

Articles

Inferring Movements and Staging Locations for Canvasbacks Using Light-Level Geolocators

Nathan A. Cook, Christopher A. Nicolai, Kevin T. Shoemaker*

Department of Natural Resources and Environmental Science, University of Nevada Reno, Reno, Nevada 89557

Present address of C. Nicolai: Delta Waterfowl Foundation, Bismarck, North Dakota 58504

Abstract

Understanding the geographic extent and timing of wildlife movements enables resource managers to inform habitat needs of target species efficiently and effectively. We use light-level geolocators—which enable researchers to estimate individual locations from light-level data—to build a more complete understanding of the geography and timing of migratory movements for canvasback *Aythya valisineria* in the Pacific Flyway. During the springs of 2015–2017, we placed 151 geolocators on canvasbacks using two alternative attachment methods (leg-band vs. nasal-saddle mounts) during spring migration (February–March) near Reno, Nevada. Eight of these geolocators (five males and three females) were successfully retrieved, representing 10 near-complete annual migration cycles (two geolocators contained data for two migration years). Eight of the 10 estimated spring canvasback migrations (five male and three female) ended at breeding sites in the Prairie Pothole Region of southern Canada and northern United States (often via stopover sites in Utah and Montana), whereas one male and one female migrated to breeding sites in Alaska. Notably, one female settled on nesting grounds in southern Saskatchewan and then in central Alaska in successive years. During spring migration, canvasbacks made an average of 3.3 ± 0.5 stopovers, with an average duration of 14.8 ± 2.2 d. Three canvasbacks made a distinct molt migration after breeding. For fall migration, canvasback made an average of 2.7 ± 0.3 stopovers, lasting an average of 12.3 ± 2.5 d, on their way to wintering sites in California's Central Valley and coastal regions near San Francisco Bay. Retrieval rate for nasal-saddle-mounted geolocators was significantly lower than leg band-mounted devices because of failure of nasal-saddle attachment. This study demonstrates the value of geolocators for assessing year-round habitat use for waterfowl species that have negative behavioral reactions to traditional backpack devices. This information complements standard band-recovery approaches and enables waterfowl managers to ensure that the spatial and temporal distributions of individuals are identified so that habitat conservation efforts can reflect the full annual habitat use cycle.

Keywords: animal movement; archival light-level data loggers; geolocators; migration; wildlife management

Received: May 2020; Accepted: May 2021; Published Online Early: May 2021; Published: December 2021

Citation: Cook NA, Nicolai CA, Shoemaker KT. 2021. Inferring movements and staging locations for canvasbacks using light-level geolocators. *Journal of Fish and Wildlife Management* 12(2):308–321; e1944-687X. <https://doi.org/10.3996/JFWM-20-032>

Copyright: All material appearing in the *Journal of Fish and Wildlife Management* is in the public domain and may be reproduced or copied without permission unless specifically noted with the copyright symbol ©. Citation of the source, as given above, is requested.

The findings and conclusions in this article are those of the author(s) and do not necessarily represent the views of the U.S. Fish and Wildlife Service.

* Corresponding author: kevinshoemaker@unr.edu

Introduction

Wildlife researchers continually strive to identify critical habitat resources for target species that support key life-history needs and ultimately maintain viable populations. For migratory populations this is complicated by the uncertain linkages and often vast distances between

breeding and the other habitats (e.g., staging areas, molting and wintering habitats) that sustain these populations through the remainder of the year (Marra et al. 2011; Hallworth et al. 2015). For nearly a century, waterfowl have exemplified the benefits and challenges of managing spatially separated habitats to sustain migratory populations. Early efforts to improve cooper-



ative management of disjunct critical habitats for migratory waterfowl across political boundaries resulted in the establishment of four administrative flyways that remain central to North American waterfowl management (Crissey 1955; Tautin 2005). However, effective management of waterfowl populations also requires an understanding of critical habitats at smaller spatial scales, including staging and refueling areas associated with long-distance migratory movements.

Historically, information about waterfowl movements and seasonal habitat use has been derived primarily from mark–recovery data, in which birds are captured and marked with metal leg bands that are subsequently reported via hunter harvest. Between 1960 and October 2020 there were 20.3 million ducks and geese banded and 3.9 million bands reported, with several species averaging over 100,000 banded and 1,000 recovered each year (2010–2019). By comparison, canvasbacks *Aythya valisineria* were banded and encountered much less frequently, with an average of 464 banded and 105 recovered each year (2010–2019; Bird Banding Laboratory 2020). However, these data only provide a snapshot of the habitats and locations used by an individual at capture and recovery. Advances in technology have expanded the potential for recording migratory paths for individual birds (López-López 2016). Very-high-frequency radio transmitters, satellite-based geographic positioning systems (GPS), global system for mobile communication devices, and archival light-level data loggers (hereafter, geolocators) have all been used to estimate positional information for migrating birds (Bridge et al. 2011; USDA Forest Service SDTDC 2012). In practice, considerations such as weight (for birds, units should weigh no more than 2.5–5% of total body mass; Naef-Daenzer et al. 2001), potential sample size (based on per-unit cost and probability of recovery), and potential behavioral effects of attachment generally determine which devices are used to study migratory movements for a particular population. Canvasbacks and other diving species have been negatively affected by backpack-style attachment of transmitters (Perry 1981; Robert et al. 2006). Furthermore, use of implant-style GPS radios have limitations because of battery life, as solar panels are not an option.

Geolocators, which record time-stamped light-level data at frequent and regular intervals, can be a cost-effective and minimally invasive method for recording waterfowl movements throughout the annual cycle (Guilford et al. 2012). Light-level geolocators typically cost \$150–\$200 and weigh ca. 0.5–3 g (Migrate Technology 2015). After geolocators are retrieved, time-stamped light levels are used to estimate daily sunrise and sunset times (Hill and Braun 2001). Subsequently, longitude and latitude are estimated on the basis of the timing and transition of light during twilight (Ekstrom 2007). Location estimates from geolocators are not exact and have been estimated to exceed 200 km (Phillips et al. 2004; Ekstrom 2007; Fudickar et al. 2012; Lisovski et al. 2012; Rakhimberdiev et al. 2016). Geolocators have been deployed on songbirds (Bairlein et al. 2012; Lemke et al. 2013), owls (Linkhart et al. 2016), shorebirds (Rakhimberdiev 2016), and other species, but have been used

infrequently on waterfowl (Eichhorn et al. 2006; Solovyeva et al. 2012; Hanssen et al. 2016; Hupp et al. 2018) to address questions about annual migrations, including estimating migration timing and identifying staging locations.

We use geolocators to build a more complete understanding of the geography and timing of migratory movements for a small sample of canvasbacks captured near Reno, Nevada (part of the Pacific Flyway) during spring migration. The Pacific Flyway accounts for approximately 25% of canvasback harvested in the United States from 1999 to 2018 (Olson 2019). Canvasbacks are one of the least abundant ducks in North America and had multiple alternating periods of population decline and growth from the 1950s to today (USFWS 2019), with boom periods generally associated with wet spring conditions on the prairies (Serie et al. 1992; Anderson et al. 2001). Little is currently known about seasonal habitat use and the timing of key seasonal movements for canvasback in the Pacific Flyway, including those that migrate through northern Nevada. Canvasbacks are listed as a “Species of Conservation Priority” (Wildlife Action Plan Team 2012) in Nevada, in part because of the species’ low population abundance relative to other waterfowl and large historical fluctuations in abundance across the region and continent (abundance estimates in adjacent years have differed by a factor of two). Springtime observations suggest two large migration corridor concentrations from central California wintering areas: one that passes due north through the Klamath Basin and another east through the Lahontan Valley of western Nevada (U.S. Fish and Wildlife Service Bill Henry and John Vradenburg, personal communication). Specifically, our research questions were: 1) Where are the important stopover sites for canvasbacks that migrate through northern Nevada, and are they different for spring and fall migrations? 2) What is the timing of key seasonal movements (e.g., arrival at breeding locations)? 3) Are some methods of geolocator attachment more effective than others? 4) Does geolocator attachment affect the rate at which individual canvasbacks are recovered?

Methods

We captured canvasbacks using cloverleaf waterfowl traps at Swan Lake (ca. 13 km north of Reno, Nevada; Figure 1) and the Canvasback Gun Club (ca. 20 km east-northeast of Fallon, Nevada; Figure 1), during February and March 2015–2017 as they started spring migration. We marked all captured birds with standard metal leg bands. For each capture, we recorded age (second year and after second year), sex, and mass. We attached light-level geolocators (Migrate Technology Ltd., Intigeo-W65A9-SEA and Intigeo-C65; 1.0 g) using one of two established methods: nasal saddles (Greenwood 1977) or plastic leg bands. We intended to attach geolocators in equal proportions to each of the age and sex classes; however, this was not possible because of unequal captures for each group. To test for possible effects of geolocator attachment on apparent recovery rates



Figure 1. Canvasbacks *Aythya valisineria* with light-level geolocators mounted using (left) the nasal-saddle method and (right) an auxiliary leg band. In this study, recovered light-level geolocators ($n = 8$) from canvasbacks originally captured in northern Nevada during the spring migration (2015–2018) were used to infer patterns of movement and broad-scale site use for individual canvasbacks. Geolocators are a lightweight and low-cost, yet imprecise, method for tracking migratory movements; geographic locations are inferred from these devices via the timing of sunrise and sunset. Locational accuracy and precision are typically highest for long stationary periods and are lowest for rapid migrations (especially adjacent to a solar equinox).

