)} = cV_d \times B_a$$

$$c \text{ (compression factor for air underwater)} = 10/(10 + d)$$

where V_d is the volume of air displaced by the transmitter (0.0225 L), M_t is the mass of the transmitter (0.0421 kg), B_a is buoyancy of air (assumed to be 9.79 N L⁻¹), g is gravitational acceleration (9.81 m sec⁻²), and d is dive depth (m).

We categorized body position and paths taken because we noted changes in both during ascent after PTT implantation. We categorized ascent path as helical, direct, or other. The helical category included paths that followed a wide to moderately wide corkscrew pattern. The direct category included ascents that were either mostly vertical but still followed a tight corkscrew path or were vertical and contained little to no corkscrew travel. Ascents falling into the category "other" usually occurred when birds switched between helical and direct paths during ascent. We categorized body angle during ascent as horizontal, semi-horizontal, or vertical in the upper (between markers A and B) and lower (between markers B and C) parts of the dive column (Fig. 1).

STATISTICAL ANALYSES

With all six birds, we used SAS 9.1 (SAS Institute 2004) in a multi-step approach to compare descent rate for dives containing all forms of propulsion, descent rate for dives with coordinated foot/wing propulsion only, ascent rate, foot-stroke frequency during foraging on the bottom, foot/wing-stroke frequency during descent, bottom time, and dive duration before and after surgery. First, we assessed normality with a Shapiro–Wilk test and applied log transformations as needed. We then used a repeated-measures mixed model (Littell et al. 1996) to test for differences across the overall time series (2–4 days prior to surgery and 1–4, 9, 15, 22, 29, 58, and 107 days after), controlling tests with a Holm–Bonferroni procedure (Holm 1979). When the null hypothesis was rejected for the overall time series, we used two-tailed paired t -tests to check for differences between baseline and post-surgery dates and conducted separate paired tests excluding bird A. In all tests, we used the daily medians for each bird. Holm–Bonferroni-corrected P values are presented in parentheses. Following Zimmerman (1996), we compared ascent path and body angle during ascent with rank-transformed proportions. We considered all tests significant at $\alpha = 0.05$. Means are presented \pm SD.

RESULTS

Descent rate for dives containing all forms of propulsion [$F_{7,35} = 5.2$, $P < 0.001$ (0.001)], descent rate for dives with coordinated foot/wing propulsion only [$F_{7,35} = 5.6$, $P < 0.001$ (0.001)], ascent rate [$F_{7,35} = 10.6$, $P < 0.001$ (<0.001)],

TABLE 1. Measures of dive performance of six Common Eiders surgically implanted with 38- to 47-g satellite transmitters with percutaneous antennas. Two-tailed paired *t*-tests were performed on means generated from daily medians for each individual.

Variable	Days since PTT implantation							
	Baseline	1-4	9	14-15	22	29	58	107
Descent rate (all forms of propulsion; m sec ⁻¹)								
Mean	0.99	0.80	0.82	0.80	0.83	0.81	0.74	0.80
SD	0.06	0.14	0.13	0.23	0.11	0.12	0.11	0.09
<i>t</i>		4.2 ^a	3.9 ^a	2.3	5.2 ^a	5.2 ^a	6.7 ^a	6.0 ^a
Descent rate (coordinated propulsion; m sec ⁻¹)								
Mean	1.01	0.88	0.85	0.90	0.88	0.84	0.81	0.81
SD	0.06	0.11	0.11	0.19	0.08	0.11	0.11	0.10
<i>t</i>		4.0 ^a	3.5 ^a	1.6	4.0 ^a	4.5 ^a	4.2 ^a	4.4 ^a
Foot/wing-stroke frequency (during descent; strokes sec ⁻¹) ^b								
Mean	2.36	2.28	2.24	2.25	2.29	2.28	2.20	2.25
SD	0.09	0.10	0.12	0.11	0.07	0.13	0.10	0.09
Bottom time (sec) ^b								
Mean	15	15	17	16	13	15	11	15
SD	2	5	3	4	3	2	3	4
Foot-stroke frequency (during foraging on the bottom; strokes sec ⁻¹)								
Mean	3.22	3.20	3.23	2.99	3.10	3.09	3.05	3.06
SD	0.13	0.15	0.11	0.15	0.12	0.10	0.22	0.16
<i>t</i>		0.7	-0.2	4.9 ^a	3.6 ^a	2.0	4.2 ^a	3.6 ^a
Ascent rate (m sec ⁻¹)								
Mean	1.09	0.60	0.76	0.89	0.80	0.81	0.81	0.84
SD	0.23	0.07	0.10	0.21	0.11	0.05	0.09	0.11
<i>t</i>		7.0 ^a	6.3 ^a	2.2	5.2 ^a	3.7 ^a	4.8 ^a	2.7 ^a
Dive duration (sec)								
Mean	28	32	32	33	30	30	29	30
SD	2	4	3	3	4	2	3	3
<i>t</i>		-4.9 ^a	-3.3 ^a	-4.6 ^a	-1.5	-1.7	-1.0	-0.7

