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Generating indicator species for bird monitoring within the humid forests of northeast Central America

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Abstract The use of indicator species can simplify bird monitoring by reducing the level of specialized skills needed, which increases the potential pool of participants and reduces training costs and complexity. To facilitate monitoring in the humid forests of northeast Central America, we conducted point count surveys for birds across gradients of disturbance in the Cockscomb Basin Wildlife Sanctuary, Belize, and analyzed the association of bird species with remotely sensed metrics of forest condition and anthropogenic disturbance using indicator species analysis. Twenty species exhibited significant associations with one or more of these metrics. We propose six species as indicators for anthropogenic disturbance based on our criteria of being associated with anthropogenically disturbed sites, or anthropogenically disturbed and riparian sites with no explicit mention in the literature of an obligate association with riparian habitats, or association of remotely sensed metrics that appeared to reflect disturbance: yellow-olive flycatcher, red-legged honeycreeper, dusky antbird, blue ground dove, buff-throated saltator, and brown jay. We propose the keel-billed motmot as an indicator of undisturbed forest based on its association with forested sites in our analyses. Green shrike vireo, collard trogon, rufous-tailed jacamar, and rufous piha were associated with a specific elevational range but not associated with disturbance, so upward shifts in elevation that might indicate response to climate change would not be confounded with habitat disturbance or degradation. This exercise yielded a much-reduced list of monitoring targets, which will greatly reduce the cost and complexity of forest bird monitoring in the region, as well as reducing barriers to participation.

Keywords Belize · Bird · Disturbance · Forest · Habitat · Remote-sensing

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Introduction

The country of Belize is fortunate to have a relatively large proportion of its land area under protection (FAO, 2015). Nevertheless, it is important to ensure that this system of protected areas is accomplishing its intended purpose of conserving the country's biodiversity. Forest-dwelling species are a key element of the fauna encompassed within protected areas, since forest loss and degradation is occurring within the commonwealth (FAO, 2015). Thus, protected forests are only fulfilling their purpose if populations of forest-dwelling species are stable or increasing, and anthropogenic disturbance of forest habitat is minimized. Monitoring can reveal changes over time that could indicate alterations of environmental conditions that might require remediation or show the impacts and effectiveness of intentional management activities to validate or guide their future implementation (Andreasen et al., 2001).

In cases like Belize, where natural communities are extremely diverse, monitoring can be challenging (Hilty & Merenlender, 2000; Wiens et al., 2008). First, identifying all species within a given community, for example, birds in forest in Belize that include hundreds of species, requires advanced skills and experience that require time and resources to develop, and thus are possessed by relatively few individuals. The lack of adequate personnel with sufficient training from the staff of conservation organizations, as well as among laypeople who could undertake monitoring activities on a volunteer basis, may impede the implementation of broad-scale monitoring. Uneven or inadequate identification skills also induce a certain amount of uncertainty into data yielded from monitoring programs such that changes in bird abundance over time, for example, could be an artifact about changes in observer skill.

One approach to monitoring that addresses the lack of monitoring capacity stemming from these challenges is the employment of "indicator species," which make the task of assessing the current condition and trends in biodiversity more tractable (Carignan & Villard, 2002; Siddig et al., 2016; Bal et al., 2018). Indicator species are defined as "the most characteristic species of sites grouped based on shared characteristics, that are found mostly in sites of that type, and present in most sites sharing those characteristics" (Dufrêne & Legendre, 1997). These attributes of indicator species mean that if an indicator species is detected at a site, that site can be assigned to a condition for which that species is assigned as an indicator. Using indicator species simplifies monitoring by reducing the number of species that need to be considered, which allows observers with less training to generate more reliable data.

The main goal of this project was to identify bird species that reflect forest degradation within the humid forests of northeast Central America, which can be used as indicators to monitor long-term changes in habitat suitability for forest-dwelling species. Birds are considered good species to use as indicators because they (1) advertise their presence through vocalizations, making them relatively easy to detect and identify; (2) can be censused efficiently over large spatial scales; (3) are of wide interest to the public; and (4) encompass a relatively large number of species with known responses to disturbance (Carignan & Villard, 2002; Hutto, 1998; Niemi & McDonald, 2004). This list of avian indicators can then be used to establish baseline conditions of ecological integrity for protected areas and other sites of interest, as well as to gauge changes over time or in response to specific influences, natural or anthropogenic. These indicators are intended to aid in more effective long-term ecological monitoring in Cockscomb Basin Wildlife Sanctuary, and throughout the northeast humid region of Central America (Howell & Webb, 1995).

