LOOP MIGRATION BY A WESTERN YELLOW-BILLED CUCKOO WINTERING IN THE GRAN CHACO

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ABSTRACT: A lack of information on the full life cycle of long-distance migrants, including nonbreeding periods, may hinder the recovery of threatened populations. In 2010, on the middle Rio Grande, Sechrist et al. (2012) recaptured a Yellow-billed Cuckoo (*Coccyzus americanus*) fitted with a light-level geolocator, revealing for the first time wintering grounds and migration routes of an individual of this species. To further this knowledge, in 2011 we placed light-level geolocators on eight Western Yellow-billed Cuckoos at breeding sites on the lower Colorado River in Arizona and California. We recaptured one female in July 2012 at her previous capture site and analyzed the stored light data. During fall migration the bird flew ~9500–9900 km, passing through the Caribbean region. It wintered from mid-November to late April in the Gran Chaco of central South America, around the junction of Paraguay, Bolivia, and Argentina. The more direct spring route back to the breeding grounds passed through Peru and Central America. Following recapture, we discovered the bird was nesting while wearing the geolocator, and she later fledged young from two nests. Before and after migration, the bird appeared to pause in southern Arizona or Sonora, paralleling the first tracked Western Yellow-billed Cuckoo, suggesting this monsoonal region may be important to the western population during these stages of the life cycle. The bird's migration timing and loop route, though reversed in direction, were also strikingly similar to those of the first bird tracked, and their overlapping wintering grounds suggests the possibility of a distinct winter range for the western population. Given the continuing expansion of agriculture into natural areas throughout this large region of South America, conservation of these forested areas is essential.

In the western U.S., the decline of the breeding population and range of the Yellow-billed Cuckoo (*Coccyzus americanus*), recently listed as threatened under the Endangered Species Act as a "distinct population segment" (U. S. Fish and Wildlife Service 2014), is attributed mainly to loss or degradation of breeding habitat following large-scale modification of rivers (Gaines and Laymon 1984, Hughes 1999). Knowledge of the conditions the cuckoo experiences during the rest of its life cycle is limited, however, prohibiting a full assessment of its year-round conservation needs. Habitat quality in the winter range can affect an individual's fitness, timing of its spring migration, and reproductive success (Marra et al. 1998, Tonra et al. 2011). The threats to western cuckoos once they leave their breeding grounds are unclear but may be driven by the loss of forest to increased human population and by the expansion and intensification of agriculture and cattle grazing, all exacerbated by climate change (Ramirez-Villegas et al. 2012).

Recent research spurred by the development of the light-level geolocator has revealed both stopover and wintering sites of many long-distance migrants (Bridge et al. 2013, McKinnon et al. 2013), and the evolution of this technology enables the tracking of smaller (<100 g) migratory birds to their stopover and wintering grounds. Although the devices' precision remains rough, particularly in latitude (in forest, error averaging close to 200 km; Fudickar et al. 2012), geolocators can reliably be used to track the movements of long-distance migrants (Ryder et al. 2011). The tracking of sufficient numbers of Yellow-billed Cuckoos could reveal the species' migratory connectivity rangewide (Webster et al. 2002), including whether the western and eastern populations use separate migration corridors or wintering grounds, as found between distinct breeding populations of other species (Delmore et al. 2012). If the two populations are allopatric during the nonbreeding season, the decline of the western population may also be associated with greater rates of forest loss on its wintering grounds.

The first geolocator-carrying Yellow-billed Cuckoo to be tracked over one year was a female captured on the middle Rio Grande, New Mexico (Sechrist et al. 2012). The data revealed a post-breeding dispersal phase in northwest Mexico, fall migration through Mexico and Central America, wintering in central South America in the Gran Chaco region of Bolivia, Brazil, Paraguay, and Argentina, spring migration back to the breeding grounds via the Caribbean and Yucatan Peninsula, and a pre-breeding stop-over again in northwest Mexico. With the year-round movements of just one individual known, our objectives were to gain further understanding of western cuckoos' migration and wintering periods, including identifying the main areas used for wintering. This information may help to clarify the birds' risks year round.