^aSignificant difference ($P < 0.05$) between baseline and number of days after implantation.

^bResult of *F*-test not significant. Paired tests not performed.

foot-stroke frequency during foraging on the bottom [$F_{7,35} = 5.9, P < 0.001$ (0.002)], and dive duration [$F_{7,35} = 2.9, P = 0.02$ (0.05)] varied across respective time series, but foot/wing-stroke frequency during descent ($F_{7,35} = 2.1, P = 0.06$) and bottom time ($F_{7,35} = 1.6, P = 0.18$) did not. In pairwise tests (Table 1), descent rate for all forms of propulsion, descent rate for coordinated foot/wing propulsion, and ascent rate were slower than the baseline rate on all days but day 15; foot-stroke frequency during foraging on the bottom was slower on days 15, 22, 58, and 107; and dive duration was longer on days 2, 8, and 15. Removing bird A from analyses did not change the significance of results of paired tests. Helical ascent was 2.6–3.0 times more frequent than before surgery on all post-surgery days except day 29 (Fig. 2). In comparison to the baseline, vertical body position between the lower and middle cameras was less frequent on days 9 and 22 after surgery, and between the middle and upper cameras it was less frequent on all days after surgery (Fig. 3).

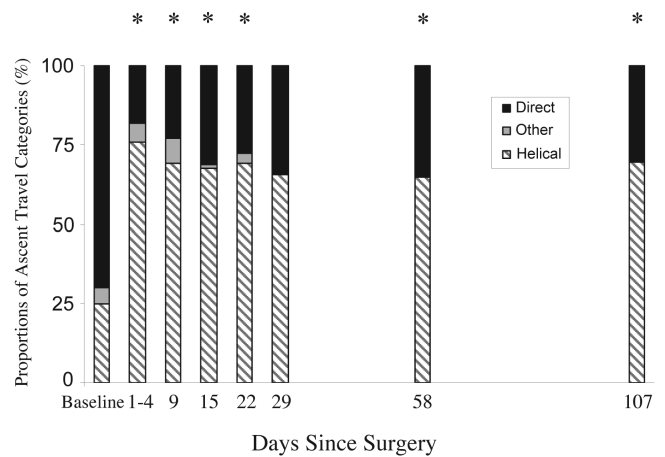


FIGURE 2. Mean daily proportions of three categories of travel during ascent (direct, helical, and other) of six Common Eiders before and after implantation of 38- to 47-g satellite transmitters with percutaneous antennas. Asterisks indicate a significant difference in helical ascent between baseline and number of days after implantation.

