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ORIGINAL ARTICLE

Evidence that dorsally mounted satellite transmitters affect migration chronology of Northern Pintails

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Abstract We compared migration movements and chronology between Northern Pintails (*Anas acuta*) marked with dorsally mounted satellite transmitters and pintails marked only with tarsus rings. During weekly intervals of spring and autumn migration between their wintering area in Japan and nesting areas in Russia, the mean distance that ringed pintails had migrated was up to 1000 km farther than the mean distance radiomarked pintails migrated. Radiomarked pintails were detected at spring migration sites on average 9.9 days (90 % CI 8.0, 11.8) later than ringed pintails that were recovered within 50 km. Although ringed and radiomarked pintails departed from Japan on similar dates, the disparity in detection of radiomarked versus ringed pintails at shared sites increased 7.7 days (90 % CI 5.2, 10.2) for each 1000 km increase in distance from Japan. Thus, pintails marked with satellite transmitters arrived at nesting areas that were 2500 km from Japan on average 19 days later than ringed birds. Radiomarked pintails were detected at autumn migration stopovers on average 13.1 days (90 % CI 9.8, 16.4) later than ringed birds that were recovered within 50 km. We hypothesize that dorsal attachment of 12–20 g satellite transmitters to Northern Pintails increased the energetic cost of flight, which resulted in more rapid depletion of energetic reserves and shortened the distance pintails could fly without refueling. Radiomarked pintails may have used more stopovers or spent longer periods at stopovers. causing their migration schedule to diverge from ringed pintails. We urge further evaluation of the effects of dorsally mounted transmitters on migration chronology of waterfowl.

Keywords *Anas acuta* · Northern Pintail · Migration chronology · Radio transmitter effects · Satellite telemetry

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Zusammenfassung

Anzeichen für einen Einfluss von dorsal angebrachten Satellitensendern auf den zeitlichen Zugverlauf von Spießenten

Wir verglichen das Muster und den zeitlichen Zugverlauf von Spießenten *Anas acuta* mit dorsal angebrachten Satellitensendern mit Spießenten, die ausschließlich beringt waren. Innerhalb einwöchiger Zeitfenster während des Frühjahrs- und Herbstzugs war die durchschnittliche Zugdistanz beringter Spießenten zwischen Japan (Überwinterungsgebiete) und Russland (Brutgebiete) bis zu 1000 km grösser als die von besenderten Spießenten. Besenderte Spießenten wurden weiterhin im Durchschnitt 9.9 Tage (90 % CI 8.0, 11.8) später in Frühjahrszuggebieten gesichtet, verglichen zu beringten Spießenten innerhalb eines Umkreises von 50 km im selben Gebiet. Obwohl sowohl beringte als auch besenderte Spießenten fast gleichzeitig aus Japan abflogen, stieg die Disparität in der Sichtung von besenderten zu beringten Spießenten in gemeinsam genutzten Aufenthaltsgebieten um 7.7 Tage (90 % CI 5.2, 10.2) pro 1000 km zurückgelegte Distanz an. Somit erreichten besenderte Spießenten ihre von Japan 2500 km entfernten Brutgebiete im Durchschnitt 19 Tage später als beringte Spießenten. Weiterhin wurden besenderte Spießenten innerhalb der Herbstrastgebiete im Durchschnitt 13.1 Tage (90 % CI 9.8, 16.4) später gesichtet als beringte Spießenten innerhalb eines Umkreises von 50 km im selben Gebiet. Unsere Hypothese ist, dass die dorsal angebrachten 12–20 g schweren Satellitentransmitter den Energieaufwand des Fliegens für Spießenten erhöhten. Dies führte zu einem schnelleren Energieverlust und verkürzte die Flugdistanz, die Spießenten zurücklegten, bevor sie ihre Energiereserven wieder aufstocken konnten. Besenderte Spießenten könnten daher mehr Rastplätze genutzt haben oder sich an diesen länger aufgehalten haben, was wohl die Ursache für das unterschiedliche Zugverhalten von besenderten und beringten Spießenten war. Wir drängen auf eine weitere Beurteilung der Auswirkungen von dorsal angebrachten Satellitensendern auf den Zugablauf von Wasservögeln.

Introduction

In recent decades, biologists have increasingly used radio transmitters and data loggers to track long-distance movements of birds (Barron et al. 2010). The number of studies that employ such devices will likely continue to increase, thanks to improvements in technology and the need to better understand migratory connectivity (Bridge et al. 2011). Among the various tracking devices deployed by ornithologists, satellite transmitters have been particularly useful to identify routes of avian migration and to establish connections between breeding, migration, and wintering areas (Rodgers 2001). Satellite telemetry has also been used to evaluate the timing of migration. For example, biologists have marked migratory birds with satellite transmitters in order to examine the timing of migration relative to resource availability (van Wijk et al. 2011; Kölzsch et al. 2015) and nest initiation (Hupp et al. 2006a), to estimate the rate at which migrants may transmit pathogens among regions (Gaidet et al. 2010; Newman et al. 2012), and to contrast migration schedules among different components of a population (Miller et al. 2005).

A critical assumption of tracking studies is that attachment of the tracking device does not influence the study animal in such a manner as to bias the studies' outcomes. As their use has become more common, the effects of transmitters and data loggers on avian species have been increasingly scrutinized (e.g., Barron et al. 2010; Vandenabeele et al. 2011; White et al. 2013). However, relatively few studies have examined whether attachment of satellite transmitters or other tracking devices can affect the timing of avian migration. An effect on migration chronology is possible if devices that are attached outside of a bird's body increase aerodynamic drag and raise energetic costs of flight (Gessaman and Nagy 1988; Irvine et al. 2007; Schmidt-Wellenburg et al. 2008). Birds that carry external tracking devices may deplete energetic reserves during migration more quickly, necessitating shorter flights between stopovers (Pennycuick et al. 2012). Additional time at stopovers to replenish reserves may cause the rate of migration for marked birds to differ from unmarked individuals, giving scientists a biased view of the timing of migration events.

