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Migratory connectivity of Golden-crowned Sparrows from two wintering regions in California

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Abstract: Knowledge of migratory connectivity is critical to understanding the consequences of habitat loss and climate change on migratory species. We used light-level geolocators to determine breeding locations and migratory routes of wintering Golden-crowned Sparrows (*Zonotrichia atricapilla*) in two regions of California, USA. Eight out of 9 birds tagged at coastal-wintering sites in Marin County went to breeding sites along the Gulf Coast of Alaska, while 7 out of 8 inland-wintering birds in Placer County migrated to interior sites in the Yukon, Northwest Territories, and British Columbia, Canada. Our estimate of the strength of migratory connectivity was relatively high ($r_m = 0.66$). Coastal-wintering birds followed a coastal migration route while inland-wintering birds migrated inland. Coastal-wintering birds migrated significantly farther than inland birds (3,624 km versus 2,442 km). Coastal birds traveled at a greater rate during spring migration (179 km/d) than did inland birds (118 km/d), but there was no statistical difference in the rate of fall migration (167 km/d and 111 km/d, respectively). Dates of arrival and departure, and duration of spring and fall migration, did not differ between groups, nor did return rates. Rates of return also did not differ between tagged and control birds. The distinct migration routes and breeding areas suggests that there may be more structuring in the migratory geography of the Golden-crowned Sparrow than in a simple panmictic population.

Keywords: Light-level geolocation, migratory divide, migratory route, rate of migration, *Zonotrichia atricapilla*, wintering grounds

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1 Introduction

Understanding migratory connectivity patterns is a critical component to the conservation of migratory birds and to understanding the consequences of habitat loss and climate change on biodiversity [1,2]. By identifying a species' migratory geography, we can increase our knowledge of the factors that limit populations, and in which season(s) of their annual cycle the limitations occur [3,4]. Additionally, determining the strength of migratory connectivity can highlight which populations may be most vulnerable: populations that have strong migratory connectivity (e.g., individuals that spend the breeding season in one area also spend the winter season in close proximity to one another) may be most sensitive to perturbations because there are fewer individuals from other areas to buffer impacts from disturbances that occur during any part of their annual cycle [5].

Recently, the proliferation of geocator studies has dramatically increased our knowledge of where migratory passerines go throughout their annual cycle, and of their migratory connectivity [6,7,8]. These studies have provided insight at a scale that has not been available from other methods, including the ability to assess migratory connectivity patterns of populations wintering or breeding close to one another. For example, with a relatively small sample size, Nelson et al. [9] demonstrated that Hermit Thrushes (*Catharus guttatus*) on the north side of San Francisco Bay in California migrate to different locations than those that winter on the south side of San Francisco Bay. Hence, on the wintering grounds, the proportion of individuals from different breeding populations may change dramatically across relatively short distances and as a result, conservation needs of a species could also vary within a small spatial scale.

Golden-crowned Sparrows (*Zonotrichia atricapilla*) breed from Alaska, USA to southern British Columbia and Alberta, Canada, and winter from British Columbia to northern Baja California, Mexico [10]. Their migratory ecology has not been well-studied, and there are no recognized subspecies [10]. Recent work has demonstrated that across their breeding range, Golden-crowned

Sparrows have distinct vocalization types [11], suggesting the possibility of a complex population structure, rather than a simple panmictic population. In our preceding study with light-level geolocators, we showed that four Golden-crowned Sparrows that wintered on the coast of California migrated to breeding sites along the Gulf Coast of Alaska [12]. Since the wintering range of Golden-crowned Sparrows in California extends from the coast inland to the foothills of the Sierra Nevada mountain range, it is possible that inland-wintering Golden-crowned Sparrows may breed in a different region than the birds that winter on the coast.

We investigated the migratory geography of Golden-crowned Sparrows captured on their wintering grounds in central California, USA. We deployed light-level geocator tags on birds at two nearby coastal study sites and one inland study site. We compared the breeding locations, migratory routes, migratory phenology, distance travelled, rates of migration, and return rates of Golden-crowned Sparrows from these two wintering areas. We predicted that coastal-wintering birds would follow a coastal migration route and breed at coastal sites, consistent with previous findings [12]; for inland-wintering birds, we investigated whether they migrated to the same or different breeding locations from the coastal-wintering birds, and calculated the strength of migratory connectivity for birds from these two wintering areas.