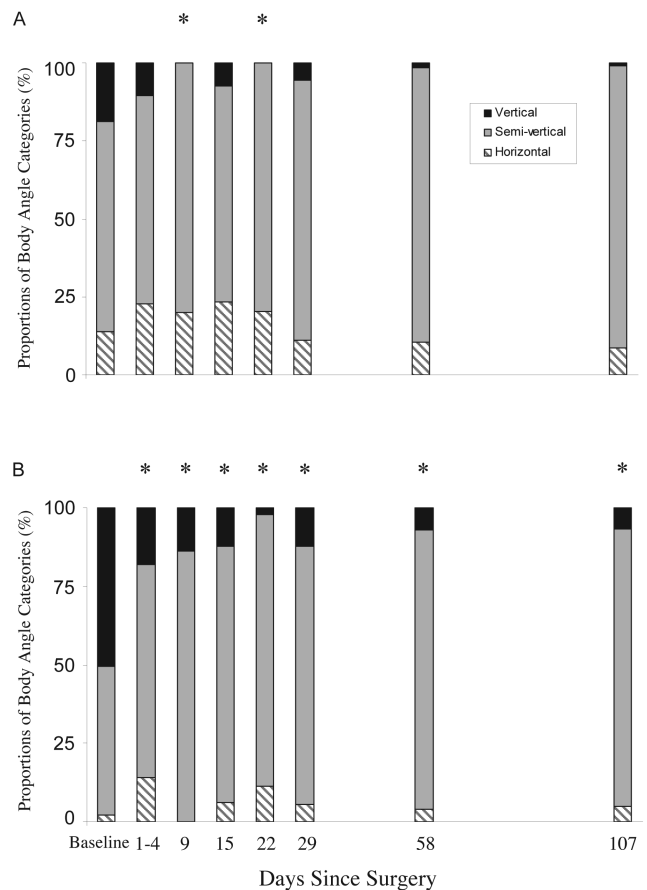


FIGURE 3. Mean daily proportions of three categories of body angle of six Common Eiders during ascent (vertical, semi-vertical, and horizontal) through the (A) lower and (B) upper portion of a 4.9-m-deep dive column before and after implantation of 38- to 47-g satellite transmitters with percutaneous antennas. Asterisks indicate a significant difference in vertical body angle between baseline and number of days after implantation.

DISCUSSION

We found that Common Eiders had slower vertical travel speeds and longer dive durations after being implanted with a PTT with a percutaneous antenna. To minimize costs and maximize foraging time, diving birds' underwater travel speeds are generally confined within relatively narrow ranges (Watanuki et al. 2005, 2006, Heath et al. 2006). In general, when descent slows, energetic cost rises because birds spend more time engaged in this expensive part of the dive cycle [2.9–3.3 times more costly than remaining at the bottom (Lovvorn et al. 1991)], but when descent speeds are high, drag rises rapidly (Lovvorn 2001, Lovvorn et al. 2001), increasing costs. Because birds traveled slower after surgery, post-surgery dives likely consumed more energy and were less efficient, i.e., the ratio of energy expended to net energy gained was higher after surgery than before.

Assessing how implanted PTTs may affect deeper dives is important because in the Common Eider, bottom time is inversely related to travel time to deeper depths (Heath et al. 2007). If the descent/ascent rates we observed are extrapolated to an 11.3-m dive, the eiders' average median travel time was 22 sec before transmitter implantation, 33 sec 1–4 days after implant, and 27 sec 107 days after implantation. Using speeds in the range found for wild Common Eiders diving to this depth (1.25 m sec^{-1}) (Heath et al. 2006, 2007), and applying the proportional changes that we observed, yield travel times of 18 sec without the PTT, 28 sec 1–4 days after surgery, and 23 sec 107 days after surgery. If Common Eiders are limited by their calculated aerobic dive limits (cADLs) and we assume a 22.5-ml loss in air-sac space due to the implanted PTT, scale the oxygen-storage compartments of the Tufted Duck (*Aythya fuligula*; Keijer and Butler 1982) to an 1800-g eider, and apply the Common Eider's estimated oxygen consumption while diving (Hawkins et al. 2000), these increased travel times would reduce the time available for aerobic foraging by 35–45% 1–4 days after implantation and 19–25% 107 days after implantation. If birds are capable of readjusting their air-sac volume to the pre-surgery value, then their cADL is 51 sec (Hawkins et al. 2000) and they have 29–39% less time to forage aerobically 1–4 days after implantation and 14–19% less on day 107 after implantation. Additionally, reduced hematocrit (Latty 2008) and possibly higher cost of transport (measured as power input per distance traveled) post-surgery may reduce cADLs. While extrapolation provides a valuable example of how deeper dives may be affected, we caution that the effects of implanted transmitters on dive performance may vary with depth and that calculated changes based on captive animals may not represent actual effects on wild birds.

