Two species of montane redstarts (*Myioborus*) in Costa Rica differ in their elevational range shifts over four decades

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ABSTRACT—Tropical montane bird species may be vulnerable to climate change as they often have narrow elevational ranges that are expected to shift upslope in response to increasing temperatures. If highland endemics near mountaintops are forced upslope, these species may be especially at risk of local extinction. We investigated the elevational ranges of two species of montane cloud forest warblers, the Slate-throated Redstart (*Myioborus miniatus*) and the Collared Redstart (*M. torquatus*), in Costa Rica between 1980 and 2019. The Collared Redstart is a highland endemic that has been projected to go locally extinct from climate change. We examined 11,856 and 7,366 checklists from sites where the Slate-throated Redstart and the Collared Redstart, respectively, have been reported to eBird, a community science project managed by the Cornell Lab of Ornithology. As expected, we found that the two species' elevational ranges were different from each other but overlapped, with the Collared Redstart showing a peak rate of detection at an elevation about 750 m to 1,050 m higher than the Slate-throated Redstart. More important, only the Slate-throated Redstart showed a shift upward in its elevation of peak detection over time. This inconsistent response to climate change reinforces the growing evidence that the impacts of climate change on tropical montane bird species are complex and difficult to forecast. Continuing to study the elevational ranges of tropical montane bird species is vital for our understanding of these birds' responses to climate change.

Keywords: climate change, cloud forest, *Myioborus miniatus*, *Myioborus torquatus*, tropics, upslope shifts.

Tropical montane bird species often have narrow elevational distributions and are habitat specialists (Stotz et al. 1996; Jankowski and Rabenold 2007; Jankowski et al. 2009, 2010). These species may be vulnerable to climate change (Şekercioğlu et al. 2008, Jankowski et al. 2010, Neate-Clegg et al. 2021b, Girish and Srinivasan 2022), and climate change may exacerbate the conservation status of already threatened species (Şekercioğlu et al. 2012). Numerous tropical montane species, such as high-elevation specialists endemic to Indonesia and nearly half of the forest bird species in the Tilarán mountains of Costa Rica, have been predicted to decline in abundance or to go extinct (Şekercioğlu et al. 2008, 2012; Gasner et al. 2010; Harris et al. 2012; Velásquez-Tibatá et al. 2013). In addition, population declines have already been observed in some tropical montane bird species (Pounds et al. 1999, 2005; Freeman et al. 2018).

Although the direct and indirect effects of climate change on tropical montane bird species' elevational ranges are not fully understood (Pounds et al. 2005, Londoño et al. 2017, Neate-Clegg et al. 2021a), these species are expected to move upslope into reduced geographic ranges in response to increasing temperatures (Parmesan and Yohe 2003, Shoo et al. 2005, Gasner et al. 2010, Forero-Medina et al. 2011, Şekercioğlu et al. 2012, Velásquez-Tibatá et al. 2013, Freeman et al. 2018, Neate-Clegg et al. 2021b). If highland endemics and other species that live near mountaintops are forced upslope, they may be especially at risk of local extinction (Pimm et al. 2006, Gasner et al. 2010, Forero-Medina et al. 2011, Şekercioğlu et al. 2012, Rosselli et al. 2017). In addition, if dominant competitors from lower elevations move upslope, high-elevation subordinate species may be forced into smaller ranges, threatening the viability of their populations (Jankowski et al. 2010). Upslope shifts have recently been observed across a range of tropical bird species in the Andes (Forero-Medina et al. 2011, Rosselli et al. 2017), Himalayas (Girish and Srinivasan 2022), East Africa (Neate-Clegg et al. 2020, Neate-Clegg et al.

2021b), and elsewhere (e.g., Campos-Cerqueira et al. 2017, Williams and de la Fuente 2021). These shifts include not only high-elevation species moving upslope but also lowland species moving into the uplands (Pounds et al. 1999, 2005; Williams and de la Fuente 2021). However, some studied species have not moved upslope, and some even appear to have shifted to lower elevations (Campos-Cerqueira et al. 2017; Neate-Clegg et al. 2021a, 2021b). Species that do not appear to have shifted upslope may be lagging behind warming due to complex responses of ecosystems to climate change (Jankowski et al. 2010, Forero-Medina et al. 2011, Alexander et al. 2018, Freeman et al. 2018, Neate-Clegg et al. 2020), though it is also possible that temperature may not be the primary driver in elevational range shifts for many birds (Currie and Venne 2017, Neate-Clegg et al. 2020).

