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Original Article

Effects of Satellite Transmitters on Captive and Wild Mallards

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ABSTRACT Satellite telemetry has become a leading method for studying large-scale movements and survival in birds, yet few have addressed potential effects of the larger and heavier tracking equipment on study subjects. We simultaneously evaluated effects of satellite telemetry equipment on captive and wild mallards (*Anas platyrhynchos*) to assess impacts on behavior, body mass, and movement. We randomly assigned 55 captive ducks to one of 3 treatment groups, including a standard body harness group, a modified harness group, and a control group. Ducks in the control group were not fitted with equipment, whereas individuals in the other 2 groups were fitted with dummy transmitters attached with a Teflon ribbon harness or with a similar harness constructed of nylon cord. At the conclusion of the 14-week captive study, mean body mass of birds in the control group was 40–105 g (95% CI) greater than birds with standard harnesses, and 28–99 g (95% CI) greater than birds with modified harnesses. Further, results of focal behavior observations indicated ducks with transmitters were less likely to be in water than control birds. We also tested whether movements of wild birds marked with a similar Teflon harness satellite transmitter aligned with population movements reported by on-the-ground observers who indexed local abundances of mid-continent mallards throughout the non-breeding period. Results indicated birds marked with satellite transmitters moved concurrently with the larger unmarked population. Our results have broad implications for field research and suggest that investigators should consider potential for physiological and behavioral effects brought about by tracking equipment. Nonetheless, results from wild ducks indicate satellite telemetry has the potential to provide useful movement data. © 2014 The Wildlife Society.

KEY WORDS *Anas platyrhynchos*, behavior, body condition, harness, mallard, movement, satellite telemetry.

Remote satellite telemetry systems, including satellite platform terminal transmitters (PTT) and PTTs combined with global positioning systems (GPS), have revolutionized the study of animal movements (Peterson and Douglas 1995, Petrie and Rogers 1997). Researchers now have the ability to monitor animals in remote locations over broad spatial scales to study ecological processes that were previously difficult to address with the limited range of very high frequency (VHF) radiotelemetry (Higuchi et al. 2004, Small et al. 2004). For example, satellite telemetry systems facilitate studies of the migratory movements in birds, which are challenging to measure by other means (Roshier et al. 2006, Gill et al. 2009, Beatty et al. 2014). Investigations that have used satellite telemetry have yielded new information about behavior, spatial distribution, and demography of wildlife populations (Woolnough et al. 2004, Shaffer et al. 2005, Mulcahy 2006, Krementz et al. 2011, Millspaugh et al. 2012). As a result, satellite telemetry has become a key tool for biologists in identifying dispersal patterns, migration routes, habitat selection, resource use, and phenology for a variety of taxa (e.g., Gill et al. 2009, Qian et al. 2009, Takekawa et al. 2010).

Satellite telemetry systems are often heavier than previous generations of VHF telemetry equipment because they require larger batteries and more sophisticated electronics to broadcast to Earth-orbiting satellites. Thus, satellite telemetry systems also have the potential to impact study subjects (Millspaugh et al. 2012). Although the equipment has been used to study marine organisms, terrestrial mammals (Bunnefeld et al. 2011), reptiles (Godley et al. 2002), and fish (Fitzpatrick et al. 2012), studies that use satellite telemetry systems have often focused on birds (Barron et al. 2010). The delicate relationship between body mass, balance and flight in birds complicates the use of transmitters, which add weight and potentially hinder mobility (Culik et al. 1994, Veasey et al. 1998, Woolnough

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et al. 2004); further, placement of transmitter devices also can affect flight energetics (Caccamise and Hedin 1985).

