

GPS-tracking reveals non-breeding locations and apparent molt migration of a Black-headed Grosbeak

Rodney B. Siegel,^{1,3} Ron Taylor,¹ James F. Saracco,¹ Lauren Helton,¹ and Sarah Stock²

¹The Institute for Bird Populations, P. O. Box 1346, Point Reyes Station, California 94956, USA

²Yosemite National Park, 5083 Foresta Road, El Portal, California 95318, USA

Received 8 November 2015; accepted 13 January 2016

ABSTRACT. Black-headed Grosbeaks (*Pheucticus melanocephalus*) have been observed to undergo prebasic molt during fall in the North American Monsoon region of the southwestern United States and northwestern Mexico, but it is unknown whether molt migration is pervasive across populations of the species. During the 2014 breeding season, we GPS-tagged (where GPS is global positioning system) nine adult Black-headed Grosbeaks in Yosemite National Park with archival GPS tags to determine specific locations where grosbeaks breeding in Yosemite spent portions of the non-breeding season, and to assess whether those locations were consistent with molt migration. On 2 June 2015, one of these birds, a male GPS-tagged on 19 June 2014, was recaptured with its GPS unit still attached. Data downloaded from the unit revealed that, by 20 August 2014, the bird had moved 1300 km from Yosemite National Park to Sonora, Mexico, where it remained until at least 15 October 2014. By 24 November 2014, the grosbeak had moved >1300 m from Sonora to the Michoacán-Jalisco border region, where it remained until the last GPS-determined location was obtained on 24 March 2015. The seasonal timing of these movements and the length of stay in Sonora are consistent with the expected behavior of a molt-migrating bird. Remote-sensed enhanced vegetation index (EVI) data indicated that the grosbeak arrived in the monsoon region near the area's annual peak in EVI, and then, as the index was declining sharply, departed for the Michoacán-Jalisco region, where the index also declined during the same period, but substantially less so than in Sonora. Climate change in the coming decades is expected to delay the annual onset of the monsoon while also accelerating the initiation of arid, summer-like conditions throughout much of western North America, possibly yielding a temporal mismatch between fall migration and the monsoon-driven conditions that may be critical for molt-migrating birds.

RESUMEN. El rastreo por GPS se revela las ubicaciones no utilizados para cría y una aparente migración de muda de un Picogordo Cabecinegro (*Pheucticus melanocephalus*)

Se han observado Picogordo Cabecinegros (*Pheucticus melanocephalus*) a someterse en muda inicial durante el otoño en la región monzónica de Norteamérica en el suroeste de los Estados Unidos y el noroeste de México, pero no se sabe si la migración de muda es un fenómeno generalizado en todas las poblaciones de la especie. Durante la temporada de cría en el 2014, rastreamos por GPS nueve adultos Picogordo Cabecinegros en el Parque Nacional de Yosemite con etiquetas de GPS de archivo para determinar lugares específicos donde los picogordos, que se reproducen en Yosemite, pasaron porciones de la estación no reproductiva, y para evaluar si esos lugares fueron consistentes con la migración de muda. El 2 de junio de 2015, una de estas aves, un macho etiquetado por GPS el 19 de junio 2014, fue recapturado con su unidad de GPS todavía unido. Los datos descargados de la unidad revelaron que, por la fecha 20 de agosto de 2014, el pájaro se había movido 1300 km del parque nacional de Yosemite de Sonora, México, donde se permaneció hasta al menos del 15 de octubre de 2014. Por la fecha 24 de noviembre de 2014, el mismo picogordo se había movido >1300 m de Sonora a la región fronteriza Michoacán-Jalisco, donde se permaneció hasta que se obtuvo el último lugar determinado por GPS en el 24 de marzo de 2015. El calendario estacional de estos movimientos y la duración de la estancia en Sonora son consistentes con el comportamiento esperado de un pájaro en migración de muda. Los datos del índice de vegetación mejorado (EVI), registrados por teledetección, indicaron que el picogordo llegó a la región monzónica cerca del pico anual de EVI, y luego, ya que el índice estaba disminuyendo drásticamente, partió para la región de Michoacán-Jalisco, donde el índice EVI también se redujo durante el mismo período, pero sustancialmente menos que en Sonora. Se espera que el cambio climático en las próximas décadas va a retrasar la aparición anual del monzón y al mismo tiempo va a acelerar la iniciación de condiciones áridas, lo cual es común en verano, a través del oeste de Norteamérica, posiblemente produciendo un desfase temporal entre la migración de otoño y las condiciones impulsadas por el monzón que puede ser crítica para las aves en la migración de muda.