(potentially due to differential survival), we marked approximately half of the canvasbacks we captured only with standard metal leg bands as a control group. We used two different methods of geolocator attachment, nasal saddles (model W65A9) and auxiliary leg bands (model C65), as we were concerned that light-level recordings from leg mounts may be hindered by turbid water conditions (Eichhorn et al. 2006; Conklin et al. 2013); we therefore used nasal saddles to ensure that some geolocators would be above the waterline at all times. Polyvinyl chloride nasal saddles (Figure 1) were form-fitted to a cast canvasback bill and each was attached via a welding rod through the nares (aluminum in 2015 and stainless steel in 2016), which we secured with stainless steel washers crimped on each end (Lokemoen and Sharp 1985). We initially used aluminum to allow the saddles to fall off if not encountered within a small number of years. However, we learned that they were falling off faster than we predicted and switched to stainless steel. We attached nasal-saddle-mounted geolocators with silicone directly under the saddle atop the bill, with a drilled hole filled with crystal epoxy to allow for passage of light. For birds with leg-mounted geolocators, we attached geolocators using a plastic (polyvinyl chloride) leg band with an ultraviolet-protected zip tie. We inscribed all plastic leg bands with the contact information necessary for hunters to report geolocators directly to us. Birds with nasal-saddle-mounted geolocators also received an inscribed plastic leg band (without geolocator attached) to facilitate retrieval of geolocators from hunters. We programmed all geolocators to measure light levels every minute and record the highest reading in each 5-min interval; battery life estimates showed up to 24 mo of data recording for

each geolocator (Giunchi et al. 2015; Migrate Technology 2015). Although we hoped to recapture geolocator-fitted canvasbacks in subsequent trapping efforts, we expected that most re-encounters would occur via hunter harvest.

We downloaded raw time-stamped light-level data from all retrieved geolocators and processed them to correct for drift in the internal clock using software provided by the manufacturer (Migrate Technology, Coton, Cambridge, UK). Using the corrected light-level data, we estimated morning and evening twilight times using a standard threshold algorithm (Hill and Braun 2001; Rakhimberdiev 2016; Wotherspoon et al. 2016) implemented in the TwGeos package for the R programming environment (see https://github.com/natehe20/CANV_movements for R scripts; Wotherspoon et al. 2016; R Core Team 2018). We then refined or removed (flagged as outliers) twilight-time estimates on the basis of: 1) visual inspection, 2) severe discrepancies with neighboring twilight times, and 3) evidence of excessive shading, each of which is described in more detail below. First, we graphically overlaid designated twilight times on light-level time-series plots and manually corrected or removed obviously incorrect twilight-time estimates (Renfrew et al. 2013, Mostello et al. 2014, Giunchi et al. 2015). We then used the twilightEdit function (TwGeos package; Wotherspoon et al. 2016) to flag outliers for which the designated twilight time was ≥ 15 min from the median of the eight nearest neighboring twilight times, the set including the four previous and four subsequent twilights. If all eight neighboring twilight times were relatively consistent, differing from one another by ≤ 10 min, suggesting the animal was stationary, we altered the flagged outlier to be equal to the median of its eight neighbors. If the neighboring

twilight times were inconsistent, suggesting the animal may have been migrating, we removed the outlier observation from subsequent analysis. Finally, we removed any twilight-time designations whose accuracy was likely compromised by excessive shading; specifically, we excluded twilights from further analysis if we recorded more than three occurrences of darkness (log-transformed light level ≤ 0) after a designated sunrise time or before a designated sunset time.

To estimate the geographic locations of each bird over time, we passed the postprocessed light-level data through a state-space model designed to partition shifts in geographic location from observational error, using an algorithm implemented in the R package FLIGHTR (particle filter using 1,000,000 particles; Rakhimberdiev et al. 2015). FLIGHTR's algorithm assigned geographic locations for each particle on the basis of the degree to which recorded light levels 1 h before and after each estimated twilight time corresponded with respective light levels expected to occur at plausible candidate locations using the template-fit method (Ekstrom 2007; Rakhimberdiev et al. 2015). The FLIGHTR algorithm selected plausible candidate locations (i.e., could the bird have flown there from the previous location) on the basis of a maximum per-day flight distance distribution that was set at high default values to enable the algorithm to freely estimate location on the basis of the light-level data (mean = 300 km, standard deviation = 500 km; Rakhimberdiev et al. 2017). Next, the algorithm used calibrated estimates of observational error to partition observational error from the resulting raw movement trajectories, resulting in a posterior distribution of probable daily locations, at sunrise and sunset, that formally represented positional uncertainty. To estimate the start and end dates of all stationary periods (e.g., stopover site, breeding grounds) we used a FLIGHTR function ("stationary.migration.summary") that used the output from the particle filter algorithm to identify consecutive twilights characterized by a low probability of movement (Rakhimberdiev et al. 2017). We defined a stationary period as a minimum of three consecutive twilights or 1.5 d (minimum stay = 3 d) for which the posterior probability of stationarity was greater than 90% (probable cutoff = 0.1).

To effectively partition observational errors from the estimated true flight path of each individual bird, the state-space model requires specification of one or more calibration periods for each bird whereby 1) light levels are actively recorded; 2) the animal, or the geolocator itself, is stationary; or 3) the geographic location is known (Porter and Smith 2013). For effective calibration of the particle-filter algorithm, calibration is performed while the unit is actively deployed (on-bird calibration), as animal behaviors (e.g., moving in and out of shaded locations) can contribute substantially to observational errors in light-level readings (Rakhimberdiev et al. 2015). However, because we tagged canvasbacks during active spring migration, no clear on-bird calibration periods could be identified, leaving a short predeployment calibration period (we allowed geolocators to run for 9 d in full sun before attachment on a bird) as the only

calibration period that met all three criteria above. To generate a reasonable estimate of observational errors in light readings, which requires an on-bird calibration, we used a three-stage approach to identify stationary periods suitable for on-bird calibration. In stage 1, we used the predeployment light-level data to calibrate the particle-filter algorithm. After running the particle-filter algorithm, we determined the mean locations for all stationary periods estimated to be more than 14 d (28 twilights) in length. In stage 2, we calibrated the particle-filter algorithm to those stationary locations identified in stage 1 that overlapped with conservative and distinct estimates of breeding (1 May–15 June) or molting (15 August–15 September) time periods (i.e., periods for which these birds were expected to be stationary; Bergman 1973; Thompson and Drobney 1995), in addition to the predeployment calibration data. Specifically, we defined stationary periods as breeding or molting if half of the twilights within an estimated stationary period occurred during the expected breeding and molting periods. We used the stage 2 results to update the estimated timing and duration of breeding and molting periods. Finally, in stage 3, we calibrated the particle-filter model to the breeding and molting periods identified in stage 2, this time excluding predeployment calibration data. Results from this final state-space model, including the timing and duration of all stationary periods longer than 1.5 d in length, were interpreted as the best possible representation of canvasback movements and staging locations. For ease of visualization and interpretation, we merged consecutive estimated staging locations less than 150 km apart into single locations, in addition to all stationary periods occurring during breeding, molting, or wintering periods, during which canvasbacks were expected to be stationary (Bergman 1973; Thompson and Drobney 1995).

We visualized the estimated sunrise and sunset locations for each canvasback as a rounded polygon encompassing the interquartile range (50% credible interval [CI]) for latitude and longitude (Bates et al. 2012; Cresswell and Edwards 2013; Hobson and Kardynal 2015) derived from the particle-filter algorithm. Within each designated stationary or stopover period, geographic locations with darker colors represent higher inclusion within the 50% CI for each twilight and were considered more plausible estimates for the true stationary period. For each individual we summarized the total number of stopover sites, the mean stopover duration in days, and the timing of entry and exit to and from breeding, molting, and winter ranges. We conducted all analyses using the R environment for statistical computing (R Core Team 2018). We tested for differences in the proportion of canvasbacks re-encountered (recapture or hunter harvest of geolocator-fitted birds) with geolocators (metal leg bands only) vs. without geolocators using a chi-square test of independence. We tested for differences in retrieval rates (physical retrieval of geolocators) between birds with leg band-mounted geolocators vs. nasal-saddle-mounted geolocators using Fisher's exact test ("fisher.test" in R).

Table 1. Summary of canvasback *Aythya valisineria* captures (Swan Lake and Fallon, Nevada, during early spring 2015–2017), recoveries (generally hunter captures), and geolocator retrievals (geolocators received by mail and data successfully downloaded), indicating age at capture (SY = second-year adults; ASY = after-second-year adults), sex (F = female; M = male), and method of marking.