Climate change encompasses more than just temperature, and temperature need not be the only feature of climate change influencing bird distributions. For instance, precipitation may be a better predictor than temperature of changing patterns of bird occurrence in some tropical systems (Neate-Clegg et al. 2020). We might particularly expect sensitivity to changing precipitation in tropical montane cloud forests that rely on consistent cloud cover, which provides frequent mists, reduces solar radiation, and suppresses evapotranspiration (Pounds et al. 1999, Still et al. 1999, Karmalkar et al. 2008, Nair et al. 2008). With climate change, cloud banks may form at higher altitudes, thus leaving former cloud forests moisture-stressed, especially during the dry season (Still et al. 1999, Karmalkar et al. 2008). Declines in dry season mists in Costa Rican cloud forests have already been implicated in upslope shifts and declines in populations of both the Resplendent Quetzal (*Pharomachrus mocinno*) and the Golden Bellied Flycatcher (*Myiodynastes hemichrysus*) (Pounds et al. 1999, 2005).

Two other cloud forest residents in Costa Rica potentially at risk from climate change are the congeneric Slate-throated Redstart (*Myioborus miniatus*) and Collared Redstart (*M. torquatus*) (Henderson 2010). The Slate-throated Redstart can be found from Northern Mexico to Peru and is common in Costa Rica at middle elevations from 700 m to 2100 m (Henderson 2010, Garrigues 2014). The Collared Redstart, a high-elevation specialist, is endemic to Costa Rica and Western Panama and is common between 1500 m and timberline (Henderson 2010, Garrigues 2014). Rising cloud banks may have forced these species to move upslope to seek out suitable habitat, and the Collared Redstart, as a highland endemic, may be especially at risk of local extinction. Gasner et al. (2010) projected the Collared Redstart would move upslope, go locally extinct, and have one of the largest declines in abundance of all forest birds in Costa Rica. In fact, the Collared Redstart has already disappeared from one 40 hectare cloud forest site in Monteverde (Pounds et al. 2005).

We investigated the elevational ranges of the Slate-throated Redstart and the Collared Redstart in Costa Rica between 1980 and 2019, using observations from eBird, a community science project of the Cornell Lab of Ornithology. We expected overlap in the elevational ranges of the two species but a higher average elevation for the Collared Redstart. More important, we expected that, due to the effects of a warming climate, the elevational ranges and peaks of occurrence of both species had shifted upward between an earlier time period (1980-2004) and a later time period (2015-2019).

Methods

We identified the elevational distributions of the Slate-throated Redstart and the Collared Redstart in Costa Rica using datasets retrieved from eBird, a community science project managed by the Cornell Lab of Ornithology. Although eBird was launched in 2002, observers may submit historical data, and so observations extend to earlier decades (Cornell Lab of Ornithology 2021). eBird is among the world's largest biodiversity-related science projects, with more than 100 million bird sightings contributed annually by birders around the world (Cornell Lab of Ornithology 2021). Birders enter when, where, and how they went birding, and they fill out a checklist of the birds seen or heard during the outing. In addition, experts review checklists to improve data quality (Cornell Lab of Ornithology 2021).

From eBird, we accessed data through September 2020, including a sampling event dataset with all of the checklists ever submitted to eBird globally and all of the Slate-throated Redstart and Collared Redstart sightings ever submitted in Costa Rica (Cornell Lab of Ornithology 2020).

We filtered the data to eliminate entries inappropriate for our analyses. We first filtered for the protocol type (method of observation/data gathering) for each checklist. We only included protocols that we expected to have a low probability of bias, including traveling, stationary, historical, random, and area counts (see Appendix A for a list of eBird protocols). These protocols all produced lists of species regardless of whether our target species were detected, therefore allowing us to compare lists with and without our target species to determine rates of detection at different elevations. We excluded data from the 'incidental' protocol because submissions of these lists are more likely to depend on the species detected.