Key words: Migration connectivity, North American Monsoon, *Pheucticus melanocephalus*

Many migratory songbird species are philopatric on both breeding and wintering grounds, and understanding migratory connec-

tivity of particular populations across the annual cycle has become a major frontier in ornithology (Webster and Marra 2005, Marra et al. 2015). Advances in light-level geolocation (Bridge et al. 2013), as well as progress working with

³Corresponding author. Email: rsiegel@birdpop.org

high-resolution genetic markers (Ruegg et al. 2014) and isotope analysis (Hobson 2011, Rundel et al. 2013), are yielding rapid improvements in the capacity to identify individual populations, link breeding and wintering sites used by those populations, and even infer their particular migratory pathways. Recent progress in miniaturizing archival global positioning system (GPS) units provides the opportunity to track individual birds across their annual cycle with unprecedented precision (Hallworth and Marra 2015). Such precise tracking can yield a more nuanced understanding of the annual migratory cycle of birds, which may be more complex than simply migrating between a breeding location and a wintering location (Rohwer et al. 2005, Pyle et al. 2009, Ruiz-Gutierrez et al., 2016).

One increasingly appreciated source of such complexity in songbird migratory patterns is molt migration, where birds stop at intermediate locations after leaving their breeding grounds to molt some or all of their feathers before continuing to wintering areas (Rohwer et al. 2005, Pyle et al. 2009). This strategy differs from the more typical patterns observed in Neotropical migrants, where species either undergo a complete prebasic molt in late summer on or near their breeding grounds, or complete this molt in wintering areas (Pyle 1997).

Among Neotropical migrants that breed in western North America, an emerging pattern is that many species suspend their southbound migration to molt in the North American Monsoon (NAM) region of the southwestern United States and northwestern Mexico (Leu and Thompson 2002, Rohwer et al. 2005, Pyle et al. 2009). The fall molt is likely a vulnerable time for birds because it is energetically taxing (Murphy and King 1991, Voelker and Rohwer 1998) and may also impair flight ability (Swaddle and Witter 1997). The NAM region, characterized by a flush of vegetation growth that begins in late summer in response to increased rainfall associated with the monsoon season (Adams and Comrie 1997, Comrie and Glenn 1998), may provide ephemeral but abundant insects, seeds, and protective cover needed by molting passerines (Rohwer et al. 2005, 2009, Chambers et al. 2011).

Black-headed Grosbeaks (*Pheucticus melanocephalus*) have been documented to undergo prebasic molt during the fall in Arizona and northwestern Mexico (Pyle et al. 2009,

Rohwer et al. 2009). However, the propensity for molt migration may vary across populations of a species (Contina et al. 2013). Black-headed Grosbeaks are one of several species we are studying as part of a long-term demographic monitoring program in Yosemite National Park, California. Determining if Black-headed Grosbeaks that breed in Yosemite are molt migrants, and identifying specific locations where they molt and spend the remainder of the non-breeding period, could allow modeling of their demographic rates as a function of annual weather variation at multiple sites used throughout their annual life cycle. We used archival GPS tags to study movements across the annual cycle of Black-headed Grosbeaks breeding in Yosemite. Our objectives were to determine specific locations where the birds spent portions of the non-breeding season, and to determine if those locations were consistent with molt migration.

METHODS

During June and July 2014, we captured Black-headed Grosbeaks at a Monitoring Avian Productivity and Survivorship (MAPS; DeSante et al. 2015) banding station at Hodgdon Meadow in Yosemite National Park, California (Fig. 1). Hodgdon Meadow is a wet montane meadow with extensive willow (*Salix* sp.) and dogwood (*Cornus nuttallii*) thickets, surrounded by Sierran Mixed Conifer forest (Mayer and Laudenslayer 1988), ~1400 m above sea level.