2 Methods

2.1 Study sites

We attached light-level geocator tags (hereafter, geolocators) to Golden-crowned Sparrows captured in two regions in central California, USA. The 15 birds from the inland population were tagged at one site on private land near Newcastle, California (latitude 38.88°, longitude -121.19°) in the foothills of the Sierra Nevada (elevation 192 m). The coastal birds were tagged at two sites approximately 2 km apart and within 2 km of the Pacific Ocean in Bolinas, California in conjunction with a long-term monitoring study at the Palomarin Field Station: 9 birds at Pine Gulch Creek (37.92°, -122.69°) in Marin County Open Space District's Bolinas Lagoon Open Space Preserve, and 14 birds on private land (37.90°, -122.70°) in a residential area. The inland and coastal sites were approximately 170 km apart, and the data from the two coastal sites are combined and treated as one coastal-wintering site in the results (Fig. 1).

Vegetation at the inland study site is dominated by California blue oak (*Quercus douglasii*) and interior live oak

(*Q. wislizeni*), with a small riparian zone nearby dominated by willows (*Salix* sp.) and Himalayan blackberry (*Rubus discolor*); the immediate trapping area is a landscaped yard with a mix of native and non-native shrubs, forbs, and lawn area. At the coastal sites, Pine Gulch Creek is a riparian site dominated by arroyo willow (*Salix lasiolepis*) and red alder (*Alnus rubra*) with an understory of blackberry (*R. ursinus* and *R. discolor*) and other species (see Samuels et al. [13] for a more detailed description), and the private land site is dominated by a mix of native and non-native shrubs, especially Himalayan blackberry.

2.2 Data Collection

2.2.1 Capture techniques

The birds at the inland and private-land coastal sites were captured in baited Potter traps and recaptured with these traps or target mist nets; at the Pine Gulch coastal site, birds were captured in mist nets as part of an existing long-term constant-effort banding program and recaptured with the same method or with target mist nets. All birds were tagged between 3 January and 22 March 2013 and recovered between 15 October 2013 and 8 April 2014.

2.2.2 Geolocators

We attached geolocators to 38 Golden-crowned Sparrows. We used P65C2J13 geolocators with 14 mm long stalks, manufactured by Migrate Technology Ltd. We attached these to Golden-crowned Sparrows with a leg-loop harness [14] of 1.0 mm Stretch Magic® jewelry cord, closed with a metal crimp bead. The average weight of the harness and tag together was 0.8 g, 2-3% of the bird's weight.

2.2.3 Additional information collected on birds

Each bird was banded with a federal aluminum band and also given a color band that provided a unique identifier for field identification. We determined the age of each bird, but did not determine the sex of the birds we captured because Golden-crowned Sparrows are sexually monomorphic. To evaluate the effect of tagging on return rates, we captured an additional 15 control birds at the coastal site on private land, and 15 control birds at the inland site; control birds received an aluminum band with 1-2 unique color band(s) and the same data were collected, but they were not fitted with a geocator tag.