A range of techniques has been used to secure traditional VHF and satellite telemetry equipment to birds, and previous studies reported attachment effectiveness and the influence of equipment on bird behavior. Abrasion and altered behavior were affiliated with backpack harnesses attached around the wings, and pathological effects were observed in birds with transmitter implants (Small et al. 2004, Mulcahy 2006, Robert et al. 2006, Mong and Sandercock 2007). Backpack harnesses were also associated with reduced feeding and elevated grooming behaviors (Garrettson et al. 2000, Robert et al. 2006). Studies of VHF telemetry transmitters on small birds demonstrated that harness-based equipment can remain attached for extended periods, even after transmitter battery failure (Doerr and Doerr 2002, Woolnough et al. 2004, but see Kesler 2011), whereas adhesive attachment techniques can deteriorate prematurely (Perry et al. 1981, Karl and Clout 1987). A common method of transmitter attachment for ducks is a body harness constructed from Teflon ribbon, consisting of a transmitter mounted between the wings on a bird's back. Investigators reported conflicting results about body harness effects (Kenward 1987, Malecki et al. 2001, Miller et al. 2005, Sousa et al. 2008). Some report few or no effects on waterfowl (Bergmann et al. 1994, Dzus and Clark 1996), whereas others detail delayed nesting, reduced clutch and egg sizes, and decreased incubation rates in ducks marked with body-style harnesses (Pietz et al. 1993, Rotella et al. 1993).

Investigations of marked animals often assume that study subjects are not affected by equipment, and thus provide data representative of the larger unmarked population (Barron et al. 2010). However, demonstrable effects of satellite telemetry equipment on behavior, movement, and energetics indicate potential to violate this no-effect assumption. Despite the potential for elevated effects from heavier and larger satellite telemetry systems, few studies have investigated the impact of the equipment on avian behavior and movement with unmarked controls (Houston and Greenwood 1993, Pietz et al. 1993, Petrie et al. 1996, Robert et al. 2006, Barron et al. 2010). We assessed the effect of satellite transmitters and harnesses on physiology and behavior of captive mallards (*Anas platyrhynchos*). In the captive duck population, we evaluated body mass and behaviors of birds fitted with dummy transmitters and a control group without equipment. Additionally, we compared migration movements of wild, free-ranging mallards harnessed with functional GPS satellite transmitters to movements of the greater population of unmarked birds during the non-breeding season.

STUDY AREA

We conducted research on a captive mallard population between July and December 2010 at the Missouri Department of Conservation Green Area (38°49′N, 93°15′E). We housed mallards in a square outdoor study enclosure (approx. 40 m × 40 m) that encompassed approximately equal areas of mowed grass (*Schedonorus arundinacea*) and a small artificial pond. The pen was constructed of mesh netting supported by 4 × 4 posts on the sides and in the center. Duck food was available *ad libitum* in an open container placed on land. The mud pond bottom sloped from the bank to an approximate 1.3-m depth at the edge of the enclosure.

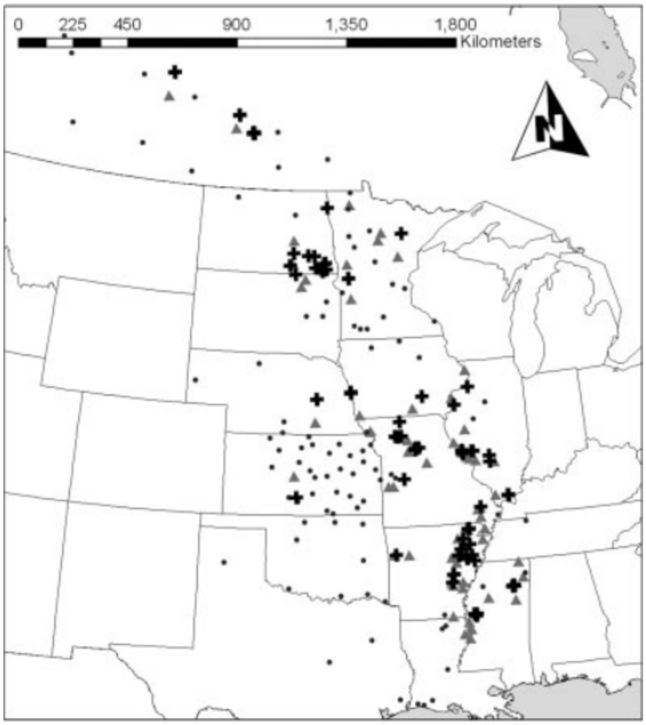

Figure 1. Mallard Migration Observation Network sites in the United States where indices were recorded (dots), and those that were within 100 km of telemetry-marked mallard females when population indices were recorded in 2010 and 2011 (triangles). Observations of mallard females that were near index sites are marked with crosses.