We captured and GPS-tagged nine adult (six males and three females) Black-headed Grosbeaks. Six birds were captured in mid-June using playback and mist nets, and three were captured passively in mist nets throughout the remainder of the breeding season. Grosbeaks were fitted with archival GPS tags (Pinpoint 8, Lotex Wireless, Inc., Newmarket, ON, Canada) secured with leg harnesses made of Teflon ribbon and crimp beads (Rappole and Tipton 1991), and then released. Birds also received numbered aluminum leg bands and a plastic, red color band to facilitate future identification of GPS-tagged individuals. GPS tags, together with harnesses and leg bands, weighed slightly under 2 g, or about 4% of body mass. GPS tags were programmed to record a location every 2–6 weeks, depending on the stage in the annual cycle, from late August 2014 through March 2015 (Table 1). During the 2015 breeding season, we again used

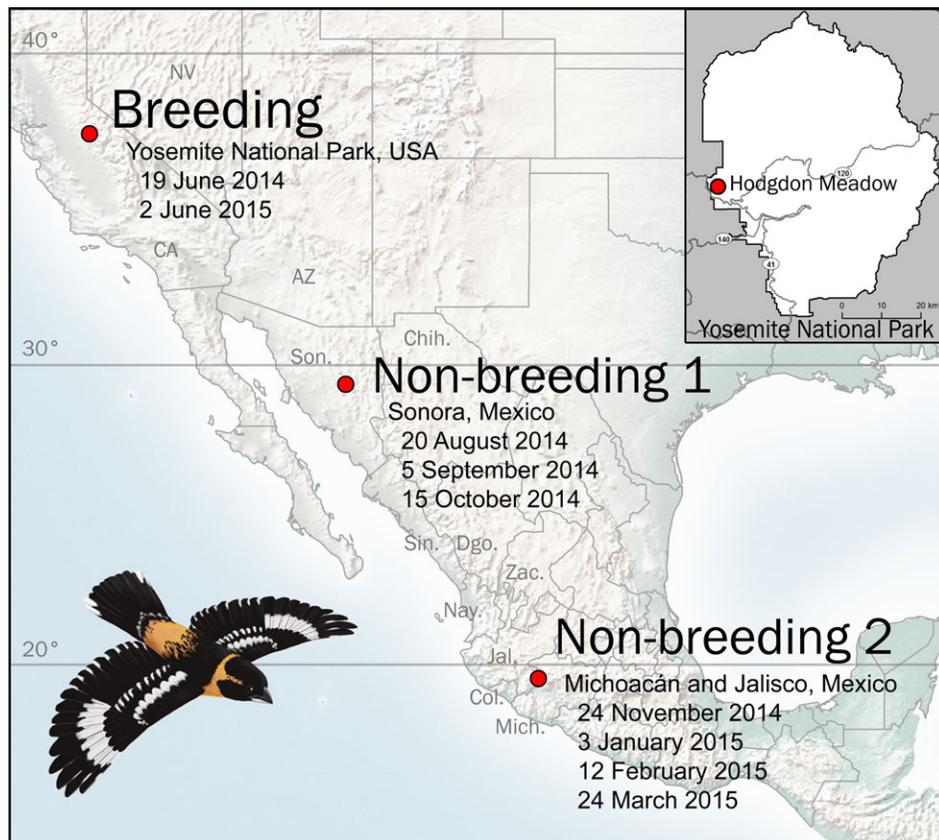


Fig. 1. Recorded locations throughout the annual cycle of a Black-headed Grosbeak GPS-tagged and recaptured a year later at Hodgdon Meadow, Yosemite National Park (inset).

target and passive netting at Hodgdon Meadow in an attempt to recapture tagged individuals and recover GPS tags.

We described seasonal patterns of vegetation greening at recorded grosbeak locations during the non-breeding season using 16-d 0.25-km resolution enhanced vegetation index (EVI) data derived from the Moderate Resolution Imaging Spectroradiometer (MODIS) instrument of NASA's Terra satellite (MODIS product MOD13Q1; <http://terra.nasa.gov/>). EVI, a composite metric of vegetation greenness, incorporates structural and seasonal components of habitat quality, including primary productivity (leaf chlorophyll content), leaf area, canopy cover, and vegetation complexity (Glenn *et al.* 2008, Park 2009, Potithepa *et al.* 2010). We extracted EVI cell values using the MODIS-Subsets function of the MODISTools package (Tuck *et al.* 2014) in the statistical software

package R (R Core Team 2013). To provide coarse land-cover classification of locations, we used 2005 0.25-km pixel resolution data from the North American Land Change Monitoring System (<http://landcover.usgs.gov/nalcms.php>). To provide finer resolution habitat information, we extracted Google Earth imagery (<https://earth.google.com/>), and derived elevation, aspect, and slope data from 90-m resolution Shuttle Radar Topography Mission digital elevation maps (Jarvis *et al.* 2008) using functions available in the R package, "raster" (Hijmans 2015).

RESULTS

On 2 June 2015, we recaptured one of the tagged grosbeaks and recovered its GPS tag. The bird was a male that had been GPS-tagged on 19 June 2014 and banded initially during the

Table 1. Locations used and minimum distances traveled by a Black-headed Grosbeak GPS-tagged in Yosemite National Park during the 2014 breeding season and recaptured at nearly the same location a year later.