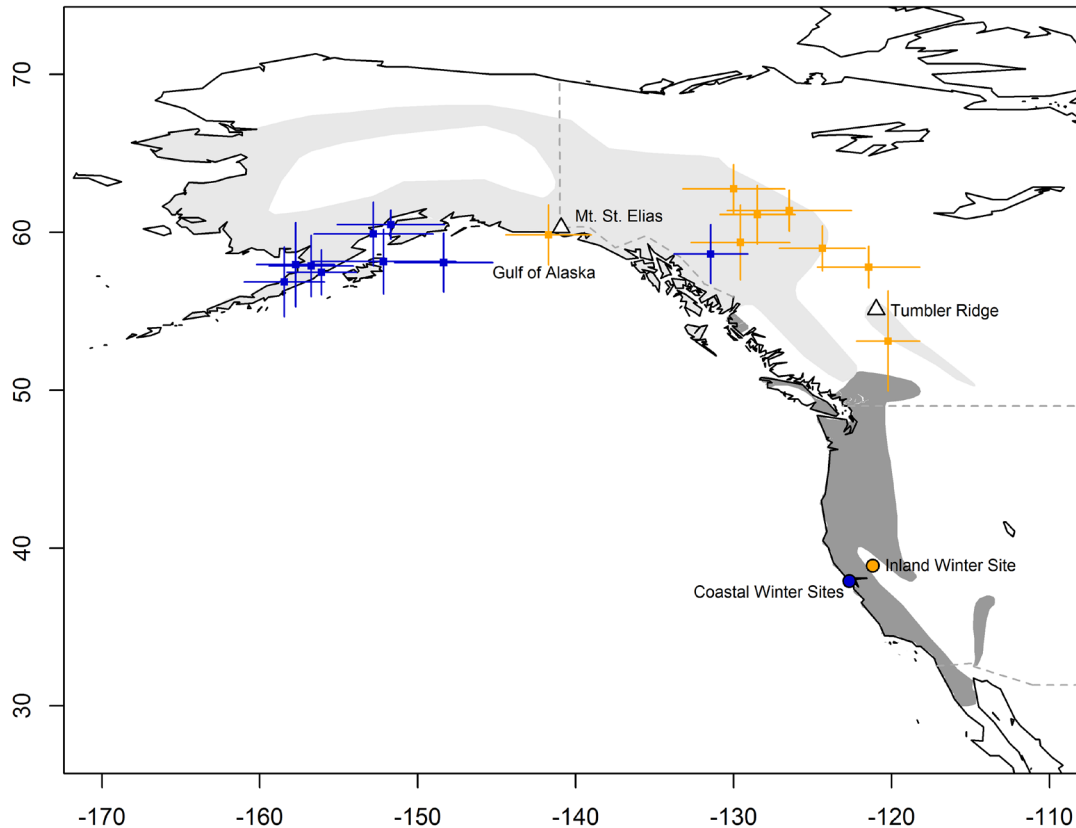


Figure 1. Mean breeding locations (blue squares = bird tagged at coastal winter site; orange squares = bird tagged at inland winter site) \pm SD are shown for 17 Golden-crowned Sparrows tagged with light-level geolocators at two wintering locations in California, USA ($n = 9$ coastal and $n = 8$ inland). Darker shading shows the species wintering range and lighter shading their breeding range [44].

2.3 Statistical Analysis

2.3.1 Light-level data processing

After recovering the geolocators, we used the IntiGeo-IF software (Migrate Technology Ltd.) to decompress data from each geocator into light files. The geolocators we used measured light intensity every 1 min and recorded the maximum measurement every 5 min. Light intensity was recorded on a scale between 1 and 74,000 lx, and before further analysis, we log transformed the light values.

2.3.2 Location processing

To convert the light files into locations, we used the threshold method performed with the BASTag [15] and GeoLight [16] packages in R (version 3.2.2 [17]). The threshold method is based on sunrise and sunset times that are identified as the time points when the light intensity passes a specific threshold. We used a threshold

value of 2.5 to identify sunrise and sunset times using the ‘BASTag’ package [15]. For all but one bird, we determined the sun elevation value using a post-deployment calibration period from 1-31 March 2013. For these birds, the calculated sun elevation angles for the 2.5 threshold ranged between -4.05 and -2.27 (average -3.45). For one additional bird, the calibration angle during March was -0.34 , but using a slightly earlier period (1-28 February) resulted in a sun elevation angle (-2.1) that was closer to the other values, and we used this earlier calibration period. We then used the elevation angle calculated for each individual to generate the location values for that individual. See Sup. Mat. Table S1 for more details on each tag.

2.3.3 Migration Phenology

We used a combination of three approaches to estimate the start and end of spring and fall migration for each individual. First, we used the “changeLight”

function (probability of change at sunrise and sunset = 0.07, minimum stationary period = 5 d) in the GeoLight package to distinguish periods of residency and movement [16]. We then used the “mergeSites” function to merge sites that were less than 350 km apart. From these two methods we extracted the dates that birds departed the wintering grounds, arrived on the breeding grounds, departed the breeding grounds, and returned to the wintering grounds. Finally, we checked the migration departure and arrival dates with re-sightings of color-banded tagged birds. If the tagged birds had been observed prior to an arrival date or after a departure date, then we returned to the changeLight movement periods and used the next earlier or later date (see Sup. Mat. Table S1 for more information on calculating arrival and departure dates). We tested for differences in departure and arrival dates for spring and fall migration between coastal-wintering and inland-wintering groups using a Mann-Whitney test. To test for differences in duration of migration, we compared the mean number of days spent on spring and fall migration for coastal-wintering and inland-wintering groups using Welch’s *t*-tests.

2.3.4 Breeding locations and migratory connectivity

We used the “coord” function in the GeoLight package [16] to determine latitude and longitude estimates for each twilight period. After determining residency periods and migration dates (see above), we calculated the mean breeding season location and \pm SD for each individual, defined as the mean of the latitude and longitude estimates after birds arrived on the breeding grounds and before they departed for the wintering grounds.

To quantify the strength of migratory connectivity, we generated two spatial matrices using the R package lmap [18]: one with pairwise great circle distance between mean breeding locations for all individuals, the second was for winter locations. We then used a Mantel test to quantify the correlation between the two matrices [19]. We performed the Mantel test with the R package “ade4” and used 100,000 random permutations to evaluate the statistical significance of the correlation coefficient [20]. We also used the breeding location matrix to calculate the average and range of distances between all breeding locations of coastal birds, the average distance between breeding locations of all inland birds, and the average distance between breeding locations of all coastal and inland birds.

2.3.5 Migration route, distance, and rate

Because there is substantial error in location estimates from geolocators, using the data to identify stopover locations is problematic when stopover durations are only a few days [21]. Thus, instead of focusing on the migration pathways of individual birds, we used kernel density estimates to summarize the location data across all inland and coastal individuals during migration. This allowed us to generate maps of the migration locations with areas of highest density representing areas where there were concentrations of locations. To generate the kernel density estimates, we used the R package “adehabitatHR” [22].