In addition, we filtered the data for the locality type recorded with each checklist and only included locations in the 'hotspot' category (see Appendix B for a complete list of eBird locality types). Hotspots are frequent birding locations nominated by eBird users. When eBird users are presented with a map and asked to identify their birding location, one option is to select an existing hotspot. Therefore, each hotspot typically has multiple checklists associated with it, and so we could treat each list from a given hotspot as a separate sampling event at that location and compare proportions of detections of our target species across elevations or time periods. Also, each hotspot is defined by a single latitude and longitude coordinate and, therefore, a single elevation. Of course, the birding area associated with each hotspot varies in elevation, especially at the montane sites in our study, but we assumed that the range in reported elevations among hotspots is much greater than the typical range of elevations explored by birders within hotspots. We found the elevation of each hotspot at which at least one of the two focal species was observed at least once using GPS Visualizer at https://www.gpsvisualizer.com/elevation (Schneider 2019).

To examine the possibility of elevational range shifts over time, we created an earlier time period from 1980-2004 and a later time period from 2015-2019. The scope of our data for the earlier time period was shaped by the availability of data, which was dramatically sparser further back in time. We excluded checklists from prior to 1980 because there were so few. The later time period spans 5 years, while the earlier time period includes 25 years to ensure similarly large datasets from both periods. In addition, we excluded checklists from 2005-2014 to allow for a 10 year gap to increase our ability to detect changes in elevational ranges between the earlier and later periods.

We created four datasets for analysis. Two datasets, one with data from the earlier time period (1980-2004) and one with data from the later time period (2015-2019), included all hotspots at which at least one of the two focal species was observed at least once during the relevant time period. These two datasets included the number of checklists at each hotspot and the number of checklists each species was detected in at each hotspot. Two additional datasets, one with data on the Slate-throated Redstart and one with data on the Collared Redstart, included all of the hotspots at which at least one member of the relevant species was detected in at least one of the two time periods. These two datasets included the number of checklists at each hotspot in each time period and the number of checklists the relevant species was detected in at each hotspot in each time period.

We compared the elevational ranges between the two species in two separate analyses, one with the dataset from the earlier time period (1980-2004) and one with the dataset from the later time period (2015-2019). We used a generalized linear model with binomial error and a logit link. The dependent variable was the ratio of the number of checklists in which each species was detected to the number of checklists for which each species was not detected at each hotspot during the given time period. The independent variables were species, elevation, elevation^2, species×elevation, and species×elevation^2. The quadratic term for elevation accounted for the expected humped shape of the relationship between elevation and detections. We included the interaction terms to assess the likely possibility that the slope of the relationship between elevation and detections differed between the two species. We used the predict function in R to generate predicted detection rate and accompanying standard error values based on our fitted statistical models across the range of elevations in our data set. We then graphed these values to visualize the elevational ranges of both species.

We compared the elevational range of each of the focal species between the earlier time period (1980-2004) and the later time period (2015-2019) in two separate analyses, one for each species. We used the same type of generalized linear model with binomial error and logit link as the previous analyses. The dependent variable was the ratio of the number of checklists in which the relevant species was detected to the number of checklists the relevant species was not detected in at each hotspot during each time period. The independent variables were time period, elevation, elevation^2, time period×elevation, and time period×elevation^2. The interaction terms assessed the possibility that the relationship between elevation and detections differed between the two time periods for each of the species. We used the predict function in R to generate predicted detection rate and accompanying standard error values based on our fitted statistical models across the range of elevations in our data set. We then graphed these values to visualize the elevational ranges of both species in both time periods.

To promote transparency, we registered our analyses prior to conducting them (Steinmetz and Parker 2021). Deviations from our registration are small and are due to an error on our registered model specification. The function of the code remained the same as we intended in our registration because after our corrections, the response variable was weighted by default according to the number of observations. In addition, we did not register the curves we fitted based on the parameter estimates to visualize the outcomes of the model. The rest of our methods are consistent with our registration (Steinmetz and Parker 2021).