	2015 (4–8 February)					2016 (27 January–24 March)					2017 (25 February–12 March)					Total
	ASY M	ASY F	SY M	SY F	Total	ASY M	ASY F	SY M	SY F	Total	ASY M	ASY F	SY M	SY F	Total	
Geolocator on leg band	13	5	2	3	23	0	0	0	0	0	41	18	10	3	72	95
Reported	3	2	0	0	5	0	0	0	0	0	4	2	0	0	6	11
Retrieved	3	1	0	0	4	0	0	0	0	0	2	2	0	0	4	8
Geolocator on nasal saddle	14	5	4	3	26	19	2	6	3	30	0	0	0	0	0	56
Reported	3	1	0	0	4	0	2	0	0	2	0	0	0	0	0	6
Retrieved	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Metal leg band only (no geolocator)	15	3	9	2	29	0	0	0	0	0	46	0	4	0	50	79
Reported	2	2	2	0	6	0	0	0	0	0	2	0	2	0	4	27
Total	42	13	15	8	78	19	2	6	3	30	87	18	14	3	122	230

Results

In total, we captured 107 canvasbacks during banding efforts at Swan Lake in 2015 and 2016, and 122 birds at Canvasback Gun Club in 2017 (Table 1). We attached geolocators via nasal saddles to 56 canvasbacks (26 in 2015 and 30 in 2016) and via auxiliary leg bands to 95 canvasbacks (23 in 2015, 0 in 2016, and 72 in 2017). We marked 79 canvasbacks (29 in 2015, 0 in 2016, and 50 in 2017) with only standard metal leg bands as a control group to test for possible effects of geolocators on recovery rates (Table 1). Twelve hunters and one outside researcher contacted us regarding birds marked with geolocators as part of this study and those that found geolocators still attached voluntarily mailed them to us (we sent replacement geolocators as requested because of their trophy status). Unfortunately, four of these birds were missing geolocators at the time of re-encounter (four mounted via nasal saddles and one mounted via leg band) and one geolocator was lost in the mail. Ultimately, we successfully retrieved 8 of a total of 151 geolocators deployed on canvasbacks from 2015 to 2017 (5% retrieval rate; Table 1). Four of the retrieved geolocators were initially deployed on 5 February 2015 and the remaining four geolocators were initially deployed during the period 2–9 March 2017 (Table 1). The eight retrieved geolocators recorded usable data for 375, 612, 605, 317, 342, 247, 243, and 290 d, respectively. Only four of eight geolocators successfully recorded data throughout the full release to recovery period. In three cases, data logging was discontinued because of battery failure several months before recovery. In addition, one geolocator's light sensor failed during its final month of deployment.

Of 49 canvasbacks originally fitted with geolocators in 2015 (26 nasal saddles and 23 leg bands), hunters (and one unaffiliated researcher) reported five canvasbacks originally fitted with leg-mounted geolocators (three after-second-year [ASY] males [M] and two ASY females [F]) and four canvasbacks (three ASY M and one ASY F) originally fitted with nasal-saddle geolocators. We successfully retrieved four of the five recovered leg-mounted geolocators (one was lost in the mail), but all nasal-saddle mounts were missing at the time of capture.

Two of the 30 canvasbacks originally fitted with geolocators in 2016 (all nasal-saddle mounts) were later captured (two ASY F), but neither had a nasal saddle attached at the time of harvest. Of the 72 canvasbacks originally fitted with geolocators in 2017 (all leg-band mounts), four (two ASY F and two ASY M) geolocators have been successfully retrieved thus far. Two additional canvasbacks originally captured in 2017 and fitted with leg-mounted geolocators (both ASY M) were reported by hunters but the geolocators were no longer attached to the plastic band. Because none of the geolocators attached via nasal saddles ($n = 56$) has been retrieved despite several hunter captures of birds originally fitted with nasal saddles, we suspect that nasal-saddle mounts may have had a failure of the metal rods used for attachment.

Of the canvasbacks marked with a metal leg band only (no geolocator), 5 birds of 29 marked in 2015 and 4 birds of 50 marked in 2017 were later captured (15% overall recovery rate; Table 1). Of the canvasbacks fitted with a leg-band geolocator, 5 of 23 birds (including the one that was lost in transit) marked in 2015 and 6 of 72 birds marked in 2017 were later captured (12% recovery rate). Of the canvasbacks originally fitted with a nasal-saddle geolocator, we recovered 4 of 26 birds marked in 2015 and 2 of 30 birds marked in 2016 (11% recovery rate). There is no strong evidence for leg-band geolocators affecting recovery rates (Fisher's exact test, $P = 0.36$) or for nasal-saddle mounts affecting recovery rates (Fisher's exact test, $P = 0.61$; however, note that many nasal-saddle mounts detached from birds). Because of the frequent failure of nasal-saddle mounts, the retrieval rate of geolocators attached via leg band (9 of 95) was significantly greater than the retrieval rate for geolocators attached via nasal saddle (0 of 55; Fisher's exact test; $P = 0.03$).

Using the light-level data from recovered geolocators, we were able to estimate geographic positions for 10 canvasback migrations: 4 in 2015, 4 in 2017, and 2 in 2018 (representing two of the four birds for which 2017 data were also available). No location data were recovered from the 2016 migration. Overall, canvasbacks made an average of 3.3 stopovers (± 0.5 , $n = 10$; sampling uncertainties here and elsewhere are reported

Table 2. Summary of the estimated timing of migratory movements for eight canvasbacks *Aythya valisineria* monitored with leg band-mounted geolocators initially deployed on 5 February 2015 (4) and 2–9 March 2017 (4) in Swan Lake and Fallon, Nevada.

Identification No.	Spring		Breeding		Molt		Fall		Winter	
	No. Stopovers	Mean stopover duration (d)	Arrival at breeding grounds	Departure from breeding grounds	Arrival at molting area	Departure from molting area	No. Stopovers	Mean stopover duration (d)	Arrival at wintering grounds	
806M 2015	2	22.2	28 March 2015	6 July 2015	9 July 2015	28 October 2015	1	11.5	15 November 2015	
809M 2015	4	15.5	18 April 2015	18 June 2015	10 July 2015	14 October 2015	3	5.8	4 November 2015	
815M 2015	4	20.8	15 May 2015	28 June 2015	30 June 2015	21 August 2015	3	12.7	—	
817F 2015	2	22.1	28 March 2015	30 July 2015	8 August 2015	4 October 2015	—	—	—	
439F 2017	2	13.5	13 April 2017	—	—	17 September 2017	4	15.8	30 November 2017	
300M 2017	5	10.3	12 May 2017	18 June 2017	24 June 2017	29 August 2017	2	24.5	31 October 2017	
364F 2017	2	24.5	8 May 2017	—	—	9 September 2017	4	15.5	3 December 2017	
385M 2017	3	13.3	20 April 2017	16 June 2017	12 Aug 2017	26 September 2017	3	6.3	11 October 2017	
300M 2018	7	9.3	3 May 2018	13 June 2018	25 June 2018	12 October 2018	3	6	—	
364F 2018	2	3.2	30 March 2018	—	—	14 October 2018	2	15	19 November 2018	
Mean (all)	3.3	14.8	21 April	27 June	13 July	26 September	2.7	12.3days	12 November	
SE (all)	0.5	2.2	5.9	6.2	7.6	7.1	0.3	2.5	7.1	

as 1 SE from the mean) during the spring migration, each of which lasted an average of 14.3 d (± 2.1 , $n = 10$; Table 2). For the fall migration, canvasbacks made an average of 2.5 stopovers (± 0.4 , $n = 9$), each of which lasted an average of 13 d (± 7.1 , $n = 9$; Table 2). The mean arrival date at breeding grounds was 4 April (± 5.9 d, $n = 10$; Table 2) and mean date for leaving breeding areas was 11 July (± 14 d, $n = 7$). The mean arrival date at molting grounds was 14 July (± 7.6 d, $n = 7$; Table 2) and mean date for leaving molting areas was 28 September (± 11.7 d, $n = 10$). In cases where breeding and molting areas were in proximity (two in 2015 and one in 2018), we treated dates for leaving breeding areas and entering molting areas as missing data because of high levels of uncertainty.

Of the 10 spring migratory routes we were able to estimate, eight (five males and three females; Figures 2 and 3) terminated at breeding grounds centered in southern Canada (Alberta and Saskatchewan) and including parts of northern Montana and North Dakota, United States. Of these eight pathways, all but one passed northeast from our northern Nevada capture site, passing through (and most stopping briefly) near a known spring staging area in northern Utah before reaching their eventual breeding grounds (Figures 2 and 3). The remaining two spring migratory pathways ended at breeding grounds in Alaska (one male and one female), one trending north from the capture site and passing through coastal Oregon and Washington (this individual, No. 815M, appeared to move directly west from the Nevada capture site and stop briefly in California's Central Valley before embarking north to Alaska) and the other taking an inland route through Idaho, Montana, and Alberta before ending in central Alaska (Figures 2 and 3). With most of our sample representing only a single year of data (beginning during spring migration and ending during the overwintering period), we were unable to estimate the timing of the initiation of spring migration for most individuals in our sample. However, we found that one male (No. 300M) left his wintering area on 12 February 2018 and one

female (No. 364F) left her wintering grounds on 19 March 2018; these were both the birds that had 2 y of data recorded (Figure 4).