Because we determined that many of the birds did not travel in a straight line between winter and summer grounds (e.g., coastal-wintering birds followed a coastal route, rather than flying directly across the Pacific Ocean), we calculated migration distance by breaking their migration into segments, instead of calculating the straight-line distance between wintering and breeding locations. While this approach resulted in longer distance estimates, it represented more realistic routes and distances. Rather than using the actual migration routes for each individual, segments were connected between common sets of points that went through the approximate centers of the kernel density estimates calculated above. We added between 0 and 3 points to connect winter and breeding locations for each bird (see Sup. Mat Table S2 for more detail). We then calculated the great circle distance for each segment between each wintering location and breeding location using the R package “fields” [23], and we calculated the sum of the great circle distances for all segments for each bird to determine the total migration distance.

We calculated rate of migration (km/d) by dividing the total distance of migration by the duration of migration; rate does not distinguish between when birds were stationary versus moving, thus does not imply speed. We compared mean migration distances and rates for coastal and inland birds using Welch’s *t*-tests.

2.3.6 Return rates

To test for differences in return rates between inland- and coastal-wintering birds, we used a Pearson’s chi-squared test and compared individuals that were recaptured or re-sighted with those that were not detected. We also compared return rates between control and tagged birds for each group using the same method. We used an alpha level of 0.05 for all statistical tests.

3 Results

3.1 Breeding locations and migratory connectivity

Of the 9 birds that wintered along the coast, 8 (89%) went to breeding sites along the Gulf Coast of Alaska, while 7 of the 8 (88%) inland-wintering birds went to inland breeding sites in the Yukon, Northwest Territories, and British Columbia, Canada (Fig. 1). We generated matrices of great circle distances for winter locations and breeding locations of the 17 individual Golden-crowned Sparrows and the Mantel correlation coefficient (r_m) for these was 0.66 ($P < 0.001$). The average distance between breeding locations of coastal breeding locations was 620 km (range 113-1,512 km) and for inland locations was 546 km (range 59-1610 km). In contrast, the average distances between inland and coastal breeding locations was 1,443 km (range 135-2,449 km).

3.2 Migration Phenology

Dates of departure and arrival did not differ statistically for spring migration between coastal-wintering and inland-wintering groups (Table 1; departure: $U = 27.5$, $P = 0.43$; arrival: $U = 25$, $P = 0.31$). The average duration of spring migration for coastal-wintering birds did not differ statistically from the average duration for inland-wintering birds (Table 1; $t = 0.34$, $df = 15$, $P = 0.74$). Dates of departure and arrival also did not differ statistically for fall migration between coastal-wintering and inland-wintering groups (Table 1; departure: $U = 33$, $P = 0.81$; arrival: $U = 30.5$, $P = 0.82$). The average duration of fall migration for coastal-wintering birds did not differ statistically from the average duration for inland-wintering birds (Table 1; $t = -1.0$, $df = 7.5$, $P = 0.33$). See Sup. Mat. Table S1 for arrival and departure dates for each tagged bird.

Table 1. Migration phenology for coastal- and inland wintering Golden-crowned Sparrows fitted with light-level geolocators on their winter grounds in California. The earliest and latest migration dates calculated for spring and fall are shown with the median date for each group in parenthesis. Average number of days spent on migration (duration) is shown in days for each group.

Winter Location	N	Spring Departure	Spring Arrival	Spring Duration (d)
coastal	9	23 Apr - 8 May (2 May)	16 May - 4 June (20 May)	23
inland	8	19 Apr - 12 May (25 Apr)	5 May - 28 May (21 May)	22.8
		Fall Departure	Fall Arrival	Fall Duration (d)
coastal	8	30 Aug - 23 Sep (11 Sep)	21 Sep - 18 Oct (4 Oct)	23.3
inland	8 (departure) 7 (arrival)	18 Aug - 20 Sep (11 Sep)	20 Sep - 25 Oct (4 Oct)	31.9

3.3 Migration route, distance, and rate

Coastal-wintering birds followed a coastal route to their breeding grounds (Fig. 2). Even in the initial legs of their migration, these birds appeared to move along or to the west of the crest of the Cascade Mountains, e.g., Mount Shasta, California and Mount Rainier, Washington (Fig. 2). Once they reached Southeast Alaska, their locations were spread along the Gulf Coast of Alaska, with some evidence of weak concentrations of points spaced regularly along this distance (Fig. 2). In contrast, the initial leg of the inland birds was clearly to the east of the crest of the Cascade Mountains, with a cluster of locations east of Mount Rainier, another in the Tumbler Ridge area of British Columbia, and then rapid movement to the breeding grounds (Fig. 2).