We captured free-ranging adult mallard females in Yorkton, Saskatchewan, Canada (51°13′N, 102°28′E). Additionally, a second group of adult mallard females was captured at various sites in Arkansas, USA, including 5-Oaks Duck Lodge (34°20′N, 91°36′E), Bayou Meto Wildlife Management Area (34°13′N, 91°31′E), and Black River Wildlife Management Area (36°03′N, 91°09′E). Satellite telemetry-marked mallards ranged across the mid-continental United States and southern Canada (Fig. 1).

METHODS

Captive Population

We purchased 59 hatch-year mallard females from a local breeder on 29 July 2010 and immediately released the birds into the Missouri study enclosure. The birds originated with a wild stock, but the number of generations removed was unknown. Work with captive birds was conducted under Animal Care and Use Protocol 6662 (University of Missouri). We allowed 8 weeks for ducks to acclimate to the surroundings and stabilize body mass. Four study subjects disappeared during the adjustment period, and likely either escaped or were preyed upon by turtles. On 16 September 2010, we captured and alternately assigned birds to 1 of 3 treatment groups: a standard harness group, a modified harness group, or a control group. We fitted mallard ducks in each of the 2 harness groups with dummy transmitters constructed to match the dimensions and mass of a 22-g transmitter (Model PTT-100; Microwave Telemetry, Inc., Columbia, MD). Dummy transmitters were constructed of plastic shaped with a band saw and a mill, and we used weighted screws and a false antenna to simulate actual units (Fig. 2). We banded each individual with numbered aluminum bands and colored, plastic-coated wrap-around bands. Each dummy transmitter was painted with colored stripes matching the colored leg bands, and colored plastic wire ties were attached to the false antennas to facilitate bird identification.

We fitted dummy transmitters to the standard harness group ($n = 18$) with a harness constructed from 2 1/4″ Teflon ribbon loops that encircled the body (e.g., Malecki et al. 2001). One loop was located anterior to the wings and fitted underneath the crop, whereas another loop was positioned posterior to the wings and anterior to the legs. Additionally, an anteroposterior section of ribbon connected the 2 loops across the breast. The dummy transmitter was attached along an anteroposterior axis, on the dorsal side, between the wings. The second harness configuration ($n = 18$) was generally similar to the standard harness, except that it was attached with light-weight nylon cord (1-mm-diam) rather than Teflon ribbon. Additionally, the posterior loop of the harnesses extended around the posterior proximal portion of the legs, rather than in front of the legs. The modified harness system has not previously been described or deployed to our knowledge, but it was being considered for deployment at the time of the test so it was included in this study. Mean mass for the traditional harness and transmitter package was 30.5 g (SD = 1.5 g), whereas mean mass for the modified system was 25.7 g (SD = 0.9 g). The control group ($n = 19$) was not fitted with transmitters or harnesses. We weighed and applied harnesses to all birds on 16 September. However, 8 birds (5 modified harness, 1 regular harness, and 2 control birds) were not weighed on 16 September because they escaped into the enclosure immediately after marking and we did not want to further stress the flock. We captured all birds, including individuals from the control group, again on 23 September and adjusted harnesses to ensure proper fit. Birds were then recaptured weekly, weighed on a portable balance scale, and inspected for harness abrasions between 23 September and 15 December 2010. We recorded the mass of dummy transmitters and associated harnesses individually at the conclusion of the project and we used those measures to adjust weekly masses of birds.

Behavior observations.—We used 10-min focal observations (Altmann 1974; $n = 224$) recorded from a nearby tower to evaluate behavior of mallards in each of the treatment groups. Behavior observations were recorded during sessions conducted approximately 3 times weekly between 15 November and 14 December 2010. Observers used a randomly ordered list to identify a focal subject prior to the start of each observation period. Individual control birds without transmitters were difficult to identify when legs were not visible because they lacked the color-markings on equipment. Thus, when the location of an unmarked individual could not be identified we selected a transmitter-marked bird from the randomized list, and then identified the nearest control group bird for the focal watch. During each focal observation, observers counted grooming behaviors, which included preening, flapping, and washing. Each movement was recorded as a single bout if a bird's head was oriented in a forward position at the behavior onset. Aggression was recorded when birds lunged at, chased, or pecked other individuals. We also recorded location of focal study subjects (on land or in the water) at the end of each 10-min focal observation.

Figure 2. Actual and dummy satellite-telemetry transmitters used to evaluate movements of mallards (September 2010 to December 2011); and assess the impacts of equipment on captive ducks (September 2010 to December 2010).