METHODS

Between mid-June and mid-August 2011, we captured, banded, and weighed 29 adult cuckoos at three riparian-forest-restoration sites managed under the Lower Colorado River Multi-Species Conservation Program (2004): Palo Verde Ecological Reserve, California (33.7° N, 114.5° W), Cibola Valley Conservation Area, Arizona (33.41° N, 114.66° W), and Cibola National Wildlife Refuge, Arizona (33.36° N, 114.69° W). We modified a targeted mist-net technique (Sogge et al. 2001), raising the top of the net to the height of the canopy (up to 12 m) to increase the likelihood of capture. We attached two to four stacked mist nets (each 2.6 m high, 9–18 m long, mesh 60 mm) between two canopy poles (Bat Conservation and Management, Inc.) placed in a vegetation gap and broadcast cuckoo vocalizations from portable speakers hidden on each side of the net. From each bird captured, we drew up to 40 μL of blood for molecular sexing (McNeil et al. 2012). We fitted eight that we knew or assumed were breeding on the basis of nest observations, proximity to nests, or residency with Mk20 ASLT geolocators (British Antarctic Survey), with light stalks 15 mm long angled at 30°. Following Rappole and Tipton (1991), we attached the geolocators to lower-back leg-loop harnesses made of 1 mm elastic cord weighing 1.1 g total (0.9 g geolocator plus 0.2 g cord attachment; 1.5–1.9% of the birds' total mass). We released the birds where captured, and the following breeding season we tried to recapture them at the same or adjacent sites to retrieve the geolocators.

We used BASTrak software to download and decompress geolocator data, and TransEdit to analyze the data (Fox 2010). We used a light threshold level of 2 to define sunrise and sunset, visually assessed each of these transitions, and rated the quality of the transitions on a scale of 0 to 9. Transitions lacking smooth curves (evidence the bird was in deep shade) received low scores. We then rejected transitions scoring less than 8. We also discounted clearly erroneous locations, such as those >1000 km apart within 12 hours or falling far off shore. We used a sun-elevation angle of –4.09°, which best calibrated to the capture location for the week after deployment (8–15 August 2011), thus assuming a similar degree of shading throughout the year. We used BirdTracker software (Fox 2010) to estimate latitude and longitude (datum WGS 84) at noon and midnight each day. Because Yellow-billed Cuckoos migrate at night (Crawford and Stevenson 1984), we compensated for longitudinal movement when estimating latitude (Fox 2010). For the periods within 15 days of the fall and spring equinoxes (23 September 2011 and 20 March 2012, respectively) when day length was similar everywhere, we inferred coordinates in longitude only. We estimated mean positional error by measuring the distance between calculated and known locations for the week after deployment and the week before recapture, when the bird was at the breeding site. We imported the locations into ArcMap 9.3 (ESRI) for visual assessment, and defined a buffer around pre- and post-breeding points and around winter points, the width equal to our mean positional error, to represent the areas of staging for migration and wintering, respectively.

RESULTS

Of four males and four females fitted with geolocators in 2011, we recaptured one female on 17 July 2012 at the Palo Verde Ecological Reserve, at the same net location where initially captured on 7 August 2011. We failed to refind the other seven or any of the 21 other cuckoos banded but not fitted with geolocators. We removed the leg harness and geolocator and examined the bird thoroughly; she appeared healthy with no obvious ill effects from the harness. She weighed 64 g on recapture, 4 g heavier than when captured in 2011. We then fitted her with a tail-mounted radio transmitter (McNeil et al. 2013) and found her to be a week into nesting, about 230 m from the capture location. We radio-tracked her until 2 September, when we lost her signal and assumed she left the site. She nested three times in 2012, the first and last attempts successfully.

The geolocator generated 687 location points over 344 days between 7 August 2011 and 16 July 2012. We omitted 409 low-quality points (59.5%), including 114 (16.6%) near the equinoxes, when geolocation data are unreliable, and another 15 that were clearly erroneous (2.2%). This left 263 points (38.3%) with which we assessed the migration routes and winter range (Figures 1, 2). After the data from the first week of deployment (8–13 August) were calibrated to the capture location, the mean positional error during that week was 87.2 km (range 46.8–146.4 km, SD = 28.2 km, n = 11 points). Longitudinal error averaged 56.3 km (range 19.1–89.1 km, SD = 19.0 km, n = 11), and latitudinal error averaged 57.2 km (range 2.9–142.9 km, SD = 41.5 km, n = 11). The geolocator stopped recording data on removal so we were unable to calibrate it after retrieval. Because the bird was a week into nesting when recaptured, so presumably at or near