Date	Location	Latitude	Longitude	Estimated distance from previous location
19 June 2014	Yosemite National Park, California, USA	37.79561	-119.86024	n/a
20 August 2014	Sonora, Mexico	29.39112	-110.06831	1300 km
5 September 2014	Sonora, Mexico	29.39134	-110.06901	72 m
15 October 2014	Sonora, Mexico	29.37536	-110.04953	2.6 km
24 November 2014	Michoacán, Mexico	19.52973	-102.60620	1324 km
3 January 2015	Michoacán, Mexico	19.52956	-102.60663	49 m
12 February 2015	Jalisco, Mexico	19.46049	-102.70539	12.9 km
24 March 2015	Jalisco, Mexico	19.46074	-102.70540	21 m
2 June 2015	Yosemite National Park, California, USA	37.79237	-119.86461	2623 km

2006 breeding season as a second-year bird (Pyle 1997), making it 10-yr-old when we recovered its GPS unit. Two additional male grosbeaks that had been GPS-tagged were recaptured or resighted at the Hodgdon Meadow MAPS station during the 2015 field season, but had shed their leg harnesses and GPS tags.

Coordinates from the recovered GPS tag revealed that the grosbeak was 1300 km south of Yosemite in Sonora, Mexico, when its first location was logged on 20 August (Fig. 1, Table 1). Subsequent locations recorded on 5 September and 15 October revealed the bird was still in Sonora and was 72 m, and then 2.6 km, respectively, from the first location recorded in Sonora (Table 1). All locations in Sonora were in subtropical or tropical deciduous forest. The first two locations were at ~934 m elevation on a slope of about 5.6° and easterly aspect of 104°. The third location was at ~861 m on a slope of 3.7° with northeasterly aspect of 23°.

Six weeks later, when the next location was collected on 24 November, the grosbeak was 1324 km further south in Michoacán, near the Jalisco border (Fig. 1). The bird was 49 m from the previous location on 3 January and 12.9 km to the southwest in Jalisco on 12 February, where it was recorded again on 24 March, the last date a location was recorded (Table 1). The two locations in Michoacán were in tropical deciduous forest. These sites were at an elevation of ~1276 m on a slope of about 7.7° and easterly aspect of 117°. Interestingly,

the Jalisco location, although classified by the land-cover data as cropland, was in a residential area in the town of Cipoco, characterized by large broadleaf evergreen shade trees (Fig. 2; Google Earth imagery from 12 February 2014). The movement to this location, sometime in January or February, coincides with the late dry season when food and cover resources in natural dry forests of the region might be expected to be at their lowest levels (Fig. 3).

EVI values varied greatly throughout the year in both presumed molting grounds in Sonora and wintering areas in Michoacán and Jalisco, but the variation was more pronounced in Sonora (Fig. 3). Both sites exhibited peak values in the summer, with the peak occurring about 1.5 mo later in Sonora. Both sites, but especially Sonora, had much lower values in the winter (Fig. 3). The grosbeak was first recorded in Sonora just after the local EVI value peaked and began to decline, although it could have arrived there sometime during the previous weeks when the index was at or approaching its peak. The bird remained in Sonora throughout most of the subsequent decline in the index, and then departed sometime between October 16 and November 24, shortly before the lowest values of the year were obtained. EVI values at the bird's wintering area in Michoacán and Jalisco were also at their lowest annual levels while the bird remained there throughout the late winter and early spring, but values were nevertheless substantially higher than at the Sonora location during the same period (Fig. 3).