Transmitter effects in captivity.—We used an analysis of variance (ANOVA; proc anova; Statistical Analysis Software [SAS]; SAS Institute, Inc., Cary, NC) to test for differences in mean body mass of birds in treatment and control groups when ducks were marked on 16 September 2010, and again at the conclusion of the study on 15 December 2010. If the ANOVA type III test indicated significant differences, pair-wise comparisons between groups were made by assessing differences in least squares means (SAS lsmeans statement; approximates *t*-test between treatment and control groups), and a Tukey adjustment was used for multiple comparisons. Eight individuals escaped before measures could be made on 16 September, but there was no reason to believe their inclusion would have changed group mean masses, or the end results in any way. Research was conducted in the autumn when mallard body mass generally increases (Heitmeyer 1988), so we further evaluated individual changes in weight using a paired *t*-test (proc means; SAS 9.2; SAS Institute, Inc.), which uses the difference in mass (individual mass change between 16 Sep 2010 and 15 Dec 2010) as the unit of interest.

We tested for differences in the frequency of grooming behavior, aggression, and location occurrence (water or land) among treatment groups. We compared counts of grooming behaviors with generalized linear models (PROC GLIMMIX, SAS 9.2; SAS Institute, Inc.) with a Poisson response distribution. The count of grooming bouts observed during each focal watch was included as a response, and treatment (standard harness, modified harness, or control) was included as an explanatory variable. Aggression was a much less frequent behavior, so we compared whether aggression occurred during each focal observation with a binomial response and similarly structured model. Bird location was also evaluated with a binomial response model.

Wild Population

We captured mallard females in Saskatchewan, Canada, ($n = 18$) using swim-in traps (Evrard and Bacon 1998) in September 2010; and in Arkansas, USA, ($n = 18$) using rocket nets (Wunz 1984) in mid-February 2011. Birds were fitted with a Teflon ribbon harness equipped with a solar-powered GPS satellite-telemetry transmitter programmed to record 4 locations/day (Model PTT-100; Microwave Telemetry, Inc.). Arkansas Game and Fish Commission personnel marked birds under United States federal banding permit 06569. The completed transmitter and harness ($\bar{x}$ mass = 28–30 g) accounted for $\leq 3\%$ of body mass ($\bar{x} = 1{,}101$ g, SD = 70) of birds marked in Arkansas.

Birds captured in Saskatchewan were also fitted with 28- to 30-g packages, except for one bird that was marked with a 38- to 40-g package. We monitored marked birds until transmitters failed, or a likely mortality event occurred. We defined a transmitter failure or mortality event as the disappearance of signal or consistent and sequential locations that were ≤ 100 m from the last recorded location for each individual. Elsewhere (Beatty et al. 2013), we reported the migration chronology for each of the wild mallards using net displacement methods (see Bunnefeld et al. 2011), which were used to exclude breeding season movements of marked birds.

Regional mallard abundances.—As an index of unmarked mallard movements in the greater mid-continent population and during the non-breeding season, we used observations from a national migration survey, the Mallard Migration Observation Network (MMON). Briefly, MMON included 159 wildlife management sites distributed throughout the mid-continent region (Fig. 1). At each site, wildlife managers were instructed to record a weekly index of mallard abundance (ranging from 0 to 10) from September 2010 to February 2011, and September 2011 to December 2011. In February of each year, observers at each site revisited data to scale the season's observations so that highest abundances were scored 10 and lowest 1. Although MMON reports do not lend insight into absolute numbers of birds, they provide an index of relative mallard abundance at each location and during each observation period, and thus, insights into general timing of movement within the population of unmarked birds. Managers at the MMON sites reported 4,350 observations of weekly abundance indices. Although index scores for each site likely differed from those at other sites, observers were entirely unaware of the presence or absence of telemetry-marked birds (within 100 km). Thus, we assumed that the scores were reasonable indices of population abundance at each site and that any bias was not associated with telemetry-marked birds and had no effect on our analysis.