Results

We first compared the elevational ranges between the two species in two separate analyses, one with data from the earlier time period (1980-2004) and one with data from the later time period (2015-2019). During the earlier time period, there were 115 hotspots at which at least one of the two species was observed at least once. From those 115 hotspots, there were 9,352 total checklists. Out of these checklists, 1,345 contained the Slate-throated Redstart, and 872 contained the Collared Redstart. During the later time period, there were 280 hotspots at which at least one of the two species was observed at least once. From those 280 hotspots, there were 119,664 total checklists. Out of these checklists, 10,511 contained the Slate-throated Redstart, and 6,494 contained the Collared Redstart. The graphed curves of the rate of detection of each species across elevations substantially differed between the two species during both the earlier and later time periods (Fig. 1, Table 1). Both species had a peak rate of detection at intermediate elevations. The Collared Redstart had a peak rate of detection about 1,050 m higher than the Slate-throated Redstart during the earlier time period and about 750 m higher during the later time period.

We compared the elevational range of the Slate-throated Redstart between the earlier time period (1980-2004) and the later time period (2015-2019). There were 270 hotspots at which the Slate-throated Redstart was observed at least once during at least one of the time periods. From those 270 hotspots, there were 63,799 total checklists, and of those checklists, 11,856 contained the Slate-throated Redstart. The graphed curves of the rate of detection of the Slate-throated Redstart across elevations substantially differed in shape between the two time periods (Fig. 2, Table 1). The curve for the later time period showed some evidence of a shift upward into higher elevations. The Slate-throated Redstart had a peak rate of detection at an intermediate elevation during both of the time periods, and this peak rate of detection was about 150 m higher during the later time period than during the earlier time period. However, the curve for the later time period indicated a narrower elevational range than the curve for the earlier time period, and the maximum elevation for detection during the later time period was lower than the maximum elevation for detection during the earlier time period.

We compared the elevational range of the Collared Redstart between the earlier time period (1980-2004) and the later time period (2015-2019). Across both time periods, there were 163 hotspots at which the Collared Redstart was observed at least once. From those 163 hotspots, there were 43,301 total checklists, and of those checklists, 7,366 contained the Collared Redstart.

The graphed curves of the rate of detection of the Collared Redstart across elevations substantially differed in shape between the two time periods (Fig. 3, Table 1). However, the curve for the later time period did not show a clear shift upward into higher elevations. The Collared Redstart had a peak rate of detection at an intermediate elevation during both of the time periods, but this peak rate of detection was about 150 m lower during the later time period than during the earlier time period. The curve for the later time period indicated a narrower elevational range than the curve for the earlier time period, and the maximum elevation for detection during the later time period was lower than the maximum elevation for detection during the earlier time period.

Discussion

We found that Collared Redstarts were detected at higher elevations on average than Slate-throated Redstarts over several decades, but only the Slate-throated Redstart appeared to have shifted its elevation of peak detection upslope over time. The clear difference in elevations between the two species was expected, and is a valuable validation of our method of using eBird hotspot records to detect patterns in these species' elevational ranges. Thus, despite our surprise in failing to find a shift upward in the elevational range of the highland endemic Collared Redstart over time, we are confident in this result. Further, recent work with other bird species in tropical highlands around the world suggests that our finding of inconsistent elevational shifts among species may be the norm (Neate-Clegg et al. 2020; Neate-Clegg et al. 2021a, 2021b).

As expected, our two study species had different elevational ranges that overlapped, and the Collared Redstart was observed at higher elevations than the Slate-throated Redstart consistently over several decades. Our graphs showed elevational ranges for both species that are consistent with Costa Rican field guides (Henderson 2010, Garrigues 2014). Again, this finding shows that our method of using eBird hotspots and checklists is reasonable and sufficient to detect patterns in these species' elevational ranges.