For many species of birds, biologists have few means other than satellite telemetry to study the timing of migration across large regions. Thus, opportunities to contrast migration movements of a radioed cohort with those of a non-radioed control group are rare. We attached dorsally mounted platform transmitter terminals (PTTs) to Northern Pintails (*Anas acuta*) at wintering areas in Japan to study their migration routes to nesting areas in Russia, and their connectivity with North American pintails (Yamaguchi et al. 2010; Hupp et al. 2011). This same population had been the subject of long-term ringing efforts (Flint et al. 2009). Pintails ringed in Japan were recovered, mainly by hunters, during their spring and autumn migrations in Russia. The dates and locations of ring recoveries provided a means to evaluate migration of pintails that were not encumbered by transmitters. Therefore, we contrasted the spatial and temporal distributions of recoveries of ringed pintails with those of pintails that were marked with satellite transmitters. Our objectives were to determine if ring recoveries and satellite telemetry provided similar estimates of the distance that pintails migrated over time, and if there were disparities, to estimate the magnitude of the transmitter effect and identify sources of its variation. We also contrasted the magnitude of any transmitter effects during spring migration to those of autumn migration 4–5 months later.

We predicted two outcomes if PTTs did not influence migration chronology. First, within a given interval of Julian dates, radiomarked and tarsus ringed pintails would have migrated similar distances. Within 7-day intervals in spring and autumn we contrasted the mean distance separating Japan from the recovery locations of ringed pintails and locations of birds marked with PTTs. We expected means to be similar between marker types if satellite transmitters had no effect on migration movements. Our second prediction was that Julian dates of detection at a common location would be comparable for birds marked with PTTs and those that were ringed. Therefore, we computed the number of days that separated first detection of a PTT at a site from the Julian dates of nearby ring recoveries. Our null hypothesis was that detection dates of pintails with PTTs would not be later than those of ringed individuals.

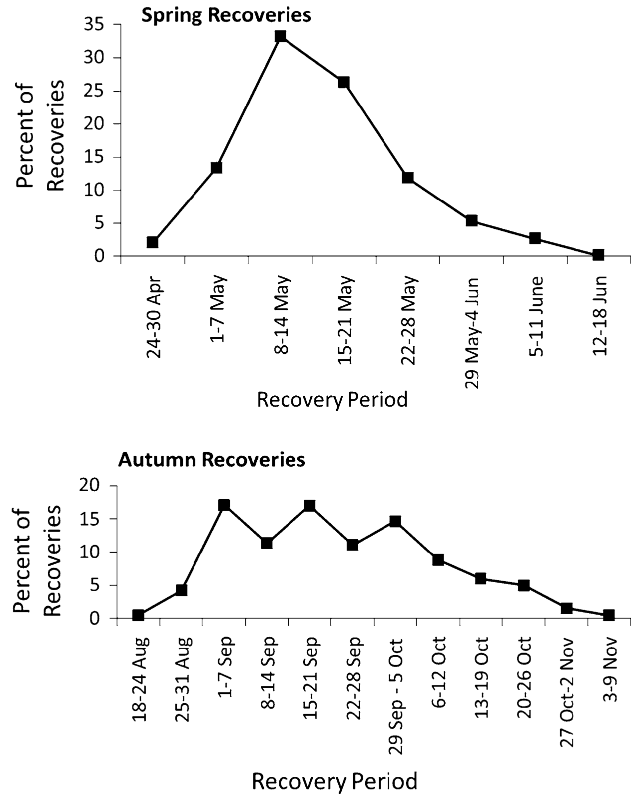

Fig. 1 Percentage of ring recoveries in each 7-day interval during spring and autumn migration for Northern Pintails that were marked in Japan and recovered in Russia, 1966–2009. In spring there were 882 recoveries and in autumn 386 recoveries of ringed pintails. In spring, most (95 %) recoveries occurred between 1 May and 4 June. In autumn, most (87 %) recoveries occurred between 1 September and 19 October

Methods

Data sets

Ring recoveries

Ring recoveries in Russia were based on pintails marked at wintering areas in Japan from 1966–2009 by the Yamashina Institute for Ornithology (YIO). During that period, the YIO ringed 111,559 pintails (median 2841 year^{-1}). Records of ring recoveries were maintained by the YIO and the Bird Ringing Centre of Russia. Most recoveries (95 %) were of pintails ringed at a winter capture site near Tokyo, Japan. We examined recoveries in Russia during spring (24 Apr–18 Jun) and autumn (18 Aug–9 Nov) between 1967 and 2009. The number of recoveries in Japan was too small for consideration in our analysis because spring harvest was not allowed and few people hunted in autumn. We used 882 spring recoveries and 386 autumn recoveries from Russia in our analysis. Recovery date was known to within one day for 96 % of recoveries, and known to within five days for the remainder. Spring recoveries mainly occurred between 1 May and 4 June, and autumn recoveries mainly occurred between 1 September and 19 October (Fig. 1). The number of recoveries declined after 1990 (Fig. 2), likely because of a reduction in the human population in the Russian Far East, and changes in government support for reporting of ring recoveries following dissolution of the Soviet Union. There was no diminishment in ringing effort in Japan after 1990 (27,592 pintails ringed from 1980 to 1989; 28,842 pintails ringed from 1990 to 1999).

PTT locations

Spatial and temporal distributions of pintails marked with PTTs were based on birds captured and marked at various locations in Japan from 2007 to 2009. Details on the capture and marking of pintails are in Hupp et al. (2011). Briefly, we captured pintails at six locations (Online Resource 1, Fig. A) and attached dorsally mounted PTTs to 198 individuals (60 % males and 40 % females). We marked from 40 to 92 birds each year. PTTs were centered between the scapulars of pintails (Online Resource 1, Fig. B) and held in place by a 0.38 cm wide Teflon ribbon harness (Miller et al. 2005). All transmitters were attached by personnel that had previous experience in securing

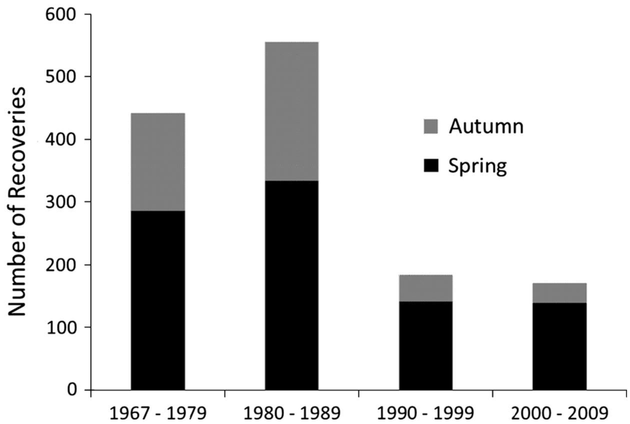

Fig. 2 Number of ringed Northern Pintails that were marked in Japan and recovered in Russia during spring and autumn migration within each 10–14 year period from 1966 to 2009. The small number of recoveries ($n = 2$) in the 1960s were combined with recoveries in the 1970s

dorsally mounted radios with a Teflon harness. In each year, we attached solar-powered PTTs that weighed 12 or 18–20 g (Online Resource 1, Table A). In 2008, our sample included 50 20-g battery-powered PTTs. Solar-powered PTTs transmitted daily, whereas battery powered PTTs transmitted once within each 3-day interval (Online Resource 1, Table A). Mass of PTTs and harnesses represented 1.7–2.6 % of the mean body mass (900 g) of pintails at capture.