We linked the locations of telemetry-marked mallards with nearby MMON survey indices. For each location of a telemetry-marked bird, we searched the MMON data set to determine whether a MMON site was within 100 km. We then assessed whether the MMON sites within 100 km of marked birds had conducted surveys within 3 days of the telemetry-marked mallard's presence. Finally, we excluded all MMON sites that had not also conducted surveys during the 2 weeks prior to the presence of the telemetry-marked bird, and during the 2 weeks after the marked bird's presence. The selection criteria resulted in a set $n = 1{,}355$ bird and MMON site dyads from 57 MMON sites. Each dyad included 5 total MMON observations, including index values for the 2 weeks prior to the telemetry-marked bird's nearby presence (T_{-2} and T_{-1} respectively), the week when the bird was near (T_0), and the 2 weeks after the bird departed (T_{+1} and T_{+2}).

Movements of wild marked birds.—We tested whether the movements of telemetry-marked mallards were similar to those of unmarked birds in the larger mid-continent population. We predicted that marked birds would be located near MMON sites during weeks with peak index scores if they were moving with the larger population (MMON index scores would be greatest at T_0 and lower at T_{-2}, T_{-1}, T_{+1} and T_{+2}). Alternatively, if satellite telemetry-marked birds lagged behind, or moved ahead of unmarked migrants, regional abundance indices would be greater prior to (MMON indices would be greater during T_{-2} and T_{-1}), or after (MMON indices would be greater during T_{+2} and T_{+1}), the presence of telemetry-marked birds.

We calculated the disparity in abundance scores (scores for the 2 weeks before and after, minus the score for the week when telemetry-marked birds were present; $\mathrm{DV} = T_i - T_0$, where i indicates the identity for weeks before and after the presence of telemetry-marked birds and T_0 denotes the week the marked birds were near the network sites) for each MMON index location. These disparity values were used as response variables in linear mixed models (proc mixed; SAS Institute, Inc.). Explanatory variables included week identity (2 weeks prior to telemetry-marked bird presence [T_{-2}], one week prior [T_{-1}], 1 week after [T_{+1}], and 2 weeks after [T_{+2}], where T_0 denotes the week the marked bird was near the network site). Bird ID and MMON site were included as random effects variables to address repeated observations of birds and sites. Parameter estimates and the associated 95% confidence intervals (95% CI) provided insights into whether abundances peaked before, during, or after the presence of telemetry-marked birds. In short, we tested whether the 95% CI for MMON index scores during the 2 weeks prior to, or the 2 weeks after, the presence of telemetry-marked birds overlapped with zero. If the confidence intervals did not overlap, we concluded that the mean index values during those periods differed from the index values when birds were present.

We also tested the sensitivity of our approach by artificially shifting the time when birds were observed near MMON sites. We subtracted 6, 3, 2, and 1 days from the observed location dates and revaluated whether those perturbed data sets showed differences in the population peaks (as reported by MMON) and the simulated presence of telemetry-marked birds. We also added 1, 2, 3, and 6 days to observations and performed a similar set of analyses. We considered differences statistically significant at $\alpha = 0.05$ for all analyses.

RESULTS

Captive Population

We identified no differences in mean body mass of captive birds among treatment and control groups at the onset of the study ($F_{2,44} = 0.81$, $P = 0.450$). At the conclusion of the captive study, body mass differed among groups ($F_{2,52} = 5.45$, $P = 0.007$). Mean body masses of birds outfitted with standard (1,093 g, SD = 67 g) and modified harnesses (1,104 g, SD = 93 g) were 7.4% and 6.4%, respectively, less than birds in the control group (1,180 g, SD = 95 g). Results indicated that birds in the control group were 87 g (95% CI = 18–156 g) heavier at the end of the study than Teflon harnessed birds, and 75 g (95% CI = 7–144 g) heavier than birds with nylon harnesses. Body mass of individual ducks in each group increased between the time they were fitted with equipment and the end of the captive study (Fig. 3). However, changes in body mass during the study indicated that birds without harnesses ($n = 16$ paired measures, $\bar{x} = 163$-g increase, 95% CI = 112–216 g) exhibited greater increases in body mass when compared with ducks with standard harnesses ($n = 17$ paired measures, $\bar{x} = 66$-g increase, 95% CI = 40–105 g) and with modified harnesses ($n = 14$ paired measures, $\bar{x} = 63$-g increase, 95% CI 28–99 g). Differences in the mass of harnessed and control birds appeared to maximize approximately 8 weeks after birds were fitted with equipment, although variability in weather conditions likely also affected the timing of mass separation.