Most (7 of 10) canvasbacks moved substantial distances from their breeding grounds to distinct molting and staging grounds (molt migration), which we were able to differentiate on the basis of light-level data (Figures 2 and 3). For example, one male (No. 809M; Figure 2b) moved northwest from his breeding site, making one stopover in Alberta (4 d) before continuing as far as northwest Alberta to his molting area (49 d). Two other males (No. 300M and 385M; Figures 3d and 3c) migrated northwest to northern Alberta and northern Northwest Territories and Alaska and stayed for 66 and 45 d, respectively. The average time spent at molting areas in 2015 was 49.5 (± 9) d (Figure 4). In general, the distance traveled to molting areas was greater for males (mean 960 km, SE = 275 km) than for females (mean 190 km, SE = 78 km; $t = 2.69$; $P = 0.03$); however, this result must be treated cautiously because of small sample size.

Three of our 10 canvasback migration pathways ended prematurely because of battery failure before or early during fall migration (No. 815M, 817F, and 300M). Of the seven total fall migration pathways we recovered, four were generally similar to spring migration routes (in reverse), heading south through southern Canada (Alberta or Saskatchewan) and into northern Utah or southern Idaho and then southwest to California. The remaining three canvasbacks took a more coastal route to California's Central Valley, heading south through Washington and Oregon from British Columbia. Geolocator data showed that one male (No. 300; Figure 3e) made three stopovers in northern mainland Canada (7, 7, and 3 d), and may have traveled west as far as Alaska before reaching his final harvest location in northern California. However, the extreme distances moved during the final 3 d of fall migration rendered the migration path highly uncertain (denoted by question marks in Figure 3e). Data for all our recovered geolocators were consistent with major overwintering sites located in California's Central Valley or coastal California

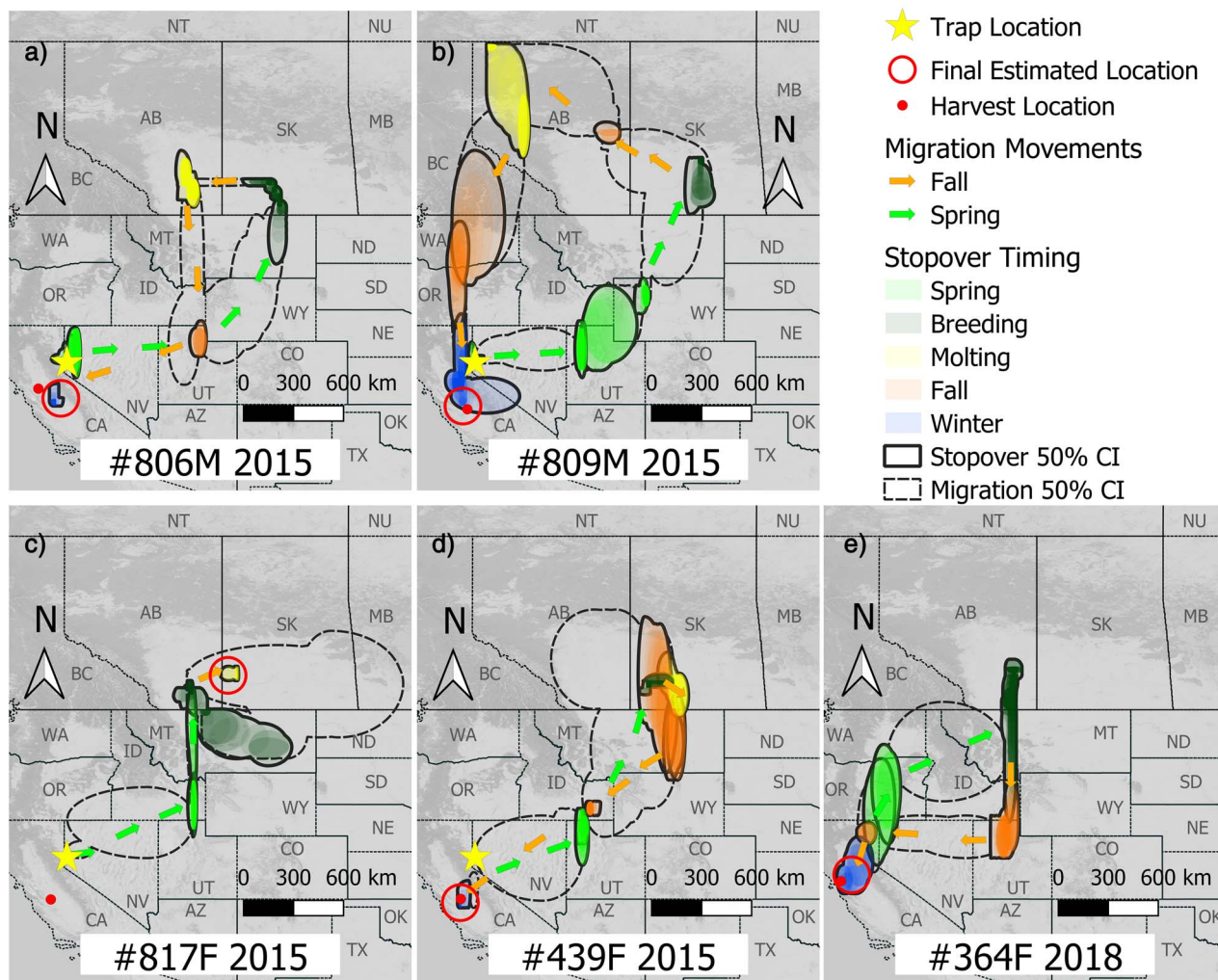


Figure 2. Canvasback *Aythya valisineria* migration paths, staging locations, and migratory end points (breeding, molting, wintering) for 5 (of 10) migrations estimated from light-level geolocator data recovered from birds originally captured in northwestern Nevada in spring (2015–2017). All five of these birds likely overwintered in California’s Central Valley, bred in the Prairie Pothole Region, and exhibited relatively short molt migrations. Estimated locations at each twilight (and associated positional error) are represented as merged, rounded polygons encompassing the interquartile range of the posterior distribution for latitude and longitude. Locations estimated to occur during active migrations are displayed with a dashed outline, whereas locations estimated to occur during a stationary period are displayed with a solid outline. Colors indicate the timing of stopovers (defined by the inset color legend) and the intensity of each color denotes the number of twilights for which a particular location was included within the interquartile range during a particular stationary period (indicating relative plausibility of being the “true” stationary location). Narrow ellipses with strong north-south orientations represent location estimates occurring during spring and fall equinoxes, for which latitudinal uncertainty is especially large. One female (No. 364; panel e) did not exhibit a distinct molt migration.

(e.g., San Francisco Bay). In fact, hunter recovery of birds in California (four Central Valley, two San Francisco Bay area, and two northern coastal bays between Arcata and Crescent City) accounted for all eight total geolocators that were successfully retrieved for this project. Arrival at overwintering grounds tended to occur around approximately mid-November (mean arrival date was 12 November, with SE = 7.1 d; Table 2; Figure 4).

Discussion

To our knowledge this study is the first to assess movements of canvasbacks using tracking technology in

the Pacific Flyway. Specifically, we used data from light-level geolocators to reveal important information about seasonal movements for canvasbacks migrating through northwestern Nevada in early spring, including locations of breeding, molting, staging, and wintering grounds, the timing of arrival and departure from these key habitats, and migratory routes used to connect them. We acknowledge that our study represents only one small part of the Pacific Flyway (e.g., a large proportion of Pacific Flyway canvasbacks are known to migrate through the Klamath Basin instead of northern Nevada), and that our sample size (10 migrations for eight birds) is too small to draw general inferences about canvasback