Latitude and longitude of PTTs at each date and time they were detected were determined through the Argos Data Collection and Location Systems (CLS America 2007). We used the Douglas Argos-filter algorithm (Douglas et al. 2012) to remove unlikely locations based on rate and direction of movement. We ignored movements suggested by low quality Argos class 0, A, B, or Z locations (CLS America 2007) unless they were confirmed by higher quality (Class 1, 2, or 3) locations. When we received >1 location within a PTT's transmission cycle, we selected the highest quality location to represent the bird's daily location.

Our analysis of spring migration chronology of PTTs was based on pintails that departed from Japan and were detected at migration or nesting areas in Russia. Spring use sites included migration stopovers in Russia and the first summer location used by a pintail. Migration stopovers of PTTs were sites separated by >25 km that were used from 1 to 27 days (Online Resource 1). The first summer location was a site where a pintail remained >27 days, a period sufficiently long for nest initiation or molt of remiges (Clark et al. 2014). We included the first summer location of PTTs in our spring migration analysis, as we thought it plausible that some harvest of ringed pintails was apt to occur as marked birds arrived at nesting areas. In autumn, the PTT sample consisted of migration stopovers used by pintails after departure from summer sites until arrival at wintering areas in Japan or the Korean Peninsula.

Data analysis

Migration distance of PTTs versus ringed pintails

We divided spring and autumn migration into 7-day intervals of Julian date, and classified each ring recovery and PTT use site according to the 7-day interval in which they occurred. We then computed the distance separating each recovery location or PTT use site from the most northern point of the Japanese island of Hokkaido. We used northern Hokkaido as a common reference point to calculate migration distance for this and subsequent analyses, because capture locations in Japan varied for marked pintails and because a high percentage of pintails passed through Hokkaido during spring and autumn migration (Hupp et al. 2011; Yamaguchi et al. 2012a). Within each 7-day interval we compared the mean distance that separated northern Hokkaido from ring recoveries versus PTT use sites. A radiomarked pintail could be detected at >1 site in a 7-day interval. However, we only used the site that indicated farthest migration in that interval to represent a radiomarked bird's location. We computed Bonferonni-adjusted 95 % confidence intervals for pairwise comparison of mean ring recovery and PTT migration distances within each 7-day period. Overlap of means and confidence intervals was evidence that ringed and radiomarked pintails had migrated similar distances within the same 7-day period.

Detection dates of PTTs and ringed pintails at common locations

If PTTs did not influence the timing of migration, Julian dates of detection should have been similar, regardless of marker type, for ringed and radiomarked pintails that occurred at the same sites. In spring and autumn, we identified ring recoveries that occurred within 50 km of a PTT use site. We then computed the number of days that separated the first Julian date of PTT detection at the site and the Julian dates of individual ring recoveries within 50 km. A single ring recovery could occur within 50 km of >1 PTT use site, and multiple ring recoveries could occur within 50 km of a single PTT site. Therefore, for each season we created 5000 data sets that consisted of one randomly selected use site for each pintail marked with a PTT, and a randomly selected ring recovery that occurred within 50 km of the site. Data sets were randomly created with replacement so that for each, all combinations of ring recoveries and PTT use sites were available for selection. By creating data sets where each PTT was represented by a single use site that was paired to a unique ring recovery within 50 km, we reduced dependencies among observations. We computed the average difference in days between the first Julian date of detection of a PTT at a site and Julian date of a nearby ring recovery across all observations in a randomly created data set. A positive value indicated that on average, PTTs were detected at later dates than the ring recoveries. We computed the mean of average differences across all 5000 iterations for each season. The 5th and 95th percentiles for average difference across all data sets served as lower and upper 90 % confidence limits for the overall mean difference. Our null hypothesis that PTTs did not delay migration chronology was rejected if the lower confidence limit was >0, indicating that on average, first detection dates of PTTs were later than the dates of nearby ring recoveries.

Pending rejection of the null hypothesis of no PTT effect, we further examined factors that might influence disparities in migration timing between ringed and radiomarked pintails. We conducted a separate linear regression for each of the 5000 iterations of the data. In each analysis, the response variable was the number of days separating first detection of a PTT at a site and the date of a nearby ring recovery. Predictor variables for the spring migration analysis were (1) distance separating the PTT site from northern Hokkaido, (2) sex of the radiomarked and ringed pintails, (3) body mass of the radiomarked pintail, (4) mass of the PTT (12 versus 18–20 g), and (5) the difference in May temperature between the year of the PTT location and the year of the ring recovery. We expected that if PTTs adversely affected some aspect of migration energetics, such as the cost of flight or the accumulation and expenditure of reserves, radiomarked birds might increasingly lag behind ring recoveries as migration progressed, resulting in a positive effect of migration distance on the disparity. Hupp et al. (2011) observed that migration routes of male pintails marked with PTTs differed slightly from radiomarked females, and suggested that because of skewed sex ratios, migration strategies of unpaired males might differ from paired males and females. Therefore, we considered sex of marked birds as predictor variables if genders of the radiomarked and ringed pintails differed. We expected that radiomarked birds that were relatively lighter in mass might migrate more slowly than heavier individuals that were potentially in better physiological condition. We measured body mass of all radiomarked pintails at capture, and expressed individual body mass as observed mass minus mean mass for that individual's sex. PTT mass could have affected migration chronology if pintails with heavier transmitters migrated more slowly. We expected that pintails would advance migration chronology in warm springs compared to years of colder spring temperatures and that temperature differences between years could affect disparities in detection dates of PTTs and ringed pintails at shared sites. We computed mean May temperature in each year from 1968 to 2009 at each of 15 Russian weather stations that were distributed across the migration region of pintails (Online Resource 1, Fig. C). We standardized annual observations from each station as normalized deviates so that data from all stations were on the same scale, and averaged standardized scores across stations within each year. We computed the difference in mean standardized temperature between the year of the PTT observation and the year of the paired ring recovery. A positive value indicated that the PTT observation occurred in a year that was warmer than a ring recovery. With the exception of body mass of the radiomarked pintail, we evaluated the effects of the same predictor variables for autumn migration. We did not include body mass as an explanatory variable in autumn, because we did not know if body mass at capture would be a valid measure of mass 7–9 months later. Autumn temperature was computed similarly to spring temperature and was based on September averages across the 15 weather stations. However, in autumn we expected that relatively warmer temperatures would result in delayed migration because birds would remain farther north.