More important, our results did not show consistent shifts upward in the two species' elevational ranges over time. Although the peak rate of detection of the Slate-throated Redstart was at a higher elevation during the later time period than during the earlier time period, the maximum elevation for detection was lower for both species during the later time period, and the peak rate of detection of the Collared Redstart was at a slightly lower elevation during the later time period. These results lend only mixed support to the projected upslope shifts of tropical montane bird species in response to climate change (Parmesan and Yohe 2003, Gasner et al. 2010, Forero-Medina et al. 2011, Şekercioğlu et al. 2012, Velásquez-Tibatá et al. 2013). However, our results are in line with a growing body of work showing inconsistent shifts in elevation by tropical montane bird species in response to climate change (Neate-Clegg et al. 2020; Neate-Clegg et al. 2021a, 2021b). Interestingly, of our two study species, it was the endemic Collared Redstart that had been forecasted to be particularly susceptible to climate change (Gasner et al. 2010), but it was the widespread Slate-throated Redstart that showed signs of upslope movement. The Slate-throated Redstart's shift upslope in its elevation of peak detection of about 150 m is equivalent to between 15 m per year (if we consider only the 10 year gap between our two sampling periods) and 5 m per year (if we consider the full 30 year span of our data). These estimates are within the range of values reported in other recent studies of tropical montane birds (Neate-Clegg et al. 2020; Neate-Clegg et al. 2021a, 2021b).

When bird species do not show predicted upslope shifts as the climate warms, it may be that they are instead responding to other climate variables, or to ecological variables impacted by climate in complex ways (Currie and Venne 2017, Neate-Clegg et al. 2020). The potential mechanisms behind climate change impacts on our two study species are not well understood, and species' responses may depend on complex interactions within the cloud forest ecosystem (Pounds et al. 2005, Londoño et al. 2017). It is reasonable to hypothesize that birds often respond to the distribution of tree species, which of course are relatively long-lived and thus are presumably limited to shift their distributions more slowly in response to climate change (Forero-Medina et al. 2011, Alexander et al. 2018, Neate-Clegg et al. 2020). Of course, redstarts' upslope movements may also especially depend on the availability of insects (Forero-Medina et al. 2011, Şekercioğlu et al. 2012), their main food source (Henderson 2010), or complex biotic interactions, such as interspecific competition (Terborgh and Weske 1975, Jankowski et al. 2010, Forero-Medina et al. 2011, Şekercioğlu et al. 2012). It is also unclear what the direct impact of temperature on these birds might be. Such direct effects might be weak if endothermy allows a flexible response to temperature changes (Forero-Medina et al. 2011). More detailed study of these redstarts' ecological niches, their tendencies to disperse, and the responses of the Costa Rican cloud forests themselves to climate change may be required to better forecast the responses of these bird species to climate change (Neate-Clegg et al. 2020, Neate-Clegg et al. 2021a).

Also notable was our observation that the elevational range curves for both species were narrower in the more recent time interval. These narrower elevational ranges during the later decades matched those in field guides for both species (Henderson 2010, Garrigues 2014). Interestingly, previously observed reductions in elevational ranges of tropical montane birds have been associated with upslope shifts (Freeman et al. 2018), but of course we observed a shift upward in only one of our two species. Instead, the indicated reductions in the two species' elevational ranges may have been driven by differences in how data were gathered between the two time periods. The dataset for the earlier time period may have been less geographically reliable than the dataset for the later time period because most of the data from the earlier time period (1980-2004) were gathered before eBird was launched in 2002 (Cornell Lab of Ornithology 2021). These older data would have been entered based on historical notes which may have been less geographically precise than eBird entries made at the time of observation.

Our results add to a growing body of evidence that responses of individual species to climate change may be more complex than are sometimes assumed. At the very least, our results should encourage empirical evaluation of forecasts regarding impending declines or extinctions due to climate change (e.g., Şekercioğlu et al. 2008, 2012; Gasner et al. 2010). Many tropical montane bird species do seem to be shifting their ranges upslope as climate changes, but many others are not, and the causal mechanisms determining elevational ranges of these species remain largely uncertain (Pounds et al. 1999, 2005; Peh 2007; Freeman et al. 2018; Neate-Clegg et al. 2021a, 2021b; Williams and de la Fuente 2021; Girish and Srinivasan 2022). Tropical ecosystems are complex, and predicting the outcome of changes in ecological interactions due to climate change is difficult (Pounds et al. 2005, Londoño et al. 2017, Neate-Clegg et al. 2020, Neate-Clegg et al. 2021a). Continuing to research the elevational ranges of tropical montane bird species is vital for our understanding of the effects of climate change on these species. This research is important for our ability to forecast future biological responses and for the conservation of these species.