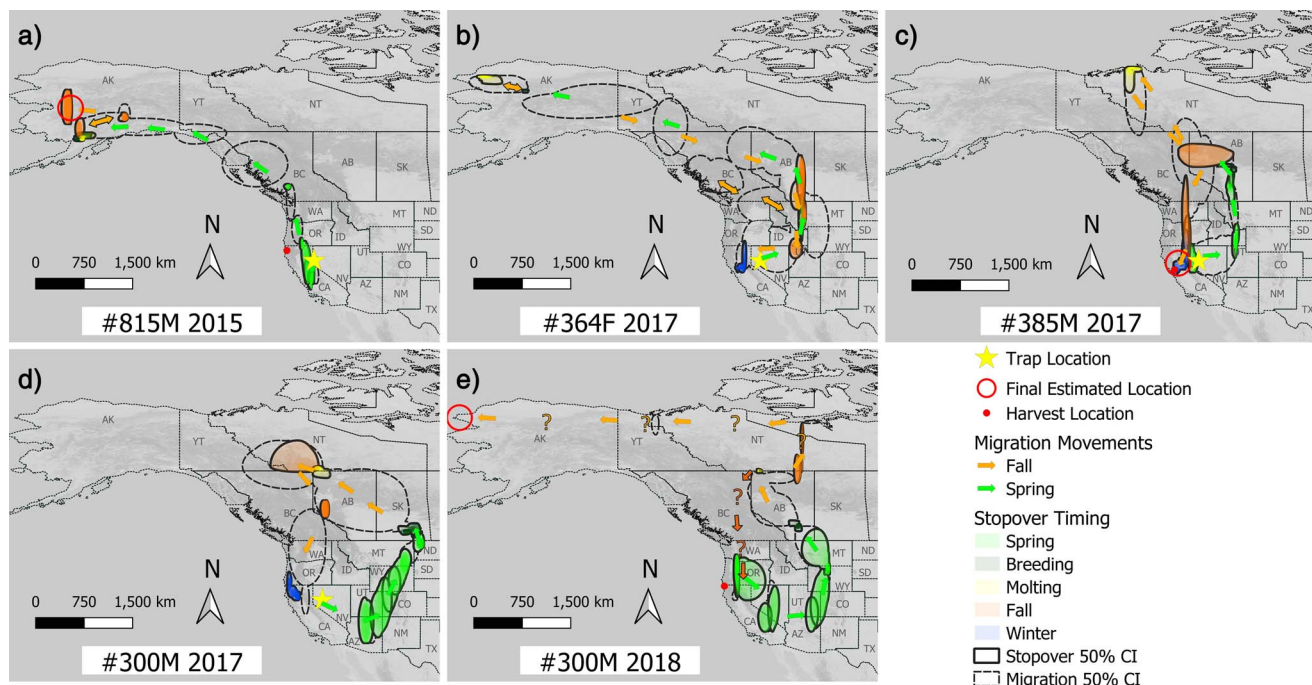


Figure 3. Canvasback *Aythya valisineria* migration paths, staging locations, and migratory end points (breeding, molting, wintering) for 5 (of 10) migrations estimated from light-level geolocator data downloaded from birds originally captured in northwestern Nevada in spring (2015–2017). All five birds likely overwintered in California’s Central Valley, bred in either the Prairie Pothole Region or Alaska, and tended to exhibit relatively long-distance molt migrations that sometimes extended into the Arctic Circle. Estimated locations at each twilight (and associated positional error) are represented as merged, rounded polygons encompassing the interquartile range of the posterior distribution for latitude and longitude. Locations estimated to occur during active migrations are displayed with a dashed outline, whereas locations estimated to occur during a stationary period are displayed with a solid outline. Colors indicate the timing of stopovers (defined by the inset color legend) and the intensity of each color denotes the number of twilights for which a particular location was included within the interquartile range during a particular stationary period (indicating relative plausibility of being the “true” stationary location). Narrow ellipses with strong north-south orientations represent location estimates occurring during spring and fall equinoxes, for which latitudinal uncertainty is especially large. The last 3 d of the fall migration for individual No. 300M (panel e) were particularly uncertain (likely due to very-long-distance daily movements with no stopovers) and we therefore suggest two possible paths for this individual, each interspersed with question marks to denote uncertainty. The more southerly route for No. 300M is more likely, since it was harvested on the northern California coast shortly after the final geolocator recording.

migrations in the Pacific Flyway. In our study, 80% (8 of 10) of canvasback migrations used breeding grounds in southwestern prairie Canada, suggesting that the western Prairie Pothole Region may potentially be more important for supporting some canvasbacks in the Pacific Flyway than previously thought (Bellrose 1980; Johnson and Grier 1988), at least for those canvasbacks migrating through northwestern Nevada. The remaining birds in our study used breeding locations on the Alaska Peninsula and central Alaska that have not previously been identified as important breeding sites for canvasbacks in the Pacific Flyway. Of great interest is the one female (No. 364 [2017] and No. 364 [2018]; Figures 3b and 2e) that apparently settled on nesting grounds in southern Saskatchewan and then in central Alaska in successive years. It is generally understood that female canvasbacks exhibit high fidelity to their nesting grounds (Lindberg et al. 2001). The migration routes estimated for canvasbacks in this study crossed multiple states and two countries, which underscores the need for continued cooperation across political boundaries to manage

habitats throughout the annual cycle. Nonetheless, small sample size limits the inferential strength of this study, and our results, although suggestive, should not be used to make broad generalizations.

Despite similarities in the timing of migratory movements and locations of breeding grounds, stopover locations often differed substantially among the four individuals documented in our study. Canvasbacks for which fall and spring migrations were fully documented ($n = 7$) used nearly the same mean number of stopover sites during the spring and fall migration periods (2.9 and 2.7 sites) and stopover duration (14 and 13 d). Some regions heavily used by several canvasbacks in this study, such as the Great Salt Lake, wintering grounds in California’s Central Valley, and our trapping locations in western Nevada, are already known to be important for canvasbacks and other migrating waterfowl. However, our results also suggest the presence of several additional stopover locations around southeast Idaho and central Washington, which may support canvasback breeding in Canada, and an additional stopover site

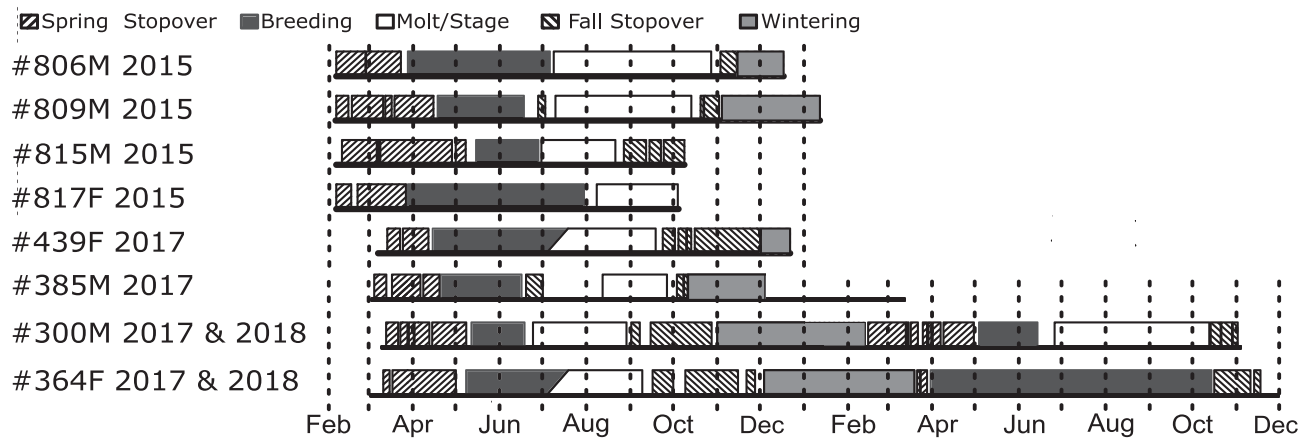


Figure 4. Timing of migratory movements, migration paths, stopovers, and migratory end points (breeding, molting, wintering) for eight canvasbacks *Aythya valisineria* originally captured in northwestern Nevada in spring (2015–2017), inferred from light-level geolocator data. Individual stopovers were merged when they were less than 150 km apart (typical positional accuracy from geolocators). A trapezoidal zone of contact between breeding and molting periods represents periods with an unknown split date (likely both activities occurring in the same general area). Note that No. 439 represents data recorded in 2017 and is therefore not directly comparable with the other birds (representing data recorded in 2015). Also note that the “molting” stopover likely includes both molting and staging in preparation for fall migration.

north of Puget Sound that may be important for canvasback breeding in Alaska. Again, we acknowledge a second exit migration corridor from the Central Valley of California through the Klamath Basin, and thus, our results are only applicable to those canvasbacks that move through western Nevada in the spring. Conservation of stopover sites such as these is important for maintaining migratory connectivity with larger well-established stopover locations (Haig et al. 1998; Webster et al. 2002; McKinnon et al. 2013). Additional stopover locations that may have been used for shorter durations were likely not detected in our analysis because of insufficient spatial resolution; detection of such sites would likely require alternative instruments (e.g., GPS tags). Some of these differences in stopover location, duration, and timing may be explained by age, sex, or individual quality. Because of our small sample sizes we cannot test for these differences, but they are important factors that should be the focus of future geolocator studies. We know that timing of molt migration is affected by sex and reproductive success (Hochbaum 1944) and timing of fall migration is driven by nest or brood success (Burger et al. 2012), but further insights are likely to be gained from geolocator research.