EXPLANATION OF EFFECTS

Biomechanical. The degree of positive buoyancy is a critical determinant of kinematics of birds during shallow dives, so decreased buoyancy is a potential cause of the changes in ascent

speed and foot-stroke frequency we observed. For an 1800-g Common Eider, if a diving bird does not adjust its air-sac volume to compensate for the displacement of air from the air sacs by the transmitter, and if transmitter implantation does not change a bird's total body volume, the PTT reduces buoyant force at the surface by 0.41 N. Accounting for air compression at depth, buoyant force is reduced approximately 0.34, 0.30, and 0.26 N at 5, 10, and 20 m, respectively. Using air-free tissue-buoyancy measurements for diving birds (-0.36 N kg^{-1} ; Stephenson 1993) and scaling the respiratory and plumage-air volumes of the Lesser Scaup (*Aythya affinis*; Stephenson 1994), these changes represent a 3.7, 4.8, 5.7, and 8.0% reduction in positive buoyancy at depths of 0, 5, 10, and 20 m, respectively. These changes compare to an approximate 20% decrease in buoyancy of the Lesser Scaup due to normal plumage air loss during dives to 1.5 m (Stephenson 1994). Implantation could also affect buoyancy in other ways, such as air-sac rupture during surgery and plumage wetting around the incisions (Latty 2008). Although a calculated 4.8% reduction in buoyancy at 5 m does not fully explain slower ascent speeds after surgery, it may in part explain the 4.3–7.9% reductions in foot-stroke frequencies during foraging on the bottom starting 14 days after surgery. We also note that changing lipid stores during the experiment could have affected buoyancy, but this change should be minimal; fat-to-lean mass probably did not change much because we ran our experiment only during winter (November–March) and birds returned to pre-surgery weights shortly after surgery (Latty 2008). Additionally, in the Lesser Scaup, a fivefold increase in body lipids increases buoyancy only 3% (Lovvorn and Jones 1991b).

Although implanting transmitters rather than mounting them externally reduces drag, percutaneous antennas still produce drag. If antenna drag was substantial, it could explain changes in speeds of both descent and ascent. Results from other studies are mixed on whether the presence of antennas affects diving in birds. For example, Chinstrap Penguins (*Pygoscelis antarctica*) fitted with a 25-g external radio transmitter with a 285-mm whip antenna and a cross-sectional area of 3.5 cm^2 made significantly longer foraging trips than did controls, while those fitted with a 107-g time–depth recorder with a cross-sectional area of 7.9 cm^2 but without antennas made foraging trips of normal duration (Croll et al. 1991). However, calculated drag produced by an antenna 200 mm long and 1 mm in diameter on a model penguin traveling at 1.0 m sec^{-1} was minimal ($\sim 0.05 \text{ N}$) (Wilson et al. 2004). Also, scoters implanted with a radio transmitter with an external whip antenna survived the first two weeks after release at a rate similar to that of birds implanted with transmitters without antennas (7.7% and 10%, respectively, Iverson et al. 2006).

Balance in the water has been suggested to alter diving in birds fitted with external devices (Healy et al. 2004) and may have affected the birds in our experiment. We found that body position during ascent through the upper dive column (between markers A and B; Fig. 1) was vertical 50% of the

time prior to PTT implantation but only 2–18% of the time after surgery. Also, on most days, the path traveled during ascent was more frequently helical after PTT implantation than before. Shallow body angles may have led to higher drag. A helical path increased the total distance birds traveled during ascent. Together, these probably account for some of the decrease in the eiders' ascent speeds after PTT implantation.