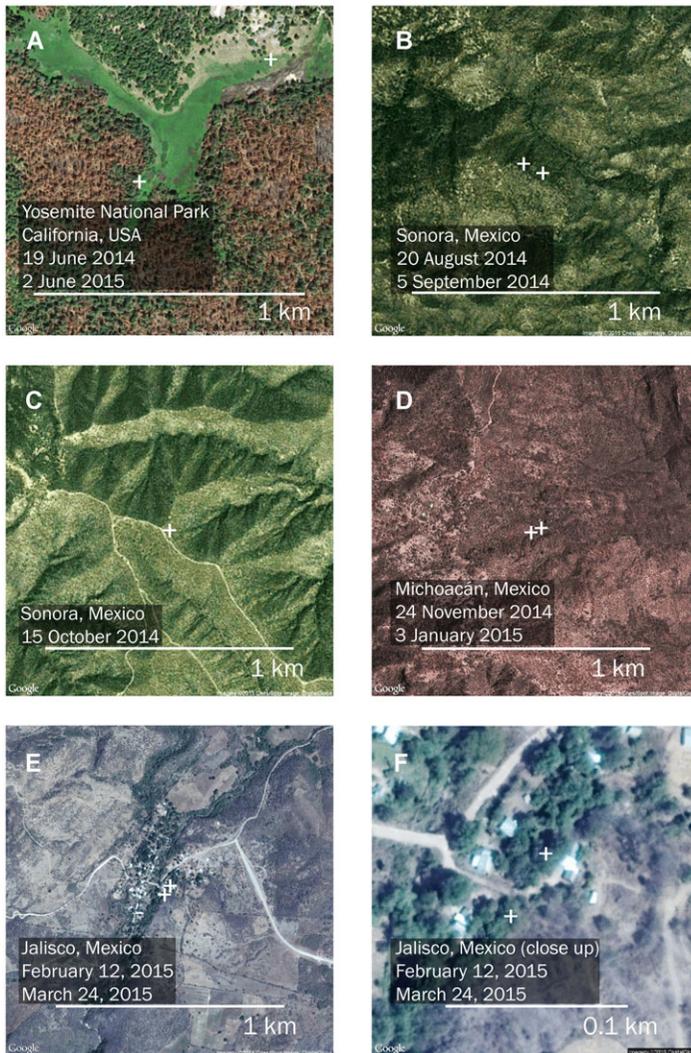


Fig. 2. Aerial imagery of landscapes around Black-headed Grosbeak tracking locations in Yosemite National Park (A); Sonora, Mexico (B and C); Michoacán, Mexico (D); and Jalisco, Mexico (E and F). Panel (F) provides a closeup view of the same locations as Panel (E).

DISCUSSION

The male Black-headed Grosbeak we tracked spent a minimum of 56 d in a small area in Sonora, Mexico, consistent with recent evidence that Black-headed Grosbeaks are molt migrants to the NAM region. It is unlikely that locations were collected on the exact arrival and departure dates, so the actual stay was almost certainly longer, potentially by a month or more. Both seasonal timing and the duration of the stopover are consistent with the expected behavior of a

molted bird. Rohwer et al. (2009) estimated that primary feather replacement for Black-headed Grosbeaks requires ~68–75 d. Two Bullock's Orioles (*Icterus bullockii*) recently tracked through molt migration with geolocators (Pillar et al. 2016) spent ~2.5 mo in the NAM region, and stable isotope analysis confirmed they grew new feathers while there.

The movements of a single individual obviously may not be representative of the annual migratory behavior of a population because migratory strategies and selection of stopover sites

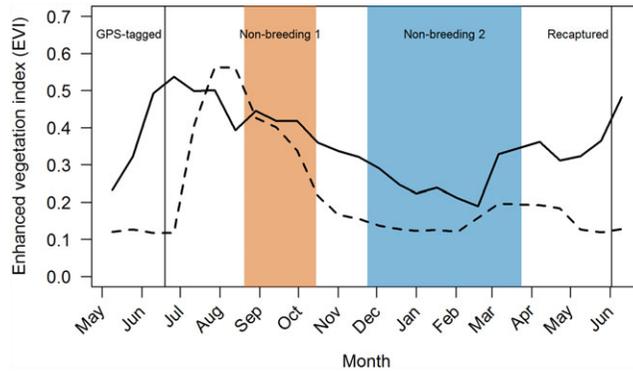


Fig. 3. Enhanced vegetation index (EVI) data obtained from May 2014 to June 2015 at locations in Mexico where a male Black-headed Grosbeak captured and GPS-tagged in Yosemite National Park spent the presumed molting period (dashed line) and the remainder of the winter (solid line). Shaded area labeled Non-breeding 1 and Non-breeding 2, respectively, represent the minimum period of time the bird spent in Sonora (Non-breeding 1), and then near the border between Michoacán and Jalisco (Non-breeding 2).

may vary among individuals within a population (Contina et al. 2013). Pyle et al. (2009) further suggested that individual birds may make different migratory and stopover choices in different years, depending on age, reproductive success and timing on the breeding grounds, variation in local weather and food resources, and perhaps other factors, although the annual variation in habitat use they reported was determined by numbers of molting individuals captured in successive years, rather than tracking individuals for multiple years.