Materials and methods

This work took place from early January to early April 2015 and 2016 in the Cockscomb Basin Wildlife Sanctuary (CBWS), which is managed by the Belize Audubon Society. The preserve consists of a 518-km^2 area of primarily second-growth tropical moist forest, which was logged from the 1930s until the area was declared a protected area in 1984 (Rabinowitz, 1986), during which the larger trees, particularly cedar (*Cedrela odorata*) and mahogany (*Swietenia macrophylla*), were removed and smaller and unmerchantable trees retained. Elevations within the sanctuary range from 38 to 1160 m above sea level.

Our approach to indicator species selection was to identify species significantly associated with disturbance, since for the purposes of monitoring, these are most useful to signal environmental changes potentially in need of remediation (Carignan & Villard, 2002; Dufrêne & Legendre, 1997; Hutto, 1998). In order to ensure our sampling represented a complete range of ecological conditions within the CBWS, we stratified sample points among ecosystem types, and along remotely sensed gradients of forest condition and elevation. Ecosystem types were based on the UNESCO classification (UNESCO, 1973) from a coverage generated by Meerman (2011). Three ecosystem types were represented within the Cockscomb Basin Wildlife Sanctuary, characterized by distinct soil, topography, and vegetation profiles. These were "riparian," which occurs largely along river sides and consists primarily of shrubs and graminoids, as well as "sandy" and "acidic" which occurred on uplands (Meerman, 2011; Table 1).

These ecosystem types were supplemented with two remotely sensed, continuous measures of forest condition: canopy height derived from light detection and ranging (LIDAR) imagery and moderate resolution imaging spectroradiometer (MODIS) enhanced vegetation index (EVI). The LIDAR-generated global canopy height data layer was used to detect major differences in canopy conditions, which we reasoned might represent damaged to or degradation of the forest canopy (Simard et al., 2011). Similarly, MODIS provides remotely sensed characterizations of vegetation conditions based on spectral transformations of LANDSAT imagery (Huete et al., 2002), and EVI is a vegetation index specifically designed to characterize canopy structure including leaf area index, canopy type, plant physiognomy, and canopy architecture. We reasoned that these characteristics would differ between disturbed and undisturbed sites (Chen & Sun, 2010; Rossia et al., 2013), and this way provides an index of forest disturbance. EVI values were captured at a 250-m landscape resolution on March 21, 2013. Although we used EVI measurements from 2013 to model associations between EVI and birds in 2015 and 2016, it is unlikely this affected our results, since 2013 values were highly significantly associated with values from 2015 ($r=0.93$, $P<0.001$) and 2016 ($r=0.95$, $P<0.001$).

Bird survey point locations were stratified among ecosystem types, and along gradients of forest condition reflected by LIDAR and EVI as well as elevation. Ecosystem type was incorporated as a categorical variable in its original form. Categories for EVI and canopy height were established by grouping sites based on their values for these remotely sensed disturbance variables using non-hierarchical k-means cluster analyses. K-means clustering establishes a user-defined "*k*" number of groups (in our analyses, we assigned three clusters) using natural cut points in the data with the aim of maximizing differences among clusters (Dufrêne & Legendre, 1997). Elevation was included since shifts in elevational distribution could signal the influenced of climate change (Auer & King, 2014). Elevation was binned into three elevational ranges: below 250 m, > 250–500 m, and > 500 m. Finally, we added points located in forested sites that had been selectively logged in 2014 ($n=7$) and cacao plantations ($n=6$) outside the perimeter of the CBWS, but located in ecosystem types represented within the protected area (acidic and sandy soils). The points were added to ensure that species associated with anthropogenically disturbed sites were also represented to contrast with the undisturbed "reference" condition within the protected area (Andreasen et al., 2001).