We used an information theoretic approach to examine the influence of predictor variables on disparities between ring recoveries and PTT occurrence at a site (Burnham and Anderson 2002). We examined a suite of 31 candidate models in spring that consisted of all combinations of predictor variables, plus a null model that only included an intercept (Online Resource 1, Table B). In autumn, our candidate set included 17 models (including the null), because we omitted those with body mass. We did not consider models with interactions, as we had no biological basis to expect such relationships. We gauged model support via Akaike's information criterion modified for small sample size (AIC_c), and Akaike weights (w_i). If no model was clearly supported, we assessed support for an effect of individual predictor variables based on the sum of Akaike weights ($\sum w_i$) and weighted parameter estimates. We averaged AIC_c and w_i across all 5000 iterations of the analysis to derive an estimate of overall model support. Weighted parameter estimates were likewise based on values averaged across all iterations. We considered the 5th and 95th percentiles for weighted parameter estimates as 90 % confidence intervals.

Results

Migration distance of PTTs versus ringed pintails

A total of 102 radiomarked pintails departed from Japan and were detected in Russia. However, the number of pintails detected within weekly intervals ranged from 44 to

76 individuals, because departure dates from Japan differed among pintails and because of transmitter failure and mortality during migration. In spring, the distance that pintails with PTTs had migrated lagged behind recovery distances of ringed pintails in most weekly intervals from 1 May to 4 June (Fig. 3). The disparity between ring recovery and PTT migration distances was relatively small (250 km) in the first week of May. However, by the fourth week of May, PTT migration distance lagged behind average ring recovery distance by approximately 1000 km. Mean recovery distance of ringed birds reached a maximum of approximately 2500 km from Japan by the fourth week of May. Recoveries between 5 and 11 June averaged slightly closer to Japan, but the sample was small ($n = 23$) and the confidence interval large. Radiomarked pintails did not reach their mean maximum spring migration distance of approximately 2200 km until the second week of June.

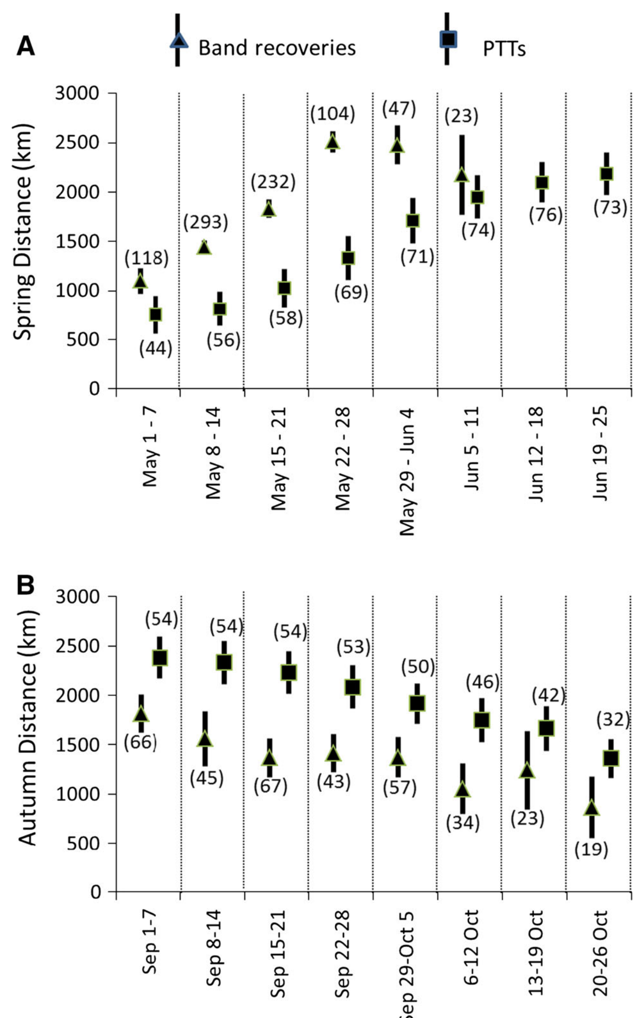

Fig. 3 Comparison of the mean distance separating Japan from recovery locations of ringed Northern Pintails versus the locations of pintails marked with satellite transmitters during 7-day intervals of spring (**a**) and autumn (**b**) migration. Solid vertical lines represent Bonferonni-adjusted 95 % confidence intervals surrounding the mean. Numbers of ring recoveries and pintails that carried satellite transmitters in each 7-day interval are indicated in parentheses

We detected between 32 and 54 pintails with PTTs during weekly intervals in autumn. After reaching an initial summer site where they remained at least 27 days, some pintails moved to more northern locations, possibly to molt remiges (Hupp et al. 2011). Thus, on average, pintails with PTTs were farther from Japan at the start of autumn migration than they were at the end of spring migration in early June. Conversely, recoveries of ringed pintails in early September were closer to Japan than in late May, possibly because migration toward the wintering area was already underway. Within weekly intervals, mean recovery distance of ringed pintails was up to 800 km closer to Japan than mean locations of radiomarked pintails (Fig. 3).

Detection dates of PTTs and ringed pintails at shared stopovers

Spring

A total of 631 ring recoveries occurred within 50 km of 361 spring stopovers or initial summer sites that were used by 101 radiomarked pintails (Online Resource 1, Fig. A). There were 4770 unique combinations of PTT spring use sites and paired ring recoveries within 50 km. From that pool, one site per PTT and one ring recovery per site were randomly selected in each of the 5000 created data sets.