Due to the coarseness of our temporal sampling, we cannot rule out the possibility that substantial movements occurred between sampling events, but the Black-headed Grosbeak we tracked appeared to make only two major migratory movements during the fall and early winter, moving from Yosemite to Sonora, Mexico, in late summer, and from Sonora to the Michoacán-Jalisco border region in late fall or early winter. Based on mark-recapture data, Ruiz-Gutierrez et al. (2016) describe alternate migratory strategies used by wintering Neotropical migrants during the non-breeding season, with some individuals in some regions exhibiting site persistence throughout the fall and winter, and others showing highly transient behavior. Within the Sonora and Michoacán-Jalisco areas, the bird we tracked appeared to move relatively short distances. For example, in Sonora, the presumed molting grounds, the locations on 20 August and 5 September were only 72 m

apart. The location on 15 October revealed that, after 5 September, the bird remained in the general vicinity, but at some point moved 2.6 km from its previous location. Similarly, in the Michoacán-Jalisco area, the locations of the grosbeak differed by <50 m on 24 November and 3 January, and then, after the bird moved 12.9 km between 3 January and 12 February, once again locations differed by <50 m on 12 February and 24 March. In both Sonora and the Michoacán-Jalisco region, mark-recapture efforts focusing on the bird's initial locations would likely have been unable to monitor its presence throughout the duration of its stay in the larger region, and light-level geolocation would not have been able to resolve either the tight clustering of some of the locations, or the intermediate-scale movements between others, underscoring the major advances that GPS-based tracking heralds for understanding passerine migration.

Identifying and understanding patterns of connectivity between breeding and overwintering areas used by populations of Neotropical migrants is increasingly recognized as critical for informing full annual-cycle conservation efforts (Webster and Marra 2005, Pekarsky et al. 2015). For molt migrant species, identifying the stopover habitats where molting occurs may also be critical. Bird conservation efforts have generally focused on breeding or wintering areas (Faaborg 2002, Leu and Thompson 2002, DeSante et al. 2005), but stopover sites used

for molting could be at least as important for some species (Leu and Thompson 2002, Pyle et al. 2009, Chambers et al. 2011, Marra et al. 2015). Moreover, seasonally dry tropical forests in Mexico, habitat apparently used by many western molt migrants, including the Black-headed Grosbeak we tracked, have undergone rapid deforestation in recent decades (Trejo and Dirzo 2000).

The greening of the monsoon region likely provides an intense, but ephemeral pulse of food and cover that molt migrants need during this vulnerable life-history stage. The grosbeak we tracked arrived in the region around the time when the EVI reached its peak, and then departed shortly before the index exhibited its lowest values, suggesting a possibly important match between migration timing and monsoon-driven phenology. During the coming decades, anthropogenic climate change is projected to have little effect on overall precipitation associated with the NAM, but to substantially change its seasonal timing (Cook and Seager 2013). Models project significant declines in early monsoon (June–July) precipitation and concomitant increases in late monsoon (September–October) precipitation, yielding an overall delayed onset and end of the monsoon (Cook and Seager 2013). This shift in timing could cause difficulties for Black-headed Grosbeaks and other molt migrants, especially because spring-like conditions across breeding ranges in much of western North America are beginning and ending increasingly earlier due to climate change, with hot, dry summer conditions starting earlier and lasting longer (U.S. Global Change Research Program 2013). Many western molt-migrant species may thus be facing pressures to breed earlier and then depart earlier from breeding areas as moisture and food decrease, even while moisture availability and greening in their molting areas is occurring increasingly later. It is unclear how or whether molt-migrant species will be able to adapt to the temporal disjunction between the need to migrate and the availability of plentiful food and cover in the molting areas that is likely to result.

ACKNOWLEDGMENTS

This project was funded by the Yosemite Conservancy, Yosemite National Park, and private donations gathered by Tyler Stuart and Jade Ajani. We thank our 2014

and 2015 field crews for assistance in capturing Black-headed Grosbeaks, including T. Alleger, B. Carnes, A. Grupenhoff, S. Harris, K. Kayano, L. Makielski, D. Mauer, D. Siegel-Zigmund, and M. Soderbergh. We also thank D. Humple and R. Cormier for advice on making and deploying leg harnesses, J. Wu for help with GIS, and P. Pyle for helpful comments on the manuscript. This research was conducted in compliance with the Guidelines to the Use of Wild Birds in Research. Bird banding and GPS-tagging were conducted under federal bird banding permit 22423 and a research permit from Yosemite National Park. This is Contribution Number 525 of The Institute for Bird Populations.