Physiological. The aforementioned changes in mechanical force we propose do not appear to fully explain slower descent speeds after PTT implantation. After surgery, levels of muscle enzymes in the eiders' blood were elevated (Latty 2008), so it is possible that muscle damage from surgery may have led to reduced propulsive force per stroke.

After surgery, in four of the six birds short-term (≤ 14 days) creatine kinase (CK) levels exceeded $1000 \text{ units L}^{-1}$, which could indicate myopathy (Bollinger et al. 1989). Each day after surgery they were measured, these four birds' median swim speeds were also slower than those of the other two. Furthermore, the individual with the highest CK level 2 days after surgery had the greatest proportional change in descent speed for the first 2 weeks after implantation. Causes of myopathy include nutritional deficiencies, capture and handling, extreme exertion, and some medications (Aktas et al. 1997, Guglielmo et al. 2001, Shivaprasad et al. 2002, Abbott et al. 2005). We propose that exertion (during capture in the pen, application of anesthesia, and post-operative handling), surgical trauma (including incisions), or other unknown factors may have contributed to elevated CK. While there appears to be a relationship between slower descent, loss of power per stroke, and CK levels, we remain cautious; elevated blood CK as an index of myopathy has not been evaluated for the Common Eider, and we cannot differentiate the causes of elevated CK. It is possible surgical trauma alone could have caused most or all of this elevation, although this possibility does not necessarily limit the importance of elevated levels of this enzyme in the blood after surgery. More study is needed before this relationship can be fully evaluated.

CONCLUSIONS

While it is premature to conclude that the effects we report would alter the health or fitness of birds in the wild or compromise the validity of PTT-derived data (survival, movement, etc.), all could be affected given the importance of dive performance to eiders. The outcome of our study suggests that further research on the effects of implanted PTTs and the development of improved implant procedures and transmitter design may be warranted.

Some caution is needed when our results are applied to eiders in the wild. We had no control group because of the limited size of the dive column and number of birds available. Without controls, we are unable to adequately address whether other factors (such as season or continued acclimation) contributed to the results. Also, because a study of captive birds

cannot reproduce conditions at sea, effects on wild Common Eiders implanted with PTTs may be different than those we observed. Some differences between wild eiders and our captive birds were fairly clear; for example, before surgery, our birds descended and ascended slower than wild Common Eiders (Heath et al. 2006, 2007). This could have occurred because of constraints of the dive column (helical ascent was probably due, in part, to limited space), dive depth, differences among subspecies, and/or physical fitness of the captive birds. Therefore, while a study of captive birds allows insight into how wild birds could be affected, care is required before a conclusion of how behavioral or physiological changes would ultimately affect birds under natural conditions.

To better understand how implanted transmitters affect sea ducks, we recommend the following: (a) empirically test how energetics are affected, (b) address how PTT mass may influence responses, (c) differentiate responses at different stages of the process of PTT implantation (i.e., capture, surgery, and post-operation), (d) determine if other implanted devices without percutaneous antennas, such as time–depth recorders, cause similar responses, (e) investigate whether all species' responses are similar, (f) investigate whether effects can be reduced by marking birds during specific seasons, and (g) assess if and when dive performance returns to baseline. Additionally, on the basis of the changes in dive performance we report and their possible effects on foraging ecology, we advise caution in studies combining implanted transmitters with percutaneous antennas and devices such as time–depth recorders that yield information on diving.

Understanding how sea ducks respond to surgery and carrying implanted PTTs is crucial for determining the devices' efficacy and interpreting the data these devices provide. Researchers planning studies using implanted PTTs with percutaneous antennas should be mindful of effects we observed and results from other studies when evaluating a device's suitability and determining censor periods adequate to ensure the validity of data for extrapolation to unmarked conspecifics.

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