Across the 5000 randomly created data sets, PTTs were first detected at spring use sites on average 9.9 days (90 % CI 8.0, 11.8) later than recovery dates of ringed pintails within 50 km. We therefore rejected the null hypothesis of no PTT effect on migration chronology. We examined covariates that might affect magnitude of the PTT effect and found that the disparity between ring recovery date and occurrence of a PTT at a site was not clearly explained by any single candidate model (Table 1). Among the predictor variables, distance separating a spring use site from Japan received the most support ($\sum w_i = 0.99$). The best supported model, which included the intercept and a term for distance from Japan, explained on average 12 % of the variation in differences between ring recovery and PTT detection dates at a site. Based on the weighted parameter estimate (Table 2), the lag in PTT detection increased by 7.7 days (90 % CI 5.2, 10.2) for each 1000 km increase in distance that separated a location from Japan (Fig. 4). Based on the modeled relationship between distance and temporal disparity, the parameter estimate for the intercept (−0.2) did not differ from 0 (90 % CI −3.8, 3.6), suggesting that radiomarked and ringed pintails departed Japan on similar Julian dates. However, at sites that were 2500 km from Japan, pintails with PTTs were first detected on average 19 days after nearby ring recoveries.

Table 1 Support for models that predicted the number of days that separated Julian dates of recoveries for ringed Northern Pintails from the first Julian detection date for pintails marked with PTTs at shared spring migration sites in Russia

Model	K[a]	AIC_c	Δ AIC_c	w_i
Distance	2	520.2	0.00	0.23
Distance + temperature	3	521.1	0.93	0.14
Distance + PTT mass	3	521.4	1.24	0.12
Distance + body mass	3	522.0	1.85	0.09
Distance + temperature + PTT mass	4	522.4	2.20	0.08
Distance + temperature + body mass	4	523.0	2.82	0.06
Distance + PTT male + ringed male	4	523.1	2.94	0.05
Distance + PTT mass + body mass	4	523.3	3.13	0.05
Distance + temperature + PTT male + ringed male	5	524.1	3.96	0.03
Distance + temperature + PTT mass + body mass	5	524.3	4.13	0.03
Distance + PTT mass + PTT male + ringed male	5	524.4	4.26	0.03
Distance + body mass + PTT male + ringed male	5	524.9	4.78	0.02
Distance + temperature + PTT mass + PTT male + ringed male	6	525.5	5.32	0.02
Distance + temperature + body mass + PTT male + ringed male	6	526.0	5.84	0.01
Distance + body mass + PTT mass + PTT male + ringed male	6	526.3	6.12	0.01
Distance + temperature + body mass + PTT mass + PTT male + ringed male	7	527.4	7.22	0.01
Null	1	528.3	8.11	0.00

Predictor variables include distance separating the site from northern Japan (Distance), difference in standardized May temperature between the year of the ring recovery versus the year of PTT detection (Temperature), body mass of the radiomarked pintail (Body mass), whether the radiomarked pintail was a female and the ringed pintail was a male (Ringed male), or the ringed bird a female and the radiomarked pintail a male (PTT male), and mass (18–20 versus 12 g) of the PTT (PTT mass). Models are ranked according to increase in Akaike's information criterion adjusted for small sample size (AIC_c) and decreasing Akaike weight (w_i). Only models with $w_i \geq 0.01$ and the null (intercept only) model are indicated

[a] Number of parameters in the model

There was also some support for models that included terms for the effect of the spring temperature difference between the year of PTT detection and the year of the ring recovery, and PTT mass (Table 1). Based on weighted parameter estimates, the lag in PTT detection was slightly smaller if the year that a pintail with a PTT used a site was warmer than the year of the paired ring recovery, and slightly larger if the PTT weighed ≥18 g (Table 2). However, the confidence intervals that surrounded those estimates encompassed 0, suggesting their effects were weak. There was little evidence that disparities between ring recovery and PTT detection dates at a site were influenced by sex of either the radiomarked or ringed pintail or body mass of the radiomarked bird (Table 2).

Autumn

A total of 159 ring recoveries occurred within 50 km of 124 stopovers that were used by 43 radiomarked pintails during autumn migration (Online Resource 1, Fig. D). There were 1232 unique combinations of PTT stopovers and ring recoveries.

Pintails with PTTs were first detected at autumn stopovers on average 13.1 days (90 % CI 9.8, 16.4) later than recovery dates of ringed pintails within 50 km. None of the candidate models for factors that influenced the disparity between PTT detection and ring recovery dates were clearly supported (Table 3). Among the predictor variables, distance separating a stopover from Japan received the most support ($\sum w_i = 0.49$). Based on the weighted parameter estimate (Table 4), the lag in PTT detection decreased by 3.5 days for each 1000 km increase in distance to Japan (90 % CI −6.4, −0.6). Thus, disparities between PTT detection and ring recovery dates at a stopover tended to be smallest at the onset of migration and increased as pintails approached Japan. However, the distance effect was weak and on average explained only 5.3 % of variation in the difference between PTT detection and ring recovery dates. There was substantial variation in the data that was not explained by that effect (Fig. 4).

There was little evidence that the disparity between ring recovery dates and PTT occurrence at autumn stopovers was influenced by annual temperatures or size of the PTT (Table 4). However, there was slight evidence for an effect of sex on the disparity. The lag in detection of pintails with PTTs was reduced by an average of 3.6 days (90 % CI −6.9, −0.3) if the radiomarked bird was a male and the ringed pintail was a female.

Table 2 Model averaged parameter estimates for variables that predicted the disparity between Julian detection dates of Northern Pintails with PTTs versus Julian recovery dates of ringed pintails at shared spring migration sites in Russia

Parameter	Averaged estimate	90 % Confidence interval
Distance[a]	7.68	5.20, 10.20
Temperature	−0.83	−2.83, 1.21
Body mass	0.00	−0.003, 0.003
Ringed male[b]	0.21	−0.94, 1.33
PTT male[c]	0.04	−1.64, 1.62
PTT mass[d]	1.38	−0.28, 3.07

Positive values indicate that an increase in a variable contributed to a lag in detection dates of PTTs compared to nearby ring recoveries. Predictor variables include distance separating the site from northern Japan (Distance), difference in standardized May temperature between the year of PTT detection versus the year of ring recovery (Temperature), body mass of the radiomarked pintail (Body mass), whether the radiomarked pintail was a female and the ringed pintail was a male (Ringed male), or the ringed bird a female and the radiomarked pintail a male (PTT male), and mass (12 versus 18–20 g) of the PTT (PTT mass)