Based on the calculated average breeding-season locations for each bird, coastal-wintering birds travelled an average of 3,624 km between winter and breeding grounds, which was significantly farther than the average distance traveled by inland-wintering birds (2,442 km; $t = 5.3$, $df = 15$, $P < 0.001$; Fig. 2). The rate of spring migration for coastal-wintering birds (179 km/d) was significantly greater than the rate of spring migration for inland-wintering birds (118 km/d; $t = 2.4$, $df = 11$, $P = 0.03$). In contrast, the rate of fall migration was not significantly different between the two regions (coastal = 167 km/d; inland = 111 km/d; $t = 2.0$, $df = 9$, $P = 0.08$). See Sup. Mat. Table S1 for migration distance, duration, and rates for each tagged bird.

3.4 Return rates

We recaptured 8 of 14 (57%) tagged inland-wintering birds (of the 15 originally-tagged birds, a ninth individual that was also recaptured was observed without a tag before leaving for the breeding grounds), and 9 of the 23 (39%) tagged coastal-wintering birds were recaptured. The rates

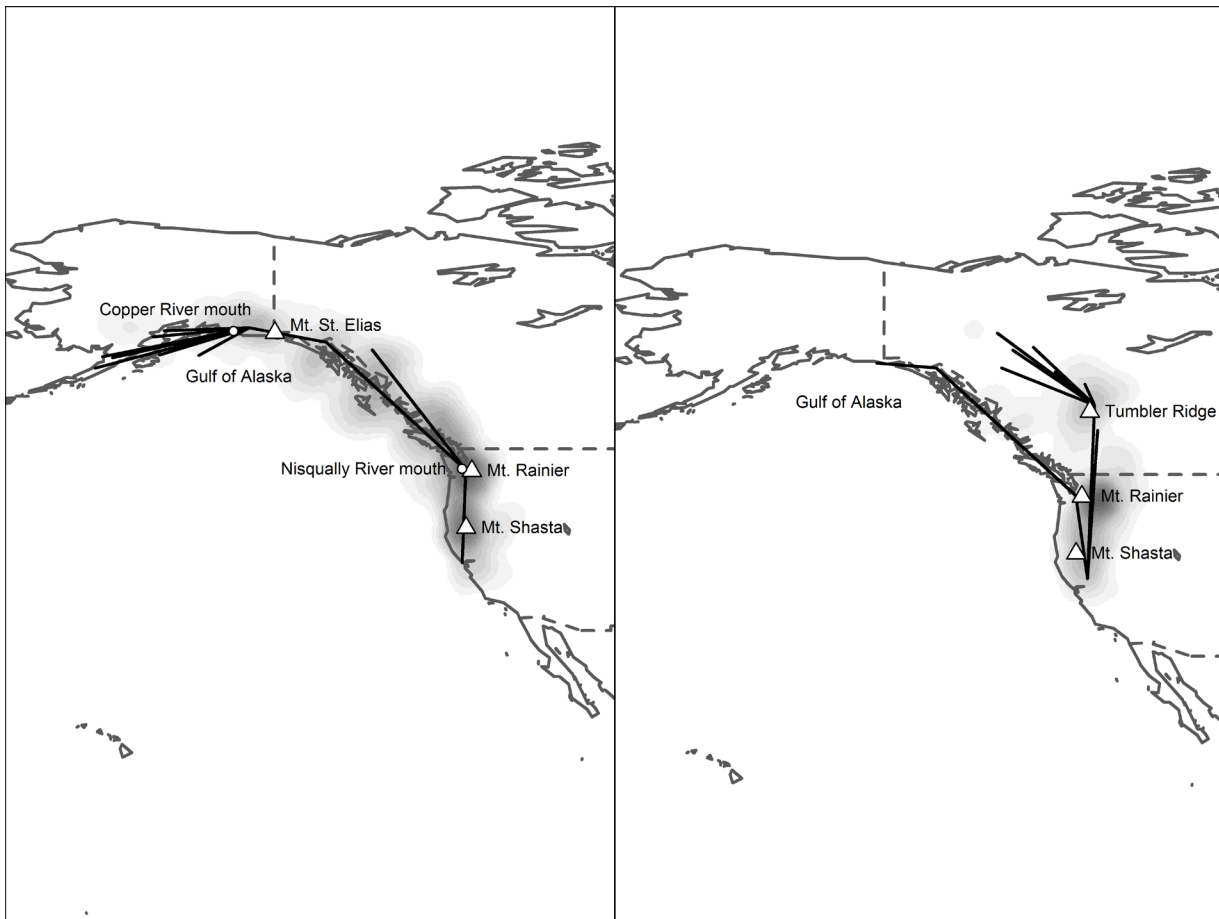


Figure 2. Kernel density estimates encompassing 85% of the maximum density for each Golden-crowned Sparrow fitted with a light-level geolocator during spring migration. Estimated migration routes are shown for birds that wintered at the coastal (left; $n = 9$) and inland (right; $n = 8$) sites. The areas with darker shading represent areas where there were concentrations of locations during the migratory period. The black lines show the migration routes (in segments) used to calculate the great circle distances between breeding and wintering locations.