We believe that light-level geolocators, combined with other tracking technologies, have great potential for studying migratory movements in waterfowl. These small, unobtrusive instruments provide advantages in terms of weight and cost effectiveness, and are well suited for addressing broad-scale questions about seasonal movements (McKinnon et al. 2013), such as long-range migration paths, important stopover sites, and the timing and location of migration movements (Niles et al. 2010; Catry et al. 2011; Johnson et al. 2011; Delmore et al. 2012; Solovyeva et al. 2012; Stach et al. 2012; Minton et al. 2013; Salewski et al. 2013; Hobson and Kardynal 2015; Linkhart et al. 2016; Rakhimberdiev et

al. 2016). Of course, there are also substantial disadvantages associated with geolocator technology, including reduced spatiotemporal resolution relative to more standard GPS telemetry methods. In addition, unlike GPS systems, the raw data of geolocators requires extensive postprocessing analyses to estimate geographic locations, adding an additional layer of locational uncertainty (analytical error). Furthermore, it is more difficult to estimate latitude than longitude from light-level geolocator data during equinox times because day length is similar throughout all latitudes during the solar equinox. Finally, low recovery rates associated with geolocators may require the deployment of hundreds of tarsal-mounted units to obtain a large-enough sample size—which may in turn cancel out any cost savings associated with geolocators (many GPS collars can transmit data remotely through satellite networks, with data recovery rates approaching 100%). However, we believe the advantages of obtaining nesting information and likely much reduced behavioral effects are beneficial. Overall, we contend that more widespread deployment of tarsal-mounted geolocators on canvasbacks and other waterfowl species at multiple capture sites within the Pacific Flyway including sites in the Klamath Basin would allow researchers to more accurately characterize habitat use and movements of migratory waterfowl. Such data would enable waterfowl managers in Nevada and other states and countries within the Pacific Flyway to ensure that the geography and timing of management actions match appropriately with the geography and timing of major waterfowl movements. Additionally, this study demonstrates that tarsal-mounted, not nasal-saddle-mounted, geolocators can be a safe and effective means for estimating the seasonal habitat use and timing of movements for diving birds, which have proven difficult to track over long distances using alternative means (e.g., GPS tags) using both external and internal attachment

(Perry 1981; Robert et al. 2006; Latty et al. 2010, 2016). Last, tarsal-mounted geolocators may lessen behavioral differences because of their weight and attachment methods when compared with larger GPS tags (Hupp et al. 2015).

Our geolocators recorded usable data for the majority of the deployment period, but they recorded a shorter period than anticipated, with a high proportion showing some form of premature failure (four of eight; three with battery failure and one with light-sensor failure). This failure rate is consistent with other published geolocator studies (Minton et al. 2010; McKinnon et al. 2013)—in fact, some studies have experienced failure of most or all geolocators (Minton et al. 2011; Bridge et al. 2013). We were unable to retrieve any nasal-saddle geolocators and suspect that nasal saddles either negatively affected survival or, more likely, were lost at high rates, but are unable to determine causes because of lack of data. Our failure to retrieve nasal-saddle geolocators prevented us from comparing the quality of data recorded vs. leg-band mounts. Nonetheless, leg-band geolocators provided light-level readings of sufficient quality to estimate stopover locations, and we detected no difference in recovery rate for canvasbacks marked with standard metal bands vs. those with leg-band-mounted geolocators, weakly suggesting no adverse effect of leg-mounted geolocators on survival rates (consistent with other studies; Bell et al. 2017). Finally, when deployed on female birds, leg band-mounted geolocators have the additional advantage of estimating the timing and duration of reproductive bouts (shading of light detectors because of incubation activities can be easily detected; Burger et al. 2012; Gosbell et al. 2012). We found evidence from our geolocator data that the two female canvasbacks each nested successfully once during 2015 and further analysis of breeding may be possible using methods similar to those of Cook (2019). Therefore, we suggest that leg bands should be the standard method for geolocator attachment for waterfowl. We do not suggest continued use of nasal saddles for mounting light-level geolocators on canvasbacks and similar waterfowl species given the sufficient light levels recorded from leg mounts.

Finally, by linking the results from our study (and similar geolocator studies) with commonly collected waterfowl survey data (collected visually from aircraft), or even citizen scientist data such as eBird (Soulliere et al. 2013), researchers should be able to refine estimates of waterfowl population abundance estimates and estimates of population-level movements around the state and region (Laughlin et al. 2013; Fleming et al. 2019). For example, our study indicated that canvasbacks remained at Nevada stopover sites no longer than 1.5 d (our minimum threshold for designating a “stationary period”). Therefore, the set of canvasback individuals observed via aerial census counts in Nevada would likely experience a nearly complete turnover between surveys conducted 2 or 3 d apart at the same location. Critically, the combination of repeated aerial counts and site-level turnover rates (determined from geolocator studies) could be used to generate estimates of the total number

of waterfowl migrating through particular states or using specific wetlands as stopovers, which would help inform habitat management decisions.

Supplemental Material

Please note: The *Journal of Fish and Wildlife Management* is not responsible for the content or functionality of any supplemental material. Queries should be directed to the corresponding author for the article.

Data S1. Summary capture data (e.g., sex, date of original geolocator deployment, capture date) for eight canvasbacks *Aythya valisineria* from which light-level geolocator data were successfully recovered for this study. All canvasbacks were originally captured in northwestern Nevada in spring (2015–2017) and recovered geolocator data (see Data S2) were used to infer migration paths, staging locations, and migratory end points (breeding, molting, wintering) for these birds. Capture summaries are provided as a comma-separated text file.

Available: <https://doi.org/10.3996/JFWM-20-032.S1> (2 KB CSV)

Data S2. Raw (preprocessed) light-level data for eight canvasbacks *Aythya valisineria* originally captured in northwestern Nevada in spring (2015–2017), downloaded from light-level geolocators attached with ancillary leg bands. These recovered geolocator data were used to infer migration paths, staging locations, and migratory end points (breeding, molting, wintering) for each individual canvasback using the R code provided (see Data S3). Raw light-level data are stored in two separate files: one containing the raw light-level data from throughout the entire deployment period for each bird and the other documenting the inferred timing of all twilight periods (dawn and dusk) during the entire deployment period for each bird. To run the code (see Data S3) the data for each bird should be stored in separate subfolders (each labeled with the unique metal leg-band number; column labeled “band” in the data files). Accompanying these data files are two metadata text files describing each column of each of the raw geolocator data files.

Available: <https://doi.org/10.3996/JFWM-20-032.S2> (63.58 MB CSV); <https://doi.org/10.3996/JFWM-20-032.S3> (424 KB CSV); <https://doi.org/10.3996/JFWM-20-032.S4> (1 KB TXT); <https://doi.org/10.3996/JFWM-20-032.S5> (1 KB TXT)

Data S3. R code for inferring waterfowl movement trajectories on the basis of light-level geolocator data (see Data S2 for the raw light-level data used for this study). In this study, we estimated canvasback *Aythya valisineria* migration paths, staging locations, and migratory end points (breeding, molting, wintering) on the basis of light-level geolocator data recovered from birds originally captured in northwestern Nevada in spring (2015–2017). The R code for performing these analyses is available as a single text file, which contains the code



needed to run the particle filter analyses and infer migratory trajectories followed by the code needed to produce the figures presented herein.

Available: <https://doi.org/10.3996/JFWM-20-032.S6> (84 KB R)

Reference S1. Fleming KK, Brasher MG, Humburg DD, Petrie MJ, Soulliere GJ. 2019. Derivation of regional, non-breeding duck population abundance objectives to inform conservation planning. Derivation of regional, non-breeding duck population abundance objectives to inform conservation planning in North America—2019 revision. North American Waterfowl Management Plan Science Support Team Technical Report 2019-01.

Available: <https://doi.org/10.3996/JFWM-20-032.S7> (2.71 MB PDF) and <https://www.fws.gov/migratorybirds/pdf/management/NAWMP/DerivationofNon-breedingDuckPopulationAbundanceObjectives.pdf>

Reference S2. Olson SM. Compiler. 2019. Pacific flyway data book, 2019. U.S. Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Vancouver, Washington.

Available: <https://doi.org/10.3996/JFWM-20-032.S8> (2.74 MB PDF) and <https://www.fws.gov/migratorybirds/pdf/surveys-and-data/DataBooks/PacificFlywayDatabook.pdf>

Reference S3. Tautin J. 2005. One hundred years of bird banding in North America.

Available: <https://doi.org/10.3996/JFWM-20-032.S9> (105 KB PDF) and https://www.fs.fed.us/psw/publications/documents/psw_gtr191/psw_gtr191_0815-0816_tatuin.pdf

Reference S4. [USFWS] U.S. Fish and Wildlife Service. 2019. Waterfowl population status, 2019. U.S. Department of the Interior, Washington, D.C.

Available: <https://doi.org/10.3996/JFWM-20-032.S10> (3.94 MB PDF) and <https://www.fws.gov/migratorybirds/pdf/surveys-and-data/Population-status/Waterfowl/WaterfowlPopulationStatusReport19.pdf>

Reference S5. USDA Forest Service SDTDC. 2012. Demonstration of satellite/GPS telemetry for monitoring fine-scale movements of lesser prairie-chickens. USDA, Forest Service, National Technology and Development Program Inventory and Monitoring, San Dimas Technology & Development Center.

Available: <https://doi.org/10.3996/JFWM-20-032.S11> (7.16 MB PDF) and https://www.fs.fed.us/t-d/programs/im/satellite_gps_telemetry/_assets/12191813hi.pdf

Reference S6. Wildlife Action Plan Team. 2012. Nevada wildlife action plan. Reno: Nevada Department of Wildlife.