[a] Effect of each 1000 km increase in distance between a spring use site and Japan on the number of days that first detection of a pintail with a PTT at the site lagged behind that of ring recoveries within 50 km

[b] Effect on PTT lag if a ringed pintail was a male and a radiomarked pintail was a female

[c] Effect on PTT lag if a radiomarked pintail was a male and a ringed pintail was a female

[d] Effect on PTT lag if PTT mass was ≥18 g

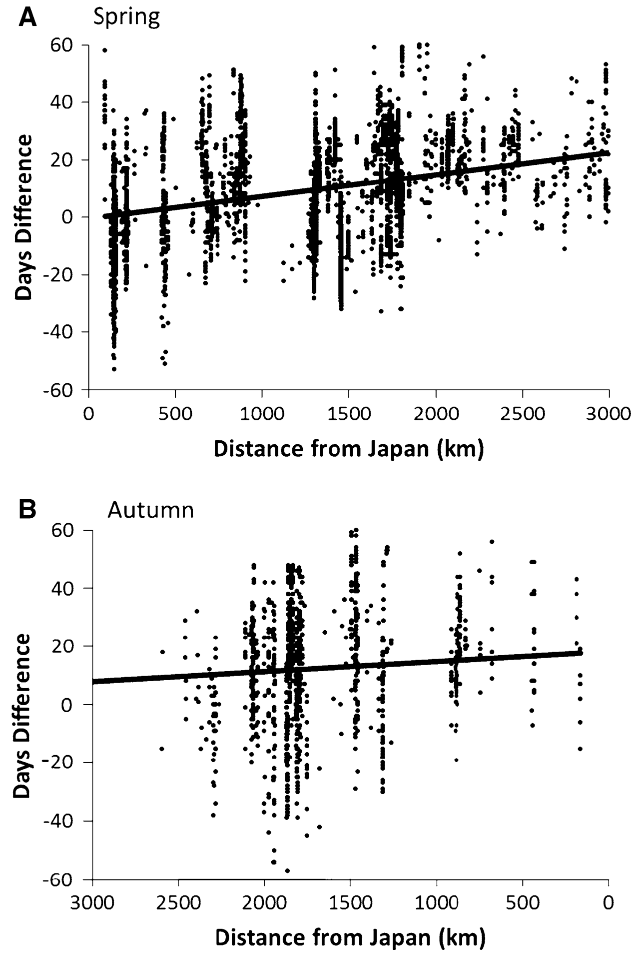

Fig. 4 The effects of distance from Japan on the number of days that separated Julian dates of detection of a Northern Pintail with a satellite transmitter at a spring (**a**) or autumn (**b**) migration use site and recovery of a ringed pintail within 50 km of the site. In spring, each point represents one of 4770 paired comparisons between a single detection of a satellite transmitter at a site and a ring recovery within 50 km. In autumn, each point represents one of 1232 paired comparisons between a single detection of a satellite transmitter at a stopover and a ring recovery within 50 km. Positive values indicate that detection of the satellite transmitter occurred after the Julian date of the ring recovery. The regression lines are based on model-averaged parameter estimates for the effects of migration distance from Japan on the disparity between Julian dates of satellite transmitter detection and nearby ring recoveries. Distance to Japan is reversed on the x-axis for autumn migration to facilitate comparison to spring migration

Discussion

There are at least several possible explanations for the disparities in spatial and temporal distributions of ringed pintails versus those marked with PTTs. Our satellite telemetry data were obtained in recent years, whereas ring recoveries occurred over a 40-year period. A later onset of spring migration or slower rates of migration in recent years compared to the 1960–1980s when most recoveries occurred could explain the disparities between ringed pintails and those with PTTs. A later onset of recent spring migration seems unlikely, given that May temperatures have increased over time in Eastern Russia (Fig. 5). We acknowledge that other weather conditions such as wind direction and atmospheric pressure systems can influence timing of avian migration (Yamaguchi et al. 2012b; Gill et al. 2014). We were unable to assess long-term changes in those conditions, and assume they did not differentially affect ringed and radiomarked pintails. We contrasted decadal differences in recovery distances of ringed pintails within 7-day intervals of spring and autumn migration, and found little evidence that movements of pintails had substantially changed over time (Online Resource 1, Fig. E).

Spatial and temporal distributions of ringed and radiomarked pintails might differ if they represented different components of the pintail population that winters in Japan, and if those components migrated on different schedules or to different regions. That scenario seems unlikely, because most (64 %) radiomarked pintails were captured within 300 km of the site where 95 % of pintails were ringed. Given the high mobility of pintails on winter areas (Cox and Afton 2000; Fleskes et al. 2002), we doubt

Table 3 Support for models that predicted the number of days that separated Julian dates of recoveries for ringed Northern Pintails from the first Julian detection date for pintails marked with PTTs at shared autumn migration stopovers in Russia

Model	K[a]	AIC_c	$\Delta\ AIC_c$	w_i
Null	1	222.5	0.00	0.13
Distance	2	222.5	0.07	0.13
Distance + PTT male + ringed male	4	222.8	0.30	0.11
PTT male + ringed male	3	223.1	0.62	0.10
PTT mass	2	223.8	1.34	0.07
Temperature	2	223.8	1.36	0.07
Distance + temperature	3	224.0	1.58	0.06
Distance + PTT mass	3	224.1	1.63	0.06
Distance + PTT male + ringed male + temperature	5	224.5	1.99	0.05
PTT male + ringed male + temperature	4	224.6	2.09	0.05
Distance + PTT male + ringed male + PTT mass	5	224.8	2.34	0.04
PTT male + ringed male + PTT mass	4	224.8	2.36	0.04
PTT mass + temperature	3	225.3	2.82	0.03
Distance + PTT mass + temperature	4	225.7	3.27	0.03
PTT male + ringed male + temperature + PTT mass	5	226.4	3.97	0.02
Distance + PTT male + ringed male + temperature + PTT mass	6	226.6	4.14	0.02

Predictor variables include distance separating the stopover from northern Japan (Distance), difference in standardized September temperature between the year of the ring recovery versus the year of PTT detection (Temperature), whether the radiomarked pintail was a female and the ringed pintail was a male (Ringed male), or the ringed bird a female and the radiomarked pintail a male (PTT male), and mass (12 versus 18–20 g) of the PTT (PTT mass). Models are ranked according to increase in Akaike's information criterion adjusted for small sample size (AIC_c) and decreasing Akaike weight (w_i)

[a] Number of parameters in the model

that population segregation would occur across that limited area. We did observe ring recoveries over a larger region of the Russian Far East than used by pintails with PTTs (Online Resource 1, Figs. A, D), but that was likely because ringing occurred over a much longer period and sampled a larger number of individuals. Satellite telemetry sampled a smaller number of individuals over a shorter interval, which has been shown to limit detection of the full range of variation in a population (Lindberg and Walker 2007). However, the region of eastern Russia most likely to be used by pintails from Japan was similar for ringed and radiomarked birds (Ostapenko et al. 1997; Flint et al. 2009; Hupp et al. 2011), and suggests they had comparable migrations.