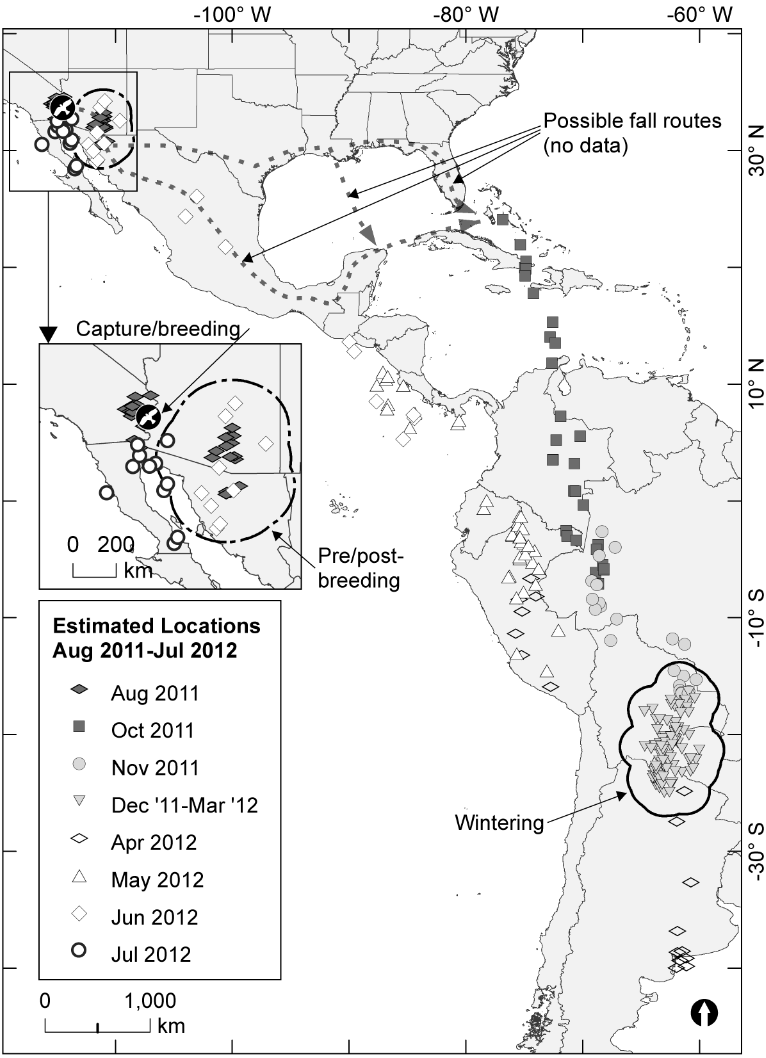

Figure 1. Estimated locations of a Western Yellow-billed Cuckoo from the lower Colorado River to/from central South America, 7 August 2011 to 17 July 2012. No latitude data are available for September 2011 because of the fall equinox; possible routes are shown as dashed arrows.

the nest the entire week, we compared the data from the week prior to recapture, 10–15 July 2012, to the location of her active nest. The mean distance between the estimated locations and the nest was 221.2 km (range 22.1–387.7 km, SD = 110 km, n = 10). We used this distance (221 km)