Available: <https://doi.org/10.3996/JFWM-20-032.S12> (3.45 MB PDF) and http://www.ndow.org/uploadedFiles/ndoworg/Content/Nevada_Wildlife/Conservation/2013-NV-WAP-Marshes-Lakes-Playas-Dunes.pdf

Archived Material

All raw data and R code needed to reproduce the results presented herein can be downloaded from our GitHub repository: https://github.com/natehe20/CANV_movements

Acknowledgments

Nevada Waterfowl Association, Nevada Department of Wildlife, and U.S. Fish and Wildlife Service—Stillwater National Wildlife Refuge provided funding and housing. U.S. Fish and Wildlife Service (Reno Field Office) provided a field vehicle. Delta Waterfowl, Ducks Unlimited, Four Flyway Outfitters, and Sportsman's Warehouse also provided funding. We thank Jerry Hupp for initial discussions on how to analyze geolocator data and Bruce Peterjohn of the U.S. Geological Survey Bird Banding Laboratory for discussions on geolocator attachment methods. We also thank Frank Baldwin for providing extra geolocators. John Carrington and Dave Stanley coordinated with members of the Canvasback Gun Club to allow us to work on their property. Mike Anderson and Frank Baldwin provided beneficial comments on an earlier draft. Many people came out to help trap canvasbacks at both sites and we especially thank the following for multiple days of running traps: John Carrington, Bill Henry, Emily Nicolai, Grace Nicolai, Alex Portillo, Ed Warman, and Lynn Warman. We also thank the duck hunters who took the time to report and mail geolocators to us: Rich Beus, Dan Sisto, Louis LaMoure, Kevin Hayes, Byron Byers, Mike Stubbs, Craig Fleckenstein, DJ Winkelman, Ricardo Calderon, and Lee Sheffler. Two anonymous reviewers and the Associate Editor provided comments that improved an earlier version of this manuscript.

Any use of trade, product, website, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

References

- Anderson MG, Lindberg MS, Emery RB. 2001. Probability of survival and breeding for juvenile female canvasbacks. *Journal of Wildlife Management* 65:385–397.
- Bairlein F, Norris DR, Nagel R, Bulte M, Voigt CC, Fox JW, Hussell DJT, Schmaljohann H. 2012. Cross-hemisphere migration of a 25 g songbird. *Biology Letters* 8:505–507.
- Bates B, Etheridge B, Elkins N, Fox J, Summers R. 2012. Pre-migratory change in mass and the migration track of a common sandpiper *Actitis hypoleucos* from Scotland. *Wader Study Group Bulletin* 119:149–154.
- Bell SC, Harouchi ME, Hewson CM, Burgess MD. 2017. No short- or long-term effects of geolocator attachment detected in pied flycatchers *Ficedula hypoleuca*. *Ibis* 159:734–743.



- Bellrose FC. 1980. Ducks, geese & swans of North America. 3rd edition. Harrisonburg, Pennsylvania: Stackpole Books.
- Bergman RD. 1973. Use of Southern boreal lakes by postbreeding canvasbacks and redheads. *Journal of Wildlife Management* 37:160–170.
- Bird Banding Laboratory. 2020. The North American bird banding program: bird banding laboratory. Available: <https://www.pwrc.usgs.gov/bbl/homepage/howmany.cfm> (October 2020)
- Bridge ES, Kelly JF, Contina A, Gabrielson RM, MacCurdy RB, Winkler DW. 2013. Advances in tracking small migratory birds: a technical review of light-level geolocation. *Journal of Field Ornithology* 84:121–137.
- Bridge ES, Thorup K, Bowlin MS, Chilson PB, Diehl RH, Fléron RW, Hartl P, Kays R, Kelly JF, Robinson WD, Wikelski M. 2011. Technology on the move: recent and forthcoming innovations for tracking migratory birds. *BioScience* 61:689–698.
- Burger J, Niles LJ, Porter RR, Dey AD. 2012. Using geolocator data to reveal incubation periods and breeding biology in red knots *Calidris canutus rufa*. *Wader Study Group Bulletin* 119:26–36.
- Catry I, Dias MP, Catry T, Afanasyev V, Fox J, Franco AMA, Sutherland WJ. 2011. Individual variation in migratory movements and winter behaviour of Iberian lesser kestrels *Falco naumanni* revealed by geolocators. *Ibis* 153:154–164.
- Conklin JR, Battley PF, Potter MA. 2013. Absolute consistency: individual versus population variation in annual-cycle schedules of a long-distance migrant bird. *PLOS ONE* 8:e54535.
- Cook NA. 2018. Geolocators as tools for inferring waterfowl movements and breeding phenology. Master's thesis. University of Nevada, Reno.
- Cresswell B, Edwards D. 2013. Geolocators reveal wintering areas of European nightjar (*Caprimulgus europaeus*). *Bird Study* 60:77–86.
- Crissey WF. 1955. The use of banding data in determining waterfowl migration and distribution. *Journal of Wildlife Management* 19:75–84.
- Delmore KE, Fox JW, Irwin DE. 2012. Dramatic intraspecific differences in migratory routes, stopover sites and wintering areas, revealed using light-level geolocators. *Proceedings of the Royal Society B: Biological Sciences* 279:4582–4589.
- Eichhorn G, Afanasyev V, Drent RH, van der Jeugd HP. 2006. Spring stopover routines in Russian barnacle geese *Branta leucopsis* tracked by resightings and geolocation. *Ardea* 94:667–678.
- Ekstrom P. 2007. Error measures for template-fit geolocation based on light. *Deep Sea Research Part II: Topical Studies in Oceanography* 54:392–403.
- Fleming KK, Brasher MG, Humburg DD, Petrie MJ, Soulliere GJ. 2019. Derivation of regional, non-breeding duck population abundance objectives to inform conservation planning. Derivation of regional, non-breeding duck population abundance objectives to inform conservation planning in North America—2019 revision. North American Waterfowl Management Plan Science Support Team Technical Report 2019-01. (see *Supplemental Material*, Reference S1).
- Fudickar AM, Wikelski M, Partecke J. 2012. Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. *Methods in Ecology and Evolution* 3:47–52.
- Giunchi D, Caccamo C, Mori A, Fox JW, Rodríguez-Godoy F, Baldaccini NE, Pollonara E. 2015. Pattern of non-breeding movements by stone-curlews *Burhinus oedicnemus* breeding in Northern Italy. *Journal of Ornithology* 156:991–998.
- Gosbell K, Minton C, Fox J. 2012. Geolocators reveal incubation and re-nesting characteristics of ruddy turnstones *Arenaria interpres* and eastern curlews *Numenius madagascariensis*. *Wader Study Group Bulletin* 119:160–171.
- Greenwood RJ. 1977. Evaluation of a nasal marker for ducks. *Journal of Wildlife Management* 41:582–585.
- Guilford T, Wynn R, McMinn M, Rodríguez A, Fayet A, Maurice L, Jones A, Meier R. 2012. Geolocators reveal migration and pre-breeding behaviour of the critically endangered Balearic shearwater *Puffinus mauretanicus*. *PLOS ONE* 7:e33753.
- Haig SM, Mehlman DW, Oring LW. 1998. Avian movements and wetland connectivity in landscape conservation. *Conservation Biology* 12:749–758.
- Hallworth MT, Sillett TS, Van Wilgenburg SL, Hobson KA, Marra PP. 2015. Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators. *Ecological Applications* 25:336–347.
- Hanssen SA, Gabrielsen GW, Bustnes JO, Bråthen VS, Skottene E, Fenstad AA, Strøm H, Bakken V, Phillips RA, Moe B. 2016. Migration strategies of common eiders from Svalbard: implications for bilateral conservation management. *Polar Biology* 39:2179–2188.
- Hill RD, Braun MJ. 2001. Geolocation by light level. Pages 315–330 in Sibert JR, Nielsen JL, editors. *Electronic tagging and tracking in marine fisheries*. New York: Springer.
- Hobson KA, Kardynal KJ. 2015. Western veeries use an eastern shortest-distance pathway: new insights to migration routes and phenology using light-level geolocators. *Auk* 132:540–550.
- Hochbaum HA. 1944. The canvasback on a prairie marsh. Washington, D.C: American Wildlife Institute. Available: <http://hdl.handle.net/2027/wu.89033412768> (October 2020)
- Hupp JW, Kharitonov S, Yamaguchi NM, Ozaki K, Flint PL, Pearce JM, Tokita K, Shimada T, Higuchi H. 2015. Evidence that dorsally mounted satellite transmitters affect migration chronology of Northern Pintails. *Journal of Ornithology* 156:977–989.
- Hupp JW, Ward DH, Soto DX, Hobson KA. 2018. Spring temperature, migration chronology, and nutrient allocation to eggs in three species of arctic-nesting