Ring recoveries could provide a biased measure of migration chronology if there were changes in the timing of hunting seasons across years, if there were errors associated with reporting of recovery dates, or if hunters mainly targeted the first pintails to arrive in an area but hunted less at the peak of migration. Spring hunting across eastern Russia traditionally started on 1 May throughout the period when we examined ring recoveries. Autumn hunting seasons have also been consistent. We do not believe that ring recoveries were biased due to errors in reporting of recovery dates or locations. Especially during the period prior to 1990, government personnel were in place throughout the Russian Far East to facilitate reporting of ring recoveries. We also think it unlikely that hunters would mainly target the first pintails to arrive in a region, but shoot fewer birds during the peak of migration when pintails would be more abundant.

The most likely explanation for disparities between marker types both for distance moved within weekly intervals, and dates of detection at shared use sites, is that attachment of dorsally mounted PTTs altered the migration chronology of pintails. Dorsal attachment of transmitters likely increased aerodynamic drag and energetic costs of flight. Those effects have been documented via experiments with captive birds (Gessaman and Nagy 1988; Irvine et al. 2007; Schmidt-Wellenburg et al. 2008), and through models of flight performance (Obrecht et al. 1988). Pennycuick et al. (2012) noted that dorsal attachment of transmitters with a low profile and small frontal area, or those sloping antennas, such as those on our PTTs, can contribute significantly to aerodynamic drag by interrupting air flow over the bird's body. Increased flight costs and use of energetic reserves would have reduced flight range (Pennycuick et al. 2012), causing radiomarked pintails to use additional spring stopovers or spend more time at stopovers than ringed birds, resulting in a slower pace of migration.

On average, the dates that radiomarked and ringed pintails used sites closest to Japan in spring were similar, suggesting that PTTs had little effect on departure dates

Table 4 Model averaged parameter estimates for variables that predicted the disparity between Julian detection dates of Northern Pintails with PTTs versus Julian recovery dates of ringed pintails at shared autumn migration stopovers in Russia

Parameter	Averaged estimate	90 % Confidence interval
Distance[a]	−3.48	−6.44, −0.62
Temperature	0.35	−2.08, 2.77
Ringed male[b]	2.59	−1.51, 6.83
PTT male[c]	−3.59	−6.89, −0.28
PTT mass[d]	1.22	−2.78, 5.77

Positive values indicate that an increase in a variable contributed to a lag in detection dates of PTTs compared to nearby ring recoveries. Predictor variables include distance separating the stopover from northern Japan (Distance), difference in standardized September temperature between the year of the ring recovery versus the year of PTT detection (Temperature), whether the radiomarked pintail was a female and the ringed pintail was a male (Ringed male), or the ringed bird a female and the radiomarked pintail a male (PTT male), and mass (12 versus 18–20 g) of the PTT (PTT mass)

[a] Effect of each 1000 km increase in distance between a stopover and Japan on the number of days that first detection of a pintail with a PTT lagged behind that of ring recoveries within 50 km

[b] Effect on PTT lag if a ringed pintail was a male and a radiomarked pintail was a female

[c] Effect on PTT lag if a radiomarked pintail was a male and a ringed pintail was a female

[d] Effect on PTT lag if PTT mass was ≥18 g

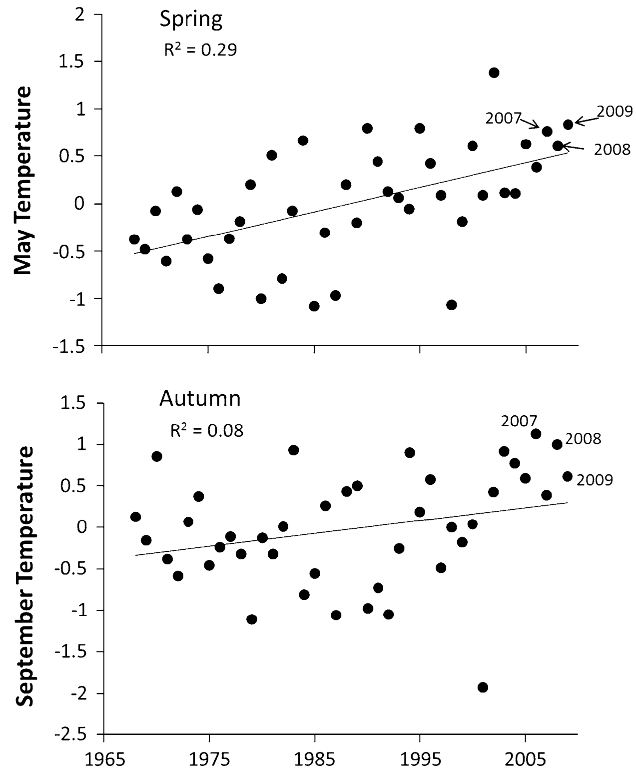

Fig. 5 Mean May and September temperatures in the Russian Far East increased from 1967 to 2009. Years when Northern Pintails were marked with satellite transmitters are labelled. Data are based on monthly mean temperatures from 15 weather stations in the Russian Far East. Normalized deviates were computed for each station and averaged across stations in each year. The regression line between averaged standardized temperature and year is indicated, as is the regression coefficient for the modeled relationship

from the winter area. For most birds marked with PTTs, there was an approximately 2.5 month period between their capture and departure from Japan. During that period there was a high rate of loss for PTTs, likely due to mortality and transmitter failure (Hupp et al. 2011). Between the time they were marked and their departure to nesting areas, pintails made relatively short flights from capture sites to staging areas in northern Japan (Yamaguchi et al. 2012a). Because flight durations were short, energetic condition of ringed and radiomarked pintails may have been similar at the onset of migration from Japan. Furthermore, pintails that had adapted most poorly to PTTs may have succumbed to mortality before leaving Japan. However, following their departure, ringed pintails advanced more rapidly than radiomarked birds and their spring migration schedules diverged. These observations are consistent with a cumulative effect of aerodynamic drag and increased flight costs over the course of migration. Ultimately, radiomarked pintails migrated about the same distance from Japan as ringed birds. But, it took them >2 weeks longer to arrive at the farthest spring migration destinations. Thus, dorsally mounted PTTs apparently affected migration chronology even though they were <3 % of pintail body mass, a percentage some biologists suggest is a desirable upper limit for transmitter weight (Barron et al. 2010).