of return did not differ statistically between the coastal and inland birds ($X^2 = 0.53$, $df = 1$, $P = 0.47$). Nine of the 15 (60%) control birds were detected at each of the coast and inland sites; differences in return rates did not differ statistically between return rates of control and tagged birds at either location (coastal: $X^2 = 0.86$, $df = 1$, $P = 0.35$; inland: $X^2 < 0.001$, $df = 1$, $P = 1$)

4 Discussion

Golden-crowned Sparrows that overwintered in one of two central-California regions of relatively close proximity took different migratory routes and went to breeding sites in predominantly disparate regions. We found that 8 out of 9 coastal-wintering birds migrated along a coastal route and went to breeding sites in coastal areas, while 7 of the 8 inland-wintering birds had a more interior migratory

path and breeding locations. Our findings are consistent with our earlier work that showed four coastal-wintering Golden-crowned Sparrows migrated to coastal breeding areas and followed a coastal migratory route [12]. However, with the larger number of individuals described, here we found that one coastal-wintering bird went to an inland breeding site, and one inland-wintering bird went to a coastal breeding site, revealing that there is some mixing between groups. Nonetheless, this suggests that coastal and inland regions might represent relatively distinct populations on both their summer and winter grounds.

We also found significant correlation between the distances between wintering and breeding sites: birds that wintered close together (e.g., in coastal versus inland California) also migrated to breeding sites that were closer together. Despite the two individuals (one from each wintering location) that migrated to the opposing breeding regions, these results suggest that Golden-

crowned Sparrows exhibit relatively strong migratory connectivity. Although only a few studies have used this method to quantitatively measure migratory connectivity for passerines, the ability of researchers to compare among and within species should increase with the increased use of geolocators [9,19,24].

We suggest that the patterns we observed may represent a migratory divide on the wintering grounds of the Golden-crowned Sparrow (a migratory divide is the zone of contact between populations that migrate in divergent directions [25,26]). Most evidence of migratory divides has been evaluated for adjacent breeding populations that migrate to dramatically different winter locations (e.g., Swainson's Thrush, *Catharus ustulatus* [27,28,29], Blackcap, *Sylvia atricapilla* [30], Willow Warblers, *Phylloscopus trochilus* [31]). However, there are other examples of species for which individuals from disparate breeding populations converge to winter in close proximity to each other (e.g., White-crowned Sparrow, *Zonotrichia leucophrys* [32,33] and Fox Sparrow, *Passerella iliaca* [34] subspecies that breed in distinct regions overlap in parts of their winter ranges), suggesting the possibility that across relatively short distances on the wintering grounds, the representation of individuals from different breeding populations may change dramatically. One of the main points of interest of migratory divides on breeding grounds is the existence of a contact zone, where there is the potential for speciation and/or hybridization [29,30]; while this would not occur for adjacent wintering populations that migrate in divergent directions to breed, there may be other ecological and evolutionary differences between the groups. To our knowledge, the existence of a migratory divide has not been described from a wintering-grounds perspective before, but we propose that this concept can also be applied to wintering birds. Because our inland and coastal sites were 170 km apart, it may be clarifying to determine the breeding locations and migratory routes for birds wintering in between these two regions (e.g., in California's Central Valley).

While there are no described subspecies of Golden-crowned Sparrow, different songs have been described in their breeding range [10], which suggests some degree of segregation. A recent analysis demonstrated that across the breeding range, Golden-crowned Sparrows exhibit at least 5 major song types, with individuals breeding on the Gulf Coast of Alaska having a distinctly different song from those in the interior [11]. The different songs, combined with distinct migratory routes suggest that the individuals from these two wintering locations may exhibit differences that extend beyond their migratory tendencies.

Despite breeding and wintering in different locations, we found no difference in migration departure or arrival dates between inland and coastal Golden-crowned Sparrows, nor in the number of days spent on migration. However, coastal-wintering birds migrated farther than inland-wintering birds and their rates of spring migration differed significantly, with coastal birds travelling, on average, more distance per day of migration. With farther to travel, coastal birds had more stopover sites, which may have accounted for the difference in rate of spring migration if they spent less time at each stopover site, accounting for the greater distance per day (Fig 2). Marra et al. [35] found that median spring arrival dates were one day earlier than the long-term average for every 1°C increase in spring temperature, suggesting that the timing of migration can be flexible and weather related. It is possible that cold or adverse weather conditions through the interior mountains prevented inland-wintering birds from migrating at the same rate as coastal birds, and also that this difference in rate may not persist in all years depending on interannual weather patterns. Alternatively, it is possible that wintering-site quality or stopover-site quality differs between coastal and inland areas, and that inland-wintering birds needed additional time at stopover sites to acquire enough fuel [36,37]; in a recent study using radio-tagged migrants, the fat score during the initial capture at a stopover site had a positive effect on probability of departure [38].