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Table 1. The results of four analyses of the rates of detection of the Slate-throated Redstart and the Collared Redstart across elevations in Costa Rica. These analyses are generalized linear models with binomial error and logit link. The first analysis compares the elevational ranges between the Slate-throated Redstart and the Collared Redstart during an earlier time period from 1980-2004. The second analysis compares the elevational ranges between the two species during a later time period from 2015-2019. The third and fourth analyses compare the elevational range of each species separately between the two time periods.

Analysis	Variable	Estimate	Standard error	z	P-value
Time period:	Intercept	-6.11	0.32	-19.3	<0.0001
1980-2004	Species	1.98	0.40	4.9	<0.0001
	Elevation	4.53×10^{-3}	3.25×10^{-4}	13.9	<0.0001
	Elevation^2	-9.12×10^{-7}	7.66×10^{-8}	-11.9	<0.0001
	Species × elevation	6.39×10^{-4}	4.76×10^{-4}	1.3	0.18
	Species × elevation^2	-8.70×10^{-7}	1.39×10^{-7}	-6.3	<0.0001
Time period:	Intercept	-18.56	0.27	-69.5	<0.0001
2015-2019	Species	6.79	0.30	22.4	<0.0001
	Elevation	1.57×10^{-2}	2.55×10^{-4}	61.5	<0.0001
	Elevation^2	-3.33×10^{-6}	5.87×10^{-8}	-56.6	<0.0001
	Species × elevation	-1.19×10^{-3}	3.18×10^{-4}	-3.7	0.0002
	Species × elevation^2	-1.22×10^{-6}	8.51×10^{-8}	-14.3	<0.0001
Slate-throated	Intercept	-4.50	0.24	-18.7	<0.0001
Redstart	Time period	-7.13	0.28	-25.5	<0.0001
	Elevation	5.53×10^{-3}	3.35×10^{-4}	16.5	<0. 0001
	Elevation^2	$-1\ .87\times10^{-6}$	1.14×10^{-7}	-16.5	<0.0001
	Time period × elevation	8.69×10^{-3}	3.86×10^{-4}	22.5	<0.0001
	Time period × elevation^2	-2.57×10^{-6}	1.29×10^{-7}	-19.9	<0.0001
Collared	Intercept	-5.56	0.33	-17.1	<0.0001
Redstart	Time period	-12.01	0.42	-28.3	<0.0001
	Elevation	4.03×10^{-3}	3.32×10^{-4}	12.1	<0.0001
	Elevation^2	-8.10×10^{-7}	7.79×10^{-8}	-10.4	<0.0001
	Time period × elevation	1.09×10^{-2}	4.21×10^{-4}	25.8	<0.0001
	Time period × elevation^2	-2.37×10^{-6}	9.80×10^{-8}	-24.2	<0.0001