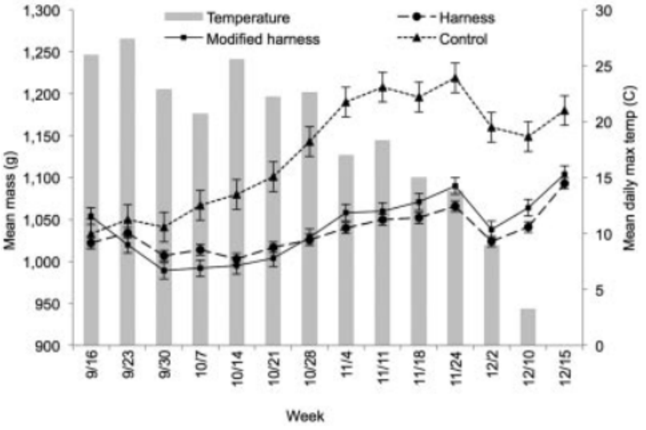

Figure 3. Mean weekly mass (g) of individual mallards marked with standard satellite-telemetry harnesses, a modified harness design, and no harness (control). Additionally, mean daily maximum temperature was collected from 16 September to 15 December 2010, Ashland, Missouri, USA.

The behavior of ducks in the captive population marked with dummy transmitters differed from those without transmitters. When compared with ducks without harnesses, which had a 42% (95% CI = 31–53%) probability of being in water at the end of the survey period, birds fitted with standard harnesses (11% probability of being in water; 95% CI = 6–21%) and those with modified harnesses (13% probability of being in water; 95% CI = 7–23%) were less likely to be in the water ($F_{2,219} = 11.76$, $P < 0.001$). There were no differences in grooming ($F_{2,220} = 1.37$, $P = 0.26$) or aggressive behaviors ($F_{2,220} = 2.38$, $P = 0.10$) in birds without harnesses and those with modified or standard harnesses.

Movements of Wild Birds

The locations of telemetry-marked mallards aligned with indices of regional abundance in the larger unmarked mid-continent population (Fig. 4). When compared with the week that unmarked birds were closest to network sites, regional abundances of mallards were lower during the 2 weeks prior (T_{-2}, T_{-1}) to the arrival of telemetry-marked birds, and during the 2 weeks after (T_{+2}, T_{+1}) the arrival of telemetry-marked birds (T_0; $F_{4,115} = 11.74$, $P < 0.001$). During the 2 weeks prior to, and during the 2 weeks after the presence of telemetry-marked birds, mean MMON population indexes were lower by 1.5 index units ($t_{73.7} = -4.87$, $P < 0.001$, 95% CI = −2.1 to −0.8), 0.7 ($t_{45.1} = -2.63$, $P = 0.0112$ 95% CI = −1.3 to −0.2), 1.2 ($t_{73.7} = -2.46$, $P < 0.016$, 95% CI = −1.4 to −0.1) and 1.8

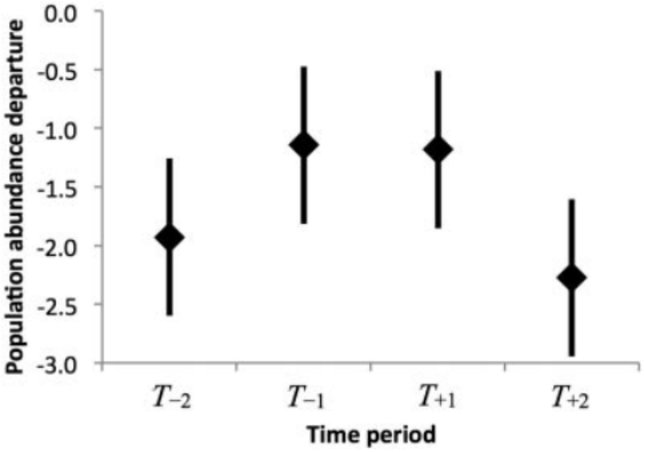

Figure 4. Mean differences in mallard population index values (diamonds) and associated 95% confidence intervals (bars) for mid-continent North American wetlands where telemetry-marked females were observed during the non-breeding season in 2010 and 2011. Indexes of unmarked birds were lower during the 2 weeks prior to the presence of telemetry-marked birds (T_{-2} and T_{-1} respectively) and during the 2 weeks following the presence of telemetry-marked birds (T_{+1} and T_{+2}). Results indicate that telemetry-marked mallards were moving with the larger population of unmarked mallards, because population indexes peaked during the week when marked birds were present.