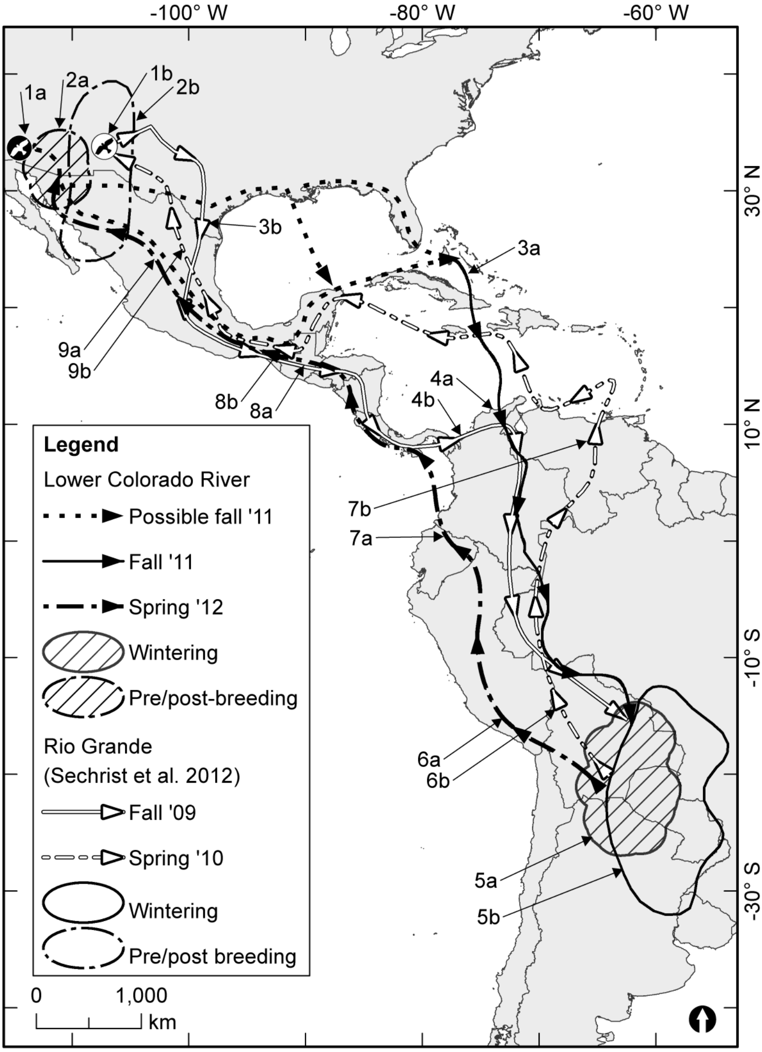

Figure 2. Comparison of migration routes, schedules, and wintering grounds of two Western Yellow-billed Cuckoos from the lower Colorado River (a) and the middle Rio Grande (b; data from Figure 2 in Sechrist et al. 2012). Points along the routes also coded as 1, capture/breeding location; 2, post-breeding, Aug–Sep, and pre-breeding, Jun; 3, fall migration, early Oct; 4, fall migration, mid-Oct; 5, winter range, Dec–Mar; 6, spring migration, late Apr; 7, spring migration. mid-May; 8, spring migration early Jun; 9, spring migration, mid-Jun.

as the width of the buffer to display positional error around the points. The mean latitudinal error from the nest was 211.2 km south (range 16.3–353.9 km, SD = 107.1 km, n = 10), or approximately 2° south, large compared to the longitudinal error (mean 57.2 km, range 10.7–158.3 km, SD = 43.6 km, n = 10). Visual assessment of the locations suggested that through the year, several other points outside the grasp of the equinoxes were shifted south by a similar amount, including a cluster of points placed in the Pacific Ocean south of Central America, when the bird was probably in Panama, Nicaragua, or Honduras during spring migration.

We inferred the following from the estimated locations:

Post-breeding Dispersal and Fall Migration

- The bird left the breeding site around 17 August, moving east toward central southern Arizona or northwest Mexico, where she remained until 13 September.
- On 14 September, she flew east to 104°–107° W longitude, staying until 27 September.
- After spending six weeks in the southwest U.S. or northern Mexico post-breeding, the bird swiftly moved east, apparently flying ~2000 km from 27 September to 1 October (mean 500 km/day). By 1 October she was at 85.5°–87.5° W longitude.
- On 3 October, she was in line with Florida, Cuba and Central America. From 6–19 October she was east of Florida's longitude.
- From 20 to 25 October, she apparently moved through eastern Colombia, then spent late October to mid-November in Amazonian Brazil.

Winter

- The bird spent mid-November through March, and probably April, in the Gran Chaco of central South America, in the region where the borders of Paraguay, Bolivia, and Argentina intersect.
- Latitude data from 12 to 29 March were unusable, the dates being too near the equinox, but longitude was static. By late March she had possibly moved south toward coastal Argentina. It is unclear if this shift was error due to weather or a prolonged effect of the equinox.