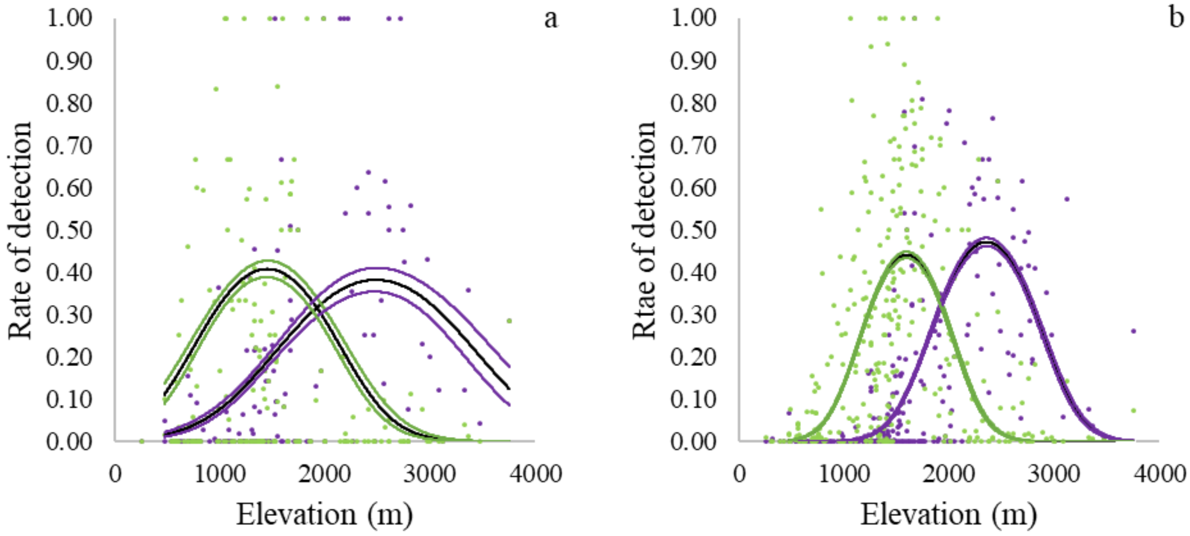

Figure 1. The estimated rates of detection of the Slate-throated Redstart (left curve in each figure, with green confidence intervals) and the Collared Redstart (right curve in each figure, with purple confidence intervals) as a function of elevation from a generalized linear model during (a) an earlier time period from 1980-2004 and (b) a later time period from 2015- 2019. The green and purple curves show the lower and upper bounds of the 95% confidence interval. The shapes of the curves differed between the two species during both of the time periods. Both species had a peak rate of detection at an intermediate elevation during both of the time periods. (a) During the earlier time period, the Slate- throated Redstart had a peak rate of detection at about 1,450 m, and the Collared Redstart had a peak rate of detection at about 2,500 m. (b) During the later time period, the Slate- throated Redstart had a peak rate of detection at about 1,600 m, and the Collared Redstart had a peak rate of detection at about 2,350 m.

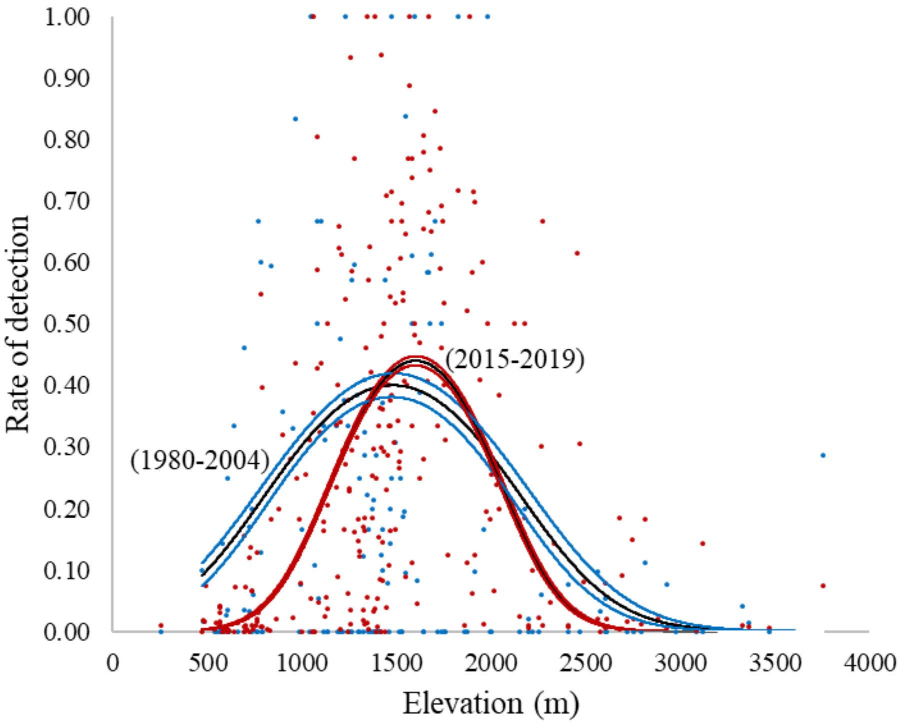

Figure 2. The estimated rate of detection of the Slate-throated Redstart as a function of elevation from a generalized linear model during an earlier time period (1980-2004) and a later time period (2015-2019). The blue and red curves show the lower and upper bounds of the 95% confidence interval for the earlier and later time periods, respectively. The shapes of the curves differed between the two time periods. The Slate-throated Redstart had a peak rate of detection at an intermediate elevation during both of the time periods: at about 1,450 m during the earlier time period and higher during the later time period at about 1,600 m. The curve for the later time period indicated a narrower elevational range than the curve for the earlier time period, and the maximum elevation for detection during the later time period was lower than the maximum elevation for detection during the earlier time period.