($t_{73.7} = -5.99$, $P < 0.001$, 95% CI $= -2.5$ to -1.2) units, respectively.

Results further indicated that our approach was sensitive enough to detect whether telemetry-marked birds traveled in advance of, or behind, the bulk of the non-breeding population, as reported by MMON. The analysis was conducted using perturbed versions of our data that included dates shifted 1–3 and 6 days before, and after, the actual observation date of the telemetry-marked bird. When observation dates were advanced by 3 days, simulating an earlier arrival of telemetry-marked birds, results indicated no significant difference in MMON index values for T_{-1} ($t_{102} = -1.33$, $P = 0.186$). Similarly, results indicated no significant differences in MMON indices during T_{+1} and the occurrence of satellite telemetry-marked birds when observation dates were delayed by 2 days ($t_{16.6} = -1.96$, $P = 0.068$), and when delayed by 3 days ($t_{16.6} = -1.96$, $P = 0.067$). The pattern was exaggerated by perturbations of 6 days (respectively, $t_{31} = 0.84$, $P = 0.407$; and $t_{62.1} = 0.07$, $P = 0.946$).

DISCUSSION

Although results demonstrated an effect of satellite telemetry equipment on body mass gain and behavior of captive mallards, movements of free-ranging birds marked with GPS satellite transmitters paralleled those of the greater mid-continent population. In the captive flock, mass gain in all 3 groups occurred with the onset of colder weather; however, birds fitted with dummy transmitters did not gain as much mass as did unmarked individuals. Birds marked with dummy transmitters also were less frequently observed in water. Transmitter effects on habitat use were likely associated with the presence or absence of harnesses, because there were no apparent differences in frequency of water use among ducks with Teflon ribbon or nylon cord harnesses. Despite the potential effects of telemetry equipment, wild mallards marked with satellite transmitter systems appeared to travel with the larger population at the mid-continent scale during autumn migration.

Results from our captive flock indicated equipment effects on waterfowl body condition, as indexed by mass, and behavior are similar to those previously presented. Investigators reported no effects on duckling or brood survival when adult females were fitted with harness-mounted transmitters similar to those used in our study (Bergmann et al. 1994), whereas others showed that harness-mounted equipment affected waterfowl behavior and reproduction through reduced incubation times and delayed clutch initiation (Pietz et al. 1993, Rotella et al. 1993, Garrettson et al. 2000, Robert et al. 2006). A meta-analysis of transmitter effects on a variety of avian taxa demonstrated that transmitter equipment substantially altered energy expenditure and the likelihood of breeding, but did not influence flying ability (Barron et al. 2010). Several investigations also reported minimal transmitter effects on behavior of nesting and brood-rearing mallards (Rotella et al. 1993, Dzus and Clark 1996). However, multiple studies emphasized differential effects on birds, depending on the type of mounting system used (Paquette et al. 1997, Guyn and Clark 1999, Phillips et al. 2003; but see Pietz et al. 1995), duration of time that birds carried equipment (Bloom et al. 2012), and transmitter mass (Hooge 1991). Satellite systems available to date have been larger and heavier than previously used VHF systems, and the harnesses we tested encircled the entire bird body. Thus, future technological developments that reduce the size of satellite transmitters and improve mounting techniques may also reduce transmitter effects.

Reduced use of water and the reduced mass of captive marked birds may have been caused by compromised thermoregulatory abilities, as a result of satellite transmitter equipment. Plumage provides the thermal insulation essential to buffer convective and radiative heat loss to the environment (Wolf and Walsberg 2000, Gill 2007). Compressed feathers underlying harnesses may have served as a vector for heat conduction away from the body, thus increasing metabolic activity and daily energetic expenditure. In another study, captive birds outfitted with transmitters exhibited 8.6% greater daily energetic expenditure, compared with control birds, and investigators attributed the greater thermoregulatory costs to feather disruption caused by harness equipment (Godfrey and Bryant 2003). In addition, mallard ducklings carrying external transmitters showed areas of increased body surface temperature, likely indicating greater heat loss as a result of the transmitter and harness (Bakken et al. 1996). Harness materials also may have wicked water to the skin, which could have further reduced body heat retention through conduction and evaporation. Prolonged elevated metabolic activity, as a result of decreased thermoregulatory ability among harnessed birds, may have caused the disparity in behaviors and mass gain that was exhibited by harnessed and unharnessed captive birds.