This approach yielded 162 possible strata consisting of all possible combinations of three ecosystem types, two disturbance states (disturbed and undisturbed), and low medium and high categories of EVI, canopy height, and elevation. Only 28 of these strata were present within our study area, however (riparian sites only occurred at low elevations, for example), which differed in areal extent from 2 to 2876 ha. Up to four survey points were randomly established in each stratum using the Create Random Points tool in ArcGIS (ESRI, 2011) with the constraint that all points were at least 500 m from the nearest other survey point. Points that were > 2 km from trails were eliminated. This yielded 114 survey points (Fig. 1) distributed among representative ecosystem types with EVI ranging from 4086 to 6637, canopy height ranging from 17 to 33 m, and elevation ranging from 56 to 524 m.

Bird surveys consisted of unlimited-radius point counts during which trained observers recorded the identity of any bird seen or heard. Audio recordings were made during each count using an Olympus

Table 1 Major ecosystems within Cockscomb Basin Wildlife Sanctuary east and west basins

Type	UNESCO classification	UNESCO code
Riparian	Deciduous broad-leaved lowland riparian shrubland in hills	IIIB1b(f)H
Sandy	Tropical evergreen seasonal broad-leaved lowland forest on poor or sandy soils	IA2a(1)(b)S
Acidic	Tropical evergreen seasonal broad-leaved lowland forest, well drained, over acidic soils	IA2a(1)(a)

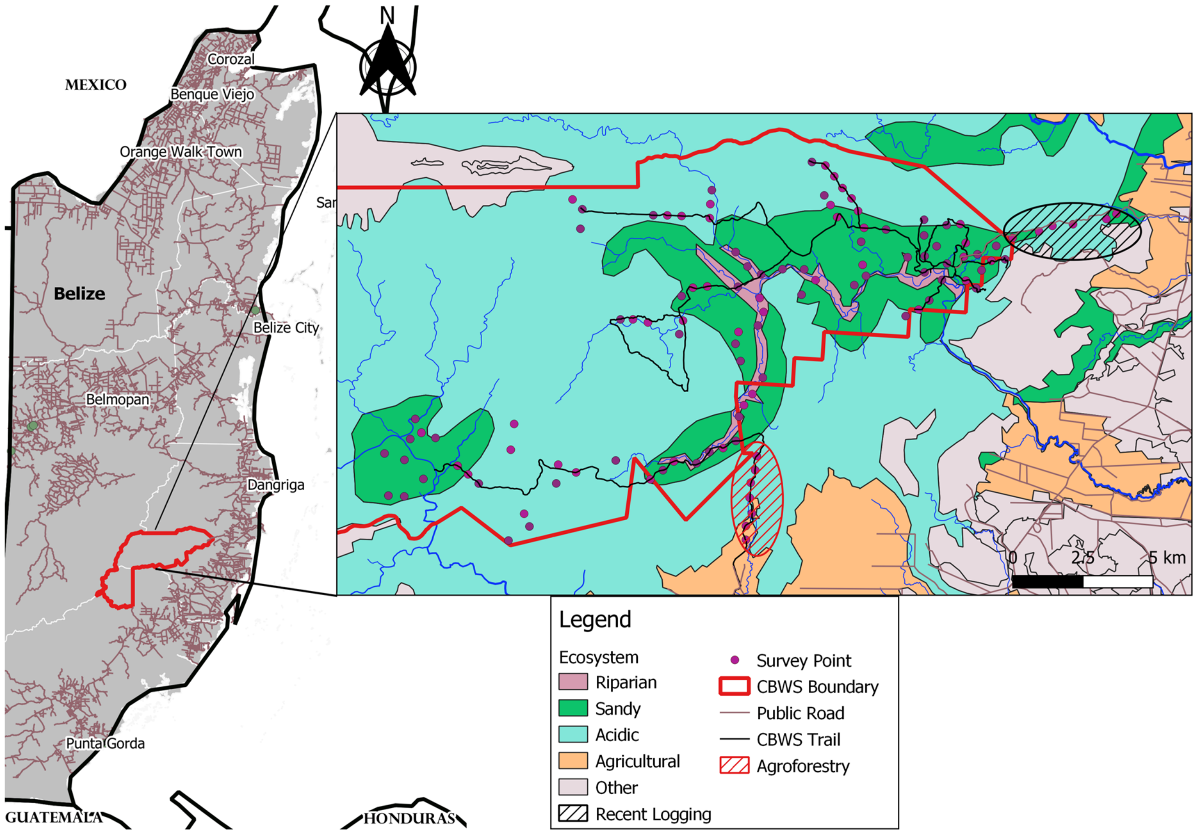

Fig. 1 A map of the Cockscomb Basin Wildlife Sanctuary showing locations of point count survey locations within the Cockscomb Basin Wildlife Sanctuary, Belize, 2015 and 2016. We were unable to establish the exact boundaries of the "recent logging" or "agroforestry" areas