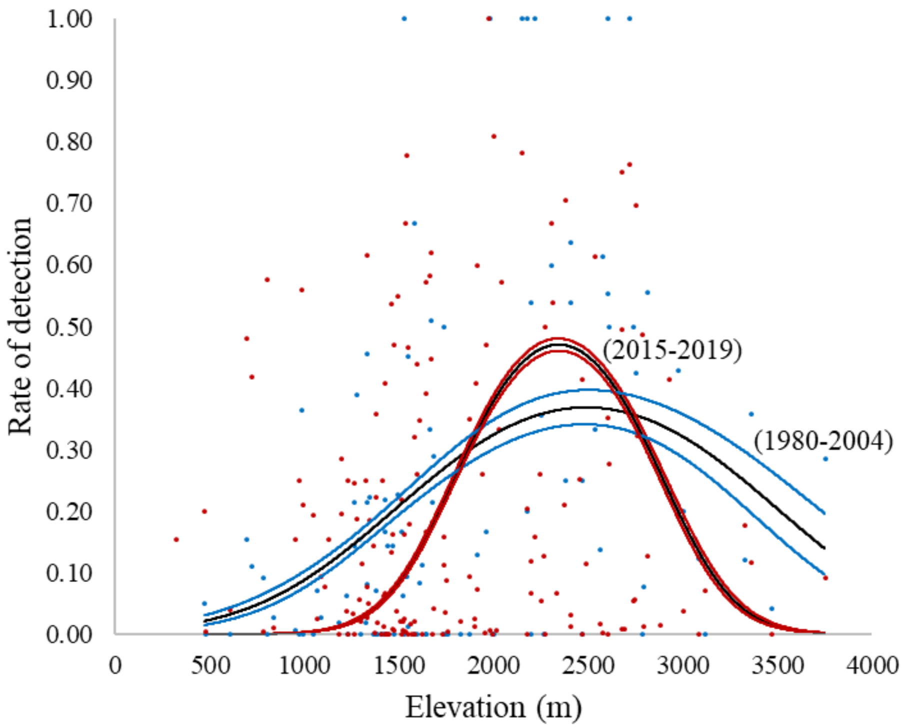

Figure 3. The estimated rate of detection of the Collared Redstart as a function of elevation from a generalized linear model during an earlier time period (1980-2004) and a later time period (2015-2019). The blue and red curves show the lower and upper bounds of the 95% confidence interval for the earlier and later time periods, respectively. The shapes of the curves differed between the two time periods. The Collared Redstart had a peak rate of detection at an intermediate elevation during both of the time periods: at about 2,500 m during the earlier time period and lower during the later time period at about 2,350 m. The curve for the later time period indicated a narrower elevational range than the curve for the earlier time period, and the maximum elevation for detection during the later time period was lower than the maximum elevation for detection during the earlier time period.

Appendix A. A partial list of the current, active protocol types available in eBird for data entry. More common protocols are at the top of the list. For our analyses, we included the protocols traveling, stationary, historical, random, and area counts, but excluded incidental and specialized protocol types not listed here. For additional information about these protocols and for a complete list of more specialized protocol types, see https://support.ebird.org/en/support/solutions/articles/48000950859-guide-to-ebird- protocols.

Protocol	Description
Traveling	Observations made over a known period of time while traveling a known distance
Stationary	Observations made over a known period of time at a single, fixed location (the observer did not go more than 30 m in any direction from the starting point)
Historical	Observations made when birding was the primary focus, but without a known start time, duration, or distance
Incidental	Observations made when birding was not the primary focus, resulting in an incomplete checklist
Area	Observations made for targeted, specialized surveys that exhaustively search a specific area
Random	Observations made at a randomly selected location over a period of at least five minutes

Appendix B. When eBird contributors submit data, they define the type of location by choosing from a list of locality types: hotspots (H), specific locations/personal (P), town (T), postal code (PC), county (C), state (S). For our analyses, we only included data from hotspots because hotspots are already existing locations on eBird maps that eBird has approved, making them more reliable than locations that contributors submit themselves. In addition, each hotspot is defined by a single latitude and longitude coordinate from which we found a single elevation for each hotspot.