Nonetheless, patterns observed in our study seem worthy of additional experiments to further elucidate mechanistic causes governing the relationship between tracking equipment, habitat use, and thermoregulation, especially among wild birds.

Wintering mallards are challenged by energy needed for molt, courtship, thermoregulation, and for nutrient reserves for spring migration and breeding (Paulus 1988). Previous research has documented conflicting results about effects of reduced body mass on waterfowl throughout the annual life cycle (Reinecke et al. 1988, Hepp et al. 1990, Gloutney and Clark 1991). Increased body mass in female mallards has been linked to increased overwinter survival (Haramis et al. 1986, Hepp et al. 1986, Bergan and Smith 1993), and earlier initiation and completion of various life-cycle events including pairing, molt, lipid accumulation, and nesting (Heitmeyer 1987, 1988; Richardson and Kaminski 1992; Devries et al. 2008). However, other researchers reported no effects of body condition on nonbreeding mallard survival in the Mississippi Alluvial Valley, Mississippi, USA, and in the San Luis Valley, Colorado, USA (Reinecke et al. 1988, Dugger et al. 1994, Jeske et al. 1994). Captive mallards marked with tracking equipment in our study showed reduced mass gain during the early winter periods compared with unmarked birds, indicating that the subjects of satellite telemetry studies may be more vulnerable to environmental conditions than individuals in the unmarked population as a whole. Thus, we suggest that investigators interested in energetics, survival, and molt should explicitly address the potential for tracking equipment to bias results in their investigations.

Observations of wild mallards did not indicate differences in the movements of marked and unmarked birds during autumn and winter. Specifically, the movements and locations of mallards marked with satellite telemetry devices coincided with those of the larger unmarked mid-continent population. This finding is particularly relevant because although numerous studies have used radio and satellite transmitters to evaluate and quantify waterfowl movements, few have assessed the effects of transmitters on bird movements (although see Ward and Flint 1995). Based on a meta-analysis of studies evaluating transmitter effects on avifauna, Barron et al. (2010) reported that although transmitters had an overall negative effect on birds and many metrics of avian ecology (nest success, body condition, behavior, etc.), flying ability was generally not affected by transmitters. Similarly, migration chronology did not differ between radiomarked brant (*Branta bernicla*) and the general population (Ward and Flint 1995). It is possible that marked birds in our study maintained their flying ability; thus allowing their movements to coincide with those observed in the general mid-continent mallard population, at the expense of increased energy consumption (Godfrey and Bryant 2003). One limitation of our study is that timing of the MMON extended from September through February, thereby preventing us from evaluating movements of marked birds in relation to the general population during spring migration. Given that body mass differences between marked and unmarked captive birds occurred during winter months, an evaluation of movements and behavior of marked birds relative to the general population during spring migration and breeding could provide valuable information on how body condition and transmitters interact during more energetically demanding time periods.

Results from captive and wild study subjects are not necessarily contradictory, in that even though transmitter-marked birds moved with the greater unmarked population of wild mallards, marked study subjects may have had lower body mass and occasionally behaved differently from unmarked birds. Nonetheless, the alignment between the unmarked population movements and the movements of birds with satellite transmitters indicates potential for obtaining useful large-scale movement and resource-use data from individuals marked with satellite transmitters.

MANAGEMENT IMPLICATIONS

Our results indicate that researchers must be cautious when designing and interpreting studies based on satellite telemetry, and that practitioners should strive to consider caveats and nuances when using those studies to guide management decisions. Our results directly demonstrate that consideration is warranted for the way in which transmitters might influence the metric of interest for a particular study. Observations from our captive population indicate potential for transmitter effects on body mass and behavior in birds, but results from the wild population suggest that studies of life-history events not strongly associated with body mass are unlikely to be substantially influenced by tracking equipment. Thus, despite potential for limited effects from larger and heavier satellite transmitters, larger scale and longer term movements of marked waterfowl are likely representative of the general population.

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