Spring Migration

- She began moving north by 28 April and was in Central America from late May to early June.
- Data from June were largely unusable (possibly because of weather or the geolocator being too shaded), but she likely moved northwest through southern Mexico to arrive in central Mexico 18–23 June. By 28 June, she was back in southern Arizona or Sonora.
- By 9 July she had returned to the breeding site, and began nesting around 12 July.

Fall migration from the southwest U.S. to South America took three weeks (mean 225–250 km/day), with another month taken to arrive on the wintering grounds (mean 117 km/day). Spring migration lasted two months, one month from the wintering grounds to Central America (mean 150 km/day), another to the southwest U.S. (mean 123 km/day). The distance from the breeding site to the core wintering grounds was 9500–9900 km (depending on the fall route), and the distance back to the breeding site was 9100–9200 km.

In comparison to that tracked by Sechrist et al. (2012), our cuckoo took a similar but reversed loop route (Figure 2). That is, she apparently migrated through the Caribbean in the fall and through Central America in the spring, whereas the cuckoo captured on the middle Rio Grande took a fall route through Central America and returned in the spring through the Caribbean. The timing of the two cuckoos' migration was also strikingly similar; both apparently left their breeding grounds around late August, arrived in northern Colombia in mid-October, and arrived on the wintering grounds mid-November. Both began spring migration in late April, and after staging in other areas in northwest Mexico or southern Arizona, they both returned to their respective breeding grounds around the end of June.

DISCUSSION

Understanding the cuckoo's migration strategies and where it stages and winters enables the expansion of management beyond the present limited scope of its breeding grounds. On a more basic ecological level, this information may help answer questions about flexibility in migration strategy and divergence of eastern and western Yellow-billed Cuckoo populations. Additionally, as geolocator technology for smaller birds is still evolving, our results support the application of this technology to smaller migratory land birds.

We did not find the geolocators to affect the cuckoos' rate of recapture or ability to breed; the fraction 1/8 recaptured is comparable to the 9.9% rate of recapture of 183 cuckoos banded along the lower Colorado River from 2009 to 2012 (McNeil et al. 2013). In a review of geolocator studies, Bridge et al. (2013) also found rates of return of birds with and without geolocators to be comparable. Though we failed to refind any of the 21 other adults captured but not fitted with geolocators in 2011, we recaptured three birds banded in the study area in earlier years (McNeil et al. 2013), suggesting some site fidelity with a relatively low probability of recapture. That all geolocator-fitted cuckoos thus far recaptured have been female (three including another female recaptured on the Pecos River whose geolocator failed soon after deployment, Sechrist and Best 2012) is somewhat unexpected because we typically capture and recapture fewer females than males (16% and 2.8% fewer, respectively; McNeil et al. 2013). Females average around 10% heavier than males (in this small sample of eight birds, the females averaged 14% heavier), though all our attachments weighed no more than 1.9% of the body mass of any bird, below the recommended limit of 3% (Gustafson et al. 1997). As birds may lose mass during migration, we recommend long-term attachments be as light as possible.

Our exclusion of over 60% of the data is consistent with other studies that have discarded as much as 62% of data from birds inhabiting forested environments (e.g., Ryder et al. 2011), the result of shade confounding the light-level readings from which locations are calculated (Fudickar et al. 2012). As we found, location error averaging over 200 km (Fudickar et al.

2012, Lisovski et al. 2012) is typical for latitude (see Hill 1994 for detailed explanation), and latitude data from the periods around the fall and spring equinoxes were largely unusable, often implying locations near the poles (data not shown). Unfortunately, our bird spent the period most affected by the fall equinox making the largest movements east. Because readings for longitude are unaffected during the equinoxes, we were able to infer possible routes for this portion of fall migration. As the first tracked cuckoo passed between the West Indies and Yucatan Peninsula (Sechrist et al. 2012), this route (though reversed in direction and season) seems the most plausible.

The apparent staging by both tracked cuckoos in southern Arizona or northern Mexico pre- and post-breeding suggests this region is important to the western population during these stages of its life cycle. The Yellow-billed Cuckoo is often described as wandering or nomadic during periods surrounding the breeding season, exploiting outbreaks of large insects (Hamilton and Hamilton 1965, Hughes 1999); birds of many species wander considerable distances after breeding but before migration (Rappole and Ballard 1987). Nomadic or exploratory behavior should aid the cuckoo in locating ephemeral patches of cottonwood–willow forest.