- geese: implications for resilience to climate warming. *Global Change Biology* 24:5056–5071.
- Johnson DH, Grier JW. 1988. Determinants of breeding distributions of ducks. *Wildlife Monographs* 100:3–37.
- Johnson OW, Fielding L, Fox JW, Gold RS, Goodwill RH, Johnson PM. 2011. Tracking the migrations of Pacific golden-plovers (*Pluvialis fulva*) between Hawaii and Alaska: new insight on flight performance, breeding ground destinations, and nesting from birds carrying light level geolocators. *Wader Study Group Bulletin* 118:26–31.
- Latty CJ, Hollmén TE, Petersen MR, Powell AN, Andrews RD. 2010. Abdominally implanted transmitters with percutaneous antennas affect the dive performance of common eiders. *Condor* 112:314–322.
- Latty CJ, Hollmén TE, Petersen MR, Powell AN, Andrews RD. 2016. Biochemical and clinical responses of common eiders to implanted satellite transmitters. *Condor* 118:489–501.
- Laughlin AJ, Taylor CM, Bradley DW, Leclair D, Clark RC, Dawson RD, Dunn PO, Horn A, Leonard M, Sheldon DR, Shutler D, Whittingham LA, Winkler DW, Norris DR. 2013. Integrating information from geolocators, weather radar, and citizen science to uncover a key stopover area of an aerial insectivore. *Auk* 130:230–239.
- Lemke HW, Tarka M, Klaassen RHG, Åkesson M, Bensch S, Hasselquist D, Hansson B. 2013. Annual cycle and migration strategies of a trans-Saharan migratory songbird: a geocator study in the great reed warbler. *PLoS ONE* 8:e79209.
- Lindberg MS, Kendall WL, Hines JE, Anderson MG. 2001. Combining band recovery data and Pollock's robust design to model temporary and permanent emigration. *Biometrics* 57:273–281.
- Linkhart BD, Fox JW, Yanco SW. 2016. Migration timing and routes, and wintering areas of flammulated owls. *Journal of Field Ornithology* 87:42–54.
- Lisovski S, Hewson CM, Klaassen RHG, Korner-Nievergelt F, Kristensen MW, Hahn S. 2012. Geolocation by light: accuracy and precision affected by environmental factors. *Methods in Ecology and Evolution* 3:603–612.
- Lokemoen JT, Sharp DE. 1985. Assessment of nasal marker materials and designs used on dabbling ducks. *Wildlife Society Bulletin* 13:53–56.
- López-López P. 2016. Individual-based tracking systems in ornithology: welcome to the era of big data. *Ardeola* 63:103–136.
- Marra PP, Hunter D, Perrault AM. 2011. Migratory connectivity and the conservation of migratory animals. *Environmental Law* 317–354.
- McKinnon EA, Fraser KC, Stutchbury BJM. 2013. New discoveries in landbird migration using geolocators, and a flight plan for the future. *Auk* 130:211–222.
- Migrate Technology. 2015. Products. Migrate Technology Ltd. Available: <http://www.migratetech.co.uk/IntigeoSummary.pdf> (October 2020)
- Minton C, Gosbell K, Johns P, Christie M, Fox JW, Afanasyev V. 2010. Initial results from light level geocator trials on ruddy turnstone *Arenaria interpres* reveal unexpected migration route. *Wader Study Group Bulletin* 117:9–14.
- Minton C, Gosbell K, Johns P, Christie M, Klaassen M, Hassell C, Boyle A, Jessop R, Fox J. 2013. New insights from geolocators deployed on waders in Australia. *Wader Study Group Bulletin* 120:37–46.
- Minton C, Gosbell K, Johns P, Christie M, Klaassen M, Hassell C, Jessop R, Fox J. 2011. Geocator studies on ruddy turnstones *Arenaria interpres* and greater sandplovers *Charadrius leschenaultii* in the East Asian–Australasia flyway reveal widely different migration strategies. *Wader Study Group Bulletin* 118:87–96.
- Mostello CS, Nisbet IC, Oswald SA, Fox JW. 2014. Non-breeding season movements of six North American roseate terns *Sterna dougallii* tracked with geolocators. *Seabird* 27:1–21.
- Naef-Daenzer B, Widmer F, Nuber M. 2001. A test for effects of radio-tagged on survival and movements of small birds. *Avian Science* 1:15–23.
- Niles LJ, Burger J, Porter RR, Dey AD, Minton CD, González PM, Baker AJ, Fox JW, Gordon C. 2010. First results using light level geolocators to track red knots in the Western Hemisphere show rapid and long intercontinental flights and new details of migration pathways. *Wader Study Group Bulletin* 117:123–130.
- Olson SM. Compiler. 2019. Pacific flyway data book, 2019. U.S. Department of Interior, Fish and Wildlife Service, Division of Migratory Bird Management, Vancouver, Washington. (see *Supplemental Material*, Reference S2).
- Perry MC. 1981. Abnormal behavior of canvasbacks equipped with radio transmitters. *Journal of Wildlife Management* 45:786–789.
- Phillips RA, Silk JRD, Croxall JP, Afanasyev V, Briggs DR. 2004. Accuracy of geolocation estimates for flying seabirds. *Marine Ecology Progress Series* 266:265–272.
- Porter RR, Smith P. 2013. Techniques to improve the accuracy of location estimation using light level geolocation to track shorebirds. *Wader Study Group Bulletin* 120:148.
- R Core Team. 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available: <https://www.R-project.org/> (October 2020)
- Rakhimberdiev E. 2016. Ornithology by light levels today: dealing with a developing teenager. *Wader Study* 123:1–3.
- Rakhimberdiev E, Saveliev A, Piersma T, Karagicheva J. 2017. FLIGHTR: an R package for reconstructing animal paths from solar geolocation loggers. *Methods in Ecology and Evolution* 8:1482–1487.
- Rakhimberdiev E, Senner NR, Verhoeven MA, Winkler DW, Bouten W, Piersma T. 2016. Comparing inferences of solar geolocation data against high-precision GPS

- data: annual movements of a double-tagged black-tailed godwit. *Journal of Avian Biology* 47:589–596.
- Rakhimberdiev E, Winkler DW, Bridge E, Seavy NE, Sheldon D, Piersma T, Saveliev A. 2015. A hidden Markov model for reconstructing animal paths from solar geolocation loggers using templates for light intensity. *Movement Ecology* 3:25.
- Renfrew RB, Kim D, Perlut N, Smith J, Fox J, Marra PP. 2013. Phenological matching across hemispheres in a long-distance migratory bird. *Diversity and Distributions* 19:1008–1019.
- Robert M, Drolet B, Savard JPL. 2006. Effects of backpack radio-transmitters on female Barrow's goldeneyes. *Waterbirds* 29:115–120.
- Salewski V, Flade M, Poluda A, Kiljan G, Liechti F, Lisovski S, Hahn S. 2013. An unknown migration route of the 'globally threatened' aquatic warbler revealed by geolocators. *Journal of Ornithology* 154:549–552.
- Serie JR, Trauger DL, Austin JE. 1992. Influence of age and selected environmental factors on reproductive performance of canvasbacks. *Journal of Wildlife Management* 56:546–556.
- Solovyeva D, Afanasiev V, Fox J, Shokhrin V, Fox A. 2012. Use of geolocators reveals previously unknown Chinese and Korean scaly-sided merganser wintering sites. *Endangered Species Research* 17:217–225.
- Soulliere GJ, Loges BW, Dunton EM, Luukkonen DR, Eichholz MW, Koch ME. 2013. Monitoring waterfowl in the Midwest during the non-breeding period: challenges, priorities, and recommendations. *Journal of Fish and Wildlife Management* 4:395–405.
- Stach R, Jakobsson S, Kullberg C, Fransson T. 2012. Geolocators reveal three consecutive wintering areas in the thrush nightingale. *Animal Migration* 1:1–7.
- Tautin J. 2005. One hundred years of bird banding in North America. (see *Supplemental Material*, Reference S3).
- Thompson JE, Drobney RD. 1995. Intensity and chronology of post-reproductive molts in male canvasbacks. *Wilson Bulletin* 107:338–358.
- [USFWS] U.S. Fish and Wildlife Service. 2019. Waterfowl population status, 2019. U.S. Department of the Interior, Washington, D.C. (see *Supplemental Material*, Reference S4).
- [USDA] U.S. Department of Agriculture Forest Service [SDTDC] San Dimas Technology and Development Center. 2012. Demonstration of satellite/GPS telemetry for monitoring fine-scale movements of lesser prairie-chickens. USDA, Forest Service, National Technology and Development Program Inventory and Monitoring, San Dimas Technology & Development Center. (see *Supplemental Material*, Reference S5).
- Webster MS, Marra PP, Haig SM, Bensch S, Holmes RT. 2002. Links between worlds: unraveling migratory connectivity. *Trends in Ecology & Evolution* 17:76–83.
- Wildlife Action Plan Team. 2012. Nevada wildlife action plan. Reno: Nevada Department of Wildlife. (see *Supplemental Material*, Reference S6).
- Wotherspoon S, Sumner M, Lisovski S. 2016. TwGeos: basic data processing for light based geolocation archival tags. Available: <https://github.com/slivoski/TwGeos> (October 2020)