The rate of return for inland Golden-crowned Sparrows (57%) was higher than the coastal birds (39%), but the difference was not significant, nor was the difference between the return rate of tagged birds versus control birds (60% for both coastal and inland control groups). To date, a number of geolocator studies have reported no statistical difference in return rates between tagged and control birds [12,24,39,40], but see [39,41,42]. Negative effects to breeding have been found in some studies, including greater fledgling mortality the year after tagging [43], later egg laying and lower nest success [41], although this was not the case for all species [42]. We recommend continued evaluation of tag effects as studies increase their sample sizes, and as more species with different life histories are fitted with geolocators.

For the Golden-crowned Sparrow, birds from relatively close winter populations may experience different conditions throughout their annual cycle, and it is possible that these two groups will also face differences in how their environments change under future conditions. In light of our results showing different breeding locations and migratory routes between birds from two wintering locations, we suggest that there may

be more structuring in the migratory geography of the Golden-crowned Sparrow than in a simple panmictic population. Continued studies of the full-annual cycles of animals will be crucial to understanding the consequences of habitat loss and climate change on migratory bird populations.

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Supplemental Material: The online version of this article

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Supplemental Material

Table S1. Data for each tag including winter locations, mean estimates of summer locations, calibration period, date of tagging, date of recapture, the Merge Sites (MS) number determined to be the breeding period calculated in the GeoLight package [16] in R, departure date/arrival date/duration for spring and fall migration, elevation angles used to estimate locations, total great circle distance between winter and summer locations, and rate of spring and fall migration. Dates in bold type were adjusted using resighting data from uniquely color banded birds, after processing locations using changeLight and mergeSites functions in R; for all arrival and departure dates not bolded, resighting data did not affect dates derived from changeLight and mergeSites functions.

Tag	Winter Site	Lon Winter	Lat Winter	Mean Lon Summer	Mean Lat Summer	Calibration Period	Date of Tagging	Date of Recapture	MS.site used as Breeding Site	Spring Departure	Spring Arrival	Duration Spring Migration (d)	Fall Departure	Fall Arrival	Duration Fall Migration (d)	Elevation Angle	Total Distance (Great Circle; km)	Rate Spring Migration (km/d)	Rate Fall Migration (km/d)
C588	INLAND	-121.19	38.88	-126.47	61.38	MARCH	4-Jan-13	15-Oct-13	3	26-Apr-13	16-May-13	20	15-Sep-13	26-Sep-13	11	-3.27	2600	130	236
C579	INLAND	-121.19	38.88	-129.57	59.36	FEBRUARY	4-Jan-13	16-Oct-13	4	4-Apr-13	5-May-13	16	15-Sep-13	4-Oct-13	19	-2.1	2564	160	134
C595	INLAND	-121.19	38.88	-120.22	53.11	MARCH	4-Jan-13	6-Nov-13	3	9-May-13	25-May-13	16	20-Sep-13	na	na	-3.8	1584	99	na
C591	INLAND	-121.19	38.88	-124.38	58.98	MARCH	4-Jan-13	6-Nov-13	3	23-Apr-13	23-May-13	30	8-Sep-13	25-Sep-13	17	-3.62	2315	77	136
C585	INLAND	-121.19	38.88	-129.99	62.75	MARCH	4-Jan-13	20-Nov-13	4	25-Apr-13	22-May-13	27	31-Aug-13	25-Oct-13	55	-3.91	2832	105	51
C584	INLAND	-121.19	38.88	-141.72	59.84	MARCH	4-Jan-13	14-Dec-13	6	19-Apr-13	20-May-13	31	18-Aug-13	20-Oct-13	63	-3.72	2877	93	46
C574	INLAND	-121.19	38.88	-128.49	61.11	MARCH	4-Jan-13	14-Dec-13	3	12-May-13	28-May-13	16	14-Sep-13	22-Oct-13	38	-3.78	2643	165	70
C590	INLAND	-121.19	38.88	-121.45	57.79	MARCH	4-Jan-13	11-Jan-14	2	26-Apr-13	14-May-13	18	31-Aug-13	20-Sep-13	20	-4.05	2116	118	106
C721	COAST	-122.68	37.91	-156.75	57.86	MARCH	19-Feb-13	23-Oct-13	4	1-May-13	20-May-13	19	9-Sep-13	3-Oct-13	24	-2.27	3915	206	163
C696	COAST	-122.68	37.91	-156.09	57.46	MARCH	26-Feb-13	27-Oct-13	4	2-May-13	29-May-13	27	8-Sep-13	26-Sep-13	18	-2.71	3904	145	217
C693	COAST	-122.68	37.91	-131.44	58.62	MARCH	19-Feb-13	27-Oct-13	3	8-May-13	16-May-13	8	23-Sep-13	4-Oct-13	11	-3.19	2437	305	222
C717	COAST	-122.68	37.91	-152.80	59.88	MARCH	19-Feb-13	29-Oct-13	2	23-Apr-13	19-May-13	26	14-Sep-13	4-Oct-13	20	-2.81	3619	139	181
C707	COAST	-122.68	37.91	-158.45	56.85	MARCH	26-Feb-13	8-Nov-13	3	6-May-13	27-May-13	21	12-Sep-13	12-Oct-13	30	-3.78	4060	193	135
C710	COAST	-122.68	37.91	-151.71	60.49	MARCH	25-Feb-13	22-Nov-13	3	6-May-13	20-May-13	14	21-Sep-13	15-Oct-13	24	-3.76	3547	253	148
C724	COAST	-122.68	37.91	-152.17	58.14	MARCH	22-Feb-13	11-Nov-13	4	23-Apr-13	20-May-13	27	30-Aug-13	21-Sep-13	22	-3.46	3667	136	167
C706	COAST	-122.68	37.91	-157.73	57.95	MARCH	23-Jan-13	9-Jan-14	8	6-May-13	4-Jun-13	29	11-Sep-13	18-Oct-13	37	-3.42	3961	137	107
C687	COAST	-122.68	37.91	-148.36	58.08	MARCH	23-Jan-13	8-Apr-14	6	25-Apr-13	31-May-13	36	na	na	na	-3.6	3503	97	na