The North American monsoon typically develops over southwest Mexico from late May to early June, arriving in northwest Mexico from mid- to late June, and in the southwest U.S. by early July (Adams and Comrie 1997)—roughly tracking the movement of our cuckoo through Mexico in June to its arrival in the southwest U.S. by early July. The spike in rainfall in July and August over the center of the monsoonal region in northwest Mexico (Douglas et al. 1993) coincides with the peak of western cuckoo nesting. If cuckoos track monsoonal flushes of new vegetation and insects (Wallace et al. 2013), they may be pursuing a multi-stage strategy for breeding and migration, as found in some other birds (e.g., Stach et al. 2013).

Sechrist et al. (2012) raised "migratory double-brooding" (breeding in two regions in one year, separated by a migration) as a possible reason for cuckoos to visit Mexico late in the breeding season. First suggested by Rohwer et al. (2009), this hypothesis is based on circumstantial evidence alone, and it appears increasingly unlikely (Rohwer and Wood 2013). Sechrist et al. (2012) also suggested molt migration as a possible cause for the stopover in Mexico, while acknowledging that the stopover was too brief; also, the Yellow-billed Cuckoo molts its flight feathers mainly in its winter range (Pyle 1997, Rohwer and Wood 2013). Tracking many more individuals, through more than one annual cycle, is needed to test these hypotheses and assess fidelity to staging areas.

The similarity in the timing of the two tracked cuckoos' migration was unsurprising. In long-distance migrants, it is often highly consistent within a population (Stanley et al. 2012) and determined genetically (Berthold and Helbig 1992), though it can be affected by factors such as energetic condition and nesting date (Stutchbury et al. 2011). Western cuckoos' breeding much later than the eastern population (Hughes 1999) also suggests the western population may winter farther south and thus travel farther from the winter to the breeding grounds (Rubolini et al. 2005), or it may begin spring migration later than the eastern population. The lack of migration data on eastern individuals currently prevents further comparison.

The reversal of the two tracked cuckoos' loop routes implies that western cuckoos' migration routes are flexible, as found in some other species (Alerstam et al. 2006, Vardanis et al. 2011, Stanley et al. 2012). Sechrist et al. (2012) already dispelled speculation that only eastern cuckoos migrate through the Caribbean (Hughes 1999), and both birds' passing through the Caribbean suggests migration of western cuckoos through this area may even be common. Within a population, migration routes are generally more flexible than timing (Delmore et al. 2012, Stanley et al. 2012), as we found. Loop routes are common (Klaassen et al. 2010, Stanley et al. 2012), though typically the movement is in a consistent direction (e.g., clockwise). Because wind direction can be the greatest predictor of flight direction (Able 1973), the direction of the wind at the start of each migration may have driven each bird's decision whether to pass through Central America or the Caribbean.

The threats to western cuckoos on their breeding grounds, primarily habitat loss and degradation (Gaines and Laymon 1984), increasingly exacerbated by long-term drought and climate change (Ault et al. 2014), may be even greater in their winter range. The Gran Chaco, containing the second largest native forest in South America after the Amazon Basin, has, over the last few decades, experienced large-scale conversion and fragmentation of forest for expanding cattle and soybean production (Berbery et al. 2006). Deforestation of the Chaco in Argentina, Paraguay, and Bolivia represents the greatest loss of forest cover globally in the 21st century (Hansen et al. 2013). From 2005 to 2010, annual rates of deforestation in this region (1.5–2.5%) surpassed Latin American and world averages (0.5% and 0.2%, respectively, reviewed by Seghezzo et al. 2011). Gasparri and Grau (2009) found deforestation of Chaco dry forest accelerating, with over 1.4 million ha destroyed in the last 35 years. Mastrangelo and Gavin (2014) encouraged alternatives to intensive agriculture, such as selective clearing, to lessen the continuing reduction of habitat for birds in this region. A better understanding of the winter range, including identifying and supporting actions to reduce these threats, will promote conservation of western cuckoos through their full life cycle.

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Yellow-billed Cuckoo

Drawing by George C. West