LITERATURE CITED

- ADAMS, D. K., AND A. C. COMRIE. 1997. The North American Monsoon. *Bulletin of the American Meteorological Society* 78: 2197–2213.
- BRIDGE, E. S., J. F. KELLY, A. CONTINA, R. M. GABRIELSON, R. B. MACCURDY, AND D. W. WINKLER. 2013. Advances in tracking small migratory birds: a technical review of light-level geolocation. *Journal of Field Ornithology* 84: 121–137.
- CHAMBERS, M. K., G. DAVID, C. RAY, B. LEITNER, AND P. PYLE. 2011. Habitats and conservation of molt migrant landbirds in the Mexican monsoon region of Arizona. *Southwestern Naturalist* 56: 204–211.
- COMRIE, A. C., AND E. C. GLENN. 1998. Principal components-based regionalization of precipitation regimes across the southwest United States and northern Mexico, with an application to monsoon precipitation variability. *Climate Research* 10: 201–215.
- CONTINA, A., E. S. BRIDGE, N. E. SEAVY, J. M. DUCKLES, AND J. F. KELLY. 2013. Using geologgers to investigate bimodal isotope patterns in Painted Buntings (*Passerina ciris*). *Auk* 130: 265–272.
- COOK, B. I., AND R. SEAGER. 2013. The response of the North American Monsoon to increased greenhouse gas forcing. *Journal of Geophysical Research (Atmospheres)* 118: 1690–1699.
- DESANTE, D. F., K. M. BURTON, P. VELEZ, D. FROELICH, AND D. R. KASCHUBE. 2015. MAPS manual: 2015 protocol. The Institute for Bird Populations, Point Reyes Station, CA.
- , T. S. SILLETT, R. B. SIEGEL, J. F. SARACCO, C. A. ROMO DE VIVAR ALVAREZ, S. MORALES, A. CEREZO, D. KASCHUBE, B. MILÁ, AND M. GROSSELET. 2005. MoSI (Monitoreo de Sobrevivencia Invernal): assessing habitat-specific overwintering survival of Neotropical migratory landbirds. In: *Bird conservation implementation and integration in the Americas* (C. J. Ralph and T. D. Rich, eds.), pp. 926–936. USDA Forest Service General Technical Report PSW-GTR-191, Pacific Southwest Research Station, Albany, CA.
- FAABORG, J. 2002. Saving migrant birds: developing strategies for the future. University of Texas Press, Austin, TX.
- GLENN, E. P., A. R. HUETE, P. L. NAGLER, AND S. G. NELSON. 2008. Relationship between remotely-sensed vegetation indices, canopy attributes and plant physiological processes: what vegetation indices can