Table S2. Locations used to calculate migration distance for each geolocator-tagged Golden-crowned Sparrow. We calculated the great circle distance between winter and summer location estimates (Lon Winter/Lat Winter and Mean Lon Summer/Mean Lat Summer). We calculated great circle distances in segments to better-reflect the actual non-linear migration pathways, and between 0-3 additional locations were added depending on the summer location (e.g., Stop 1 Lat/Stop 1 Lon).

Tag	Winter Site	Lon Winter	Lat Winter	Stop 1 Lat	Stop 1 Lon	Stop 2 Lat	Stop2 Lon	Stop 3 Lat	Stop 3 Lon	Mean Lon Summer	Mean Lat Summer
C588	INLAND	-121.19	38.88	55.75	-120.19	NA	NA	NA	NA	-126.47	61.38
C579	INLAND	-121.19	38.88	55.75	-120.19	NA	NA	NA	NA	-129.57	59.36
C595	INLAND	-121.19	38.88	NA	NA	NA	NA	NA	NA	-120.22	53.11
C591	INLAND	-121.19	38.88	55.75	-120.19	NA	NA	NA	NA	-124.38	58.98
C585	INLAND	-121.19	38.88	55.75	-120.19	NA	NA	NA	NA	-129.99	62.75
C584	INLAND	-121.19	38.88	46.94	-122.33	59.36	-135.92	NA	NA	-141.72	59.84
C574	INLAND	-121.19	38.88	55.75	-120.19	NA	NA	NA	NA	-128.49	61.11
C590	INLAND	-121.19	38.88	55.75	-120.19	NA	NA	NA	NA	-121.45	57.79
C721	COAST	-122.68	37.91	46.94	-122.33	59.36	-135.92	60.77	-143.42	-156.75	57.86
C696	COAST	-122.68	37.91	46.94	-122.33	59.36	-135.92	60.77	-143.42	-156.09	57.46
C693	COAST	-122.68	37.91	46.94	-122.33	NA	NA	NA	NA	-131.44	58.62
C717	COAST	-122.68	37.91	46.94	-122.33	59.36	-135.92	60.77	-143.42	-152.80	59.88
C707	COAST	-122.68	37.91	46.94	-122.33	59.36	-135.92	60.77	-143.42	-158.45	56.85
C710	COAST	-122.68	37.91	46.94	-122.33	59.36	-135.92	60.77	-143.42	-151.71	60.49
C724	COAST	-122.68	37.91	46.94	-122.33	59.36	-135.92	60.77	-143.42	-152.17	58.14
C706	COAST	-122.68	37.91	46.94	-122.33	59.36	-135.92	60.77	-143.42	-157.73	57.95
C687	COAST	-122.68	37.91	46.94	-122.33	59.36	-135.92	60.77	-143.42	-148.36	58.08