A published account of spring migration chronology of Northern Pintails in the Russian Far East provides additional evidence of delayed arrival of radiomarked pintails at nesting areas. Krechmar and Kondratyev (2006) noted that average peak arrival of pintails at nesting areas on the Anadyr River from 1975 to 1989 was approximately 25 May. Mean recovery date for 42 ringed pintails in the same region was 22 May (range 26 Apr–3 Jun). The Anadyr River was the most common spring migration destination of radiomarked pintails (Hupp et al. 2011). Average date that 21 pintails with PTTs were first detected near the Anadyr River was 9 June (range 19 May–20 Jul), more than 2 weeks later than the mean date of ring recoveries and observed arrival noted by Krechmar and Kondratyev (2006).

The mean difference in detection dates between ringed pintails and radiomarked birds at shared stopovers was slightly larger in autumn (13 days) than in spring (9.9 days). However, in autumn there was less evidence that disparities in detection dates of marked birds at shared stopovers changed as pintails migrated toward Japan.

Interpretation of the differences in migration schedules of ringed versus radiomarked pintails is more difficult in autumn because of smaller samples of each. However, once autumn migration was initiated, rates of movement may have been more similar between radiomarked and ringed pintails than in spring. By autumn, only birds that were least affected by transmitter attachment may have been alive. But, even if their rates of migration were more similar in autumn, the radiomarked pintails initiated migration later than ringed birds, resulting in spatial and temporal differences between birds marked in different manners. Pintails required time on summer sites for nesting, molt, and accumulation of autumn premigratory energetic reserves. Delayed arrival of radiomarked birds in spring could delay timing of other seasonal events, and result in a later onset of autumn migration. Therefore, there may be a carryover effect of radiotransmitters from one season to another, even if birds acclimate to radios. The trend toward warmer September temperatures in recent years (Fig. 5) may also have contributed to radiomarked pintails remaining longer at higher latitudes compared to the ringed cohort in earlier decades. However, we found little evidence that differences in annual temperature influenced the disparity in detection dates of ringed and radiomarked pintails at shared autumn stopovers.

Although we observed that on average pintails with PTTs were detected at use sites later than ringed birds, we could explain no more than 12 % of the variation surrounding that effect. Ring recoveries at PTT use sites occurred as much as 60 days before to 60 days after the first detection of radiomarked birds. Some of that variation may have been due to the effect of weather events on migration of individual pintails. We could not assess those effects, given that we had a single recovery location for each ringed bird, but did not know its migration schedule or route prior to recovery. There was also considerable variation in recovery dates of ringed birds, likely because the data set was based on a large sample of individuals marked over a 40-year period and recovered across a broad geographic region. Finally, the difference in detection dates of PTTs and ringed pintails at shared sites may have varied if individual pintails responded differently to radios. Among pintails marked with PTTs, some individuals may have adapted more poorly to radios, while others were affected less for reasons that are unknown. The variation in temporal disparity between markers contributed to uncertainty regarding model selection, especially in autumn when there were fewer recoveries and PTTs. Unexplained variation should not be interpreted as evidence that a transmitter effect did not exist. Rather, it indicates that the covariates we examined did not account for much of the observed difference in detection dates of PTTs and ringed pintails at shared sites.

Outcomes of other studies that have contrasted migration schedules of ringed and radiomarked birds are varied. van Wijk et al. (2011) found no differences in dates White-fronted Geese (*Anser albifrons*) marked with dorsally mounted satellite transmitters and those that were ringed used shared stopover sites. Strandberg et al. (2009) noted that migration of common buzzards (*Buteo buteo*) marked with dorsally mounted satellite transmitters lagged relative to ringed individuals, an effect they attributed to behavioral changes following radio attachment. However, Strandberg et al. (2009) also observed that for some other raptor species, birds marked with satellite transmitters migrated farther and more rapidly than suggested by ring recoveries. They attributed that to a lower likelihood of ring recoveries in areas that were sparsely settled by people. Hupp et al. (2006b) found only minor differences in migration chronology of Canada geese (*Branta canadensis*) marked with tarsus bands versus those that carried abdominally implanted radio transmitters.

The effects of dorsally attached transmitters on avian migration schedules are likely to vary among taxa, depending on how a species' body size, frontal profile, and wing length affect its aerodynamic performance and ability to carry a transmitter. The method of attachment can also affect aerodynamic drag and potentially influence migration behavior. We do not imply that dorsal attachment of radio transmitters uniformly affects migration chronology of waterfowl. Indeed, there is not agreement on the effects of dorsally mounted transmitters on Northern Pintails. Miller et al. (2005) concluded that pintails marked with dorsally mounted transmitters in North America arrived at migration destinations within the range of published arrival dates for unmarked birds, although they acknowledged that transmitter attachment likely affected migration of some individuals.

We emphasize that we are not disputing the results of previous studies that have used dorsally mounted satellite transmitters to study the timing of avian migration. Nor do we believe our findings based on a single study of Northern Pintails warrant broader conclusions about the effects of dorsally mounted transmitters on migration schedules of other species. However, we do contend that very few ornithologists have used independently collected data sets to critically examine the assumption that radio attachment has no effect on migration chronology of birds. Physical scientists have long recognized that instrumentation can affect the behavior of natural systems (Fitzpatrick 2013). To promote animal welfare and ensure the integrity of research findings, ornithologists must also be aware of how marking techniques may influence the outcomes of avian behavioral and life history studies (e.g., Gauthier-Clerc et al. 2004; Sheldon et al. 2008; White et al. 2013). Satellite telemetry has greatly improved our understanding of the migratory linkages of birds and has proven to be an important research and conservation tool (Higuchi 2012). However, we urge caution when ornithologists assume that dorsal attachment of a satellite transmitter has no effect on the timing of a bird's migration. We encourage additional contrasts of migration chronology between birds marked with transmitters and those marked via other means, where opportunities permit.

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