- and cannot tell us about the landscape. *Sensors* (Basel, Switzerland) 8: 2136–2160.
- HALLWORTH, M. T., AND P. MARRA. 2015. Miniaturized GPS tags identify non-breeding territories of a small breeding migratory songbird. *Scientific Reports* 5: 11069. DOI: 10.1038/srep11069.
- HIJMANS, R. J. [online]. 2015. raster: Geographic data analysis and modeling. R package version 2.3–40. <<http://CRAN.R-project.org/package=raster>> (Accessed 22 December 2015).
- HOBSON, K. A. 2011. Isotopic ornithology: a perspective. *Journal of Ornithology* 152: 49–66.
- JARVIS, A., H. I. REUTER, A. NELSON, AND E. GUEVARA [online]. 2008. Hole-filled SRTM for the globe version 4. <<http://srtm.csi.cgiar.org>> (Accessed 22 December 2015).
- LEU, M., AND C. W. THOMPSON. 2002. The potential importance of migratory stopover sites as flight feather molt staging areas: a review for Neotropical migrants. *Biological Conservation* 106: 45–56.
- MARRA, P. P., E. B. COHEN, S. R. LOSS, J. E. RUTTER, AND C. M. TONRA. 2015. A call for full annual cycle research in animal ecology. *Biology Letters* 11: 20150552. <http://dx.doi.org/10.1098/rsbl.2015.0552>.
- MAYER, K. E., AND W. F. LAUDENSLAYER, JR. (eds.). 1988. A guide to wildlife habitats of California. Department of Fish and Game, State of California, Resource Agency, Sacramento, CA.
- MURPHY, M. E., AND J. R. KING. 1991. Nutritional aspects of avian moult. *Acta Congressus Internationalis Ornithologici* 20: 2186–2193.
- PARK, S. 2009. Synchronicity between satellite-measured leaf phenology and rainfall regimes in tropical forests. *Photogrammetric Engineering & Remote Sensing* 75: 1231–1237.
- PEKARSKY, S., A. ANGERT, B. HAESE, M. WERNER, K. A. HOBSON, AND R. NATHAN. 2015. Enriching the isotopic toolbox for migratory connectivity analysis: a new approach for migratory species breeding in remote or unexplored areas. *Diversity and Distributions* 21: 416–427.
- PILLAR, A. G., P. P. MARRA, N. J. FLOOD, AND M. W. REUDINK. 2016. Molt migration in Bullock's Orioles (*Icterus bullockii*) confirmed by geolocators and stable isotope analysis. *Journal of Ornithology* 157: 265–275.
- POTTITHEPA, P., N. K. NASAHARAB, H. MURAOKAC, S. NAGAIA, AND R. SUZUKIA. 2010. What is the actual relationship between LAI and VI in a deciduous broadleaf forest? *International Archives of the Photogrammetry, Remote Sensing and Spatial Information Science* 38: 609–614.
- PYLE, P. 1997. Identification guide to North American birds. Part 1. Slate Creek Press, Bolinas, CA.
- , W. A. LEITNER, L. LOZANO-ANGULO, F. AVILEZ-TERAN, H. SWANSON, E. GÓMEZ-LIMÓN, AND M. K. CHAMBERS. 2009. Temporal, spatial, and annual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. *Condor* 111: 583–590.
- R CORE TEAM. 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- RAPPOLE, J. H., AND A. R. TIPTON. 1991. New harness design for attachment of radio transmitters to small passerines. *Journal of Field Ornithology* 62: 335–337.
- ROHWER, S., L. K. BUTLER, AND D. FROELICH. 2005. Ecology and demography of east–west differences in molt scheduling of Neotropical migrant passerines. In: *Birds of two worlds: the ecology and evolution of migratory birds* (R. Greenberg and P. P. Marra, eds.), pp. 87–105. Johns Hopkins University Press, Baltimore, MD.
- ROHWER, V. G., S. ROHWER, AND M. F. ORTIZ RAMIREZ. 2009. Molt biology of resident and migrant birds of the monsoon region of west Mexico. *Ornitologia Neotropical* 20: 565–584.
- RUEGG, K., E. ANDERSON, K. PAXTON, V. APKENAS, S. LAO, R. B. SIEGEL, D. F. DESANTE, F. MOORE, AND T. SMITH. 2014. Mapping migration in a songbird using high-resolution genetic markers. *Molecular Ecology* 23: 5726–5739.
- RUIZ-GUTIERREZ, V., W. L. KENDALL, J. F. SARACCO, AND G. C. WHITE. 2016. Overwintering strategies of migratory birds: a novel approach for estimating movement patterns of residents and transients. *Journal of Applied Ecology*. DOI: 10.1111/1365-2664.12655.
- RUNDEL, C., M. WUNDER, A. ALVARADO, K. RUEGG, R. HARRIGAN, A. SCHUH, J. KELLY, R. B. SIEGEL, D. F. DESANTE, T. SMITH, AND J. NOVEMBRE. 2013. Novel statistical methods for integrating genetic and stable isotopic data to infer individual-level migratory connectivity. *Molecular Ecology* 22: 4163–4176.
- SWADDLE, J. P., AND M. S. WITTER. 1997. The effects of molt on the flight performance, body mass, and behavior of European Starlings (*Sturnus vulgaris*): an experimental approach. *Canadian Journal of Zoology* 75: 1135–1146.
- TREJO, I., AND R. DIRZO. 2000. Deforestation of seasonally dry tropical forest: a national and local analysis in Mexico. *Biological Conservation* 94: 133–142.
- TUCK, S. L., H. R. PHILLIPS, R. E. HINTZEN, J. P. SCHARLEMANN, A. PURVIS, AND L. N. HUDSON. 2014. MODISTools—downloading and processing MODIS remotely sensed data in R. *Ecology and Evolution* 4: 4658–4668.
- U.S. GLOBAL CHANGE RESEARCH PROGRAM. 2013. Our changing climate. U.S. Global Change Research Program, Subcommittee on Global Change Research, Washington, D.C.
- VOELKER, G., AND S. ROHWER. 1998. Contrasts in scheduling of molt and migration in eastern and western Warbling Vireos. *Auk* 115: 142–155.
- WEBSTER, M. S., AND P. P. MARRA. 2005. Importance of understanding migratory connectivity. In: *Birds of two worlds: ecology and evolution of migration* (R. S. Greenberg, ed.), pp. 199–209. Johns Hopkins University Press, Baltimore, MD.