DM-620 voice recorder equipped with both directional and omnidirectional microphones, and recordings were reviewed during data entry to confirm both the presence and identity of birds during the count period. Each point was surveyed three times each season and the average count for each species used in the analyses. In 2015, surveys took place from 11 January to 10 April and were 17.5 min long, consisting of 10-min passive listening period followed by 5-min broadcast of wood thrush (*Hylocichla mustelina*) song and alarm calls at approximately 100 db followed by a final 2.5 min of passive listening. The addition of wood thrush songs and calls was part of an associated project to test whether wood thrushes might be an effective indicator species, given their reported association with forest as well as the high level of interest in the conservation of this species (National Audubon Society, 2010). In 2016, surveys took place from 15 January to 9 April and were 25 min long, consisting of the same protocol as in 2015 but with an additional 5-min broadcast of Neotropical owls and mobbing track followed by a final 2.5-min passive listening period. Owl mobbing playback is known to increase detection probability of point count surveys in the Neotropics (Bennett et al., 2018). The addition of mobbing playback in 2016 resulted in the detection of only slightly more (7%) species than were detected in 2015 (probably because wood thrush alarm calls used in both years elicited a similar response as mobbing), and none of these species were abundant enough to include in the indicator species analysis. Thus, we conclude that the slight difference in protocol between years did not affect our results.

To determine which species were indicators of anthropogenic disturbance, undisturbed forest, or climate change, we employed indicator species analysis using the Indicspecies package in Program R (De Cáceres & Jansen, 2015) to identify species associated with ecosystem type, EVI, canopy height, anthropogenic disturbance, or elevation. For each species, an indicator value index ("IndVal") was calculated for its association with each of the categories of environmental conditions, and the species is assigned as an indicator for the variable with the highest association value. IndVal is calculated as the product of the A_{ij}, which is the mean abundance of species i in the sites of group j compared to all groups in the study, by B_{ij}, which is the relative frequency of occurrence of species i in the sites of group j, expressed as a percent (Dufrêne & Legendre, 1997). IndVal illustrates how much the target site group matches the set of sites where the species is found, and the statistical significance of this relationship was tested ($P \leq 0.05$) using a permutation test (Dufrêne & Legendre, 1997). These analyses were carried out separately by year (2015 and 2016) and for both years combined. Finally, indicator species analyses were conducted for combinations of the ecosystem types, disturbance variables, and elevation classes to further test the association of species with these conditions.

We attempted to validate our remotely sensed habitat variables by comparing them among ecosystem types to verify that they differed between closed-canopy conditions (sandy and acidic forested sites) and anthropogenically disturbed sites. Because these habitat variables were non-normally distributed, we employed a Kruskal–Wallis test and multiple comparisons with Steel–Dwass test in JMP (Version 14.1, SAS Institute, 2019). We then selected candidate indicator species for (1) anthropogenic disturbance based on an association with disturbed sites, EVI, or canopy conditions that characterized disturbed sites, or (2) undisturbed sites based on association with ecosystems within the protected area that were undisturbed, or (3) climate change based on associations with a specific elevational zone.

Species were only selected if their association with ecosystem type or disturbance variables was significant in both years at the $P < 0.05$ level of significance, with one exception (see below). In addition, we consulted reference works to ensure that the associations of species with disturbance variables from these analyses were reasonable. These consisted of peer-reviewed journal articles describing the habitat associations of birds in Belize, as well as more general reference works based on literature review and expert opinion (Howell & Webb, 1995; Jones, 2003; Vallely & Dyer, 2018). Species that were associated with riparian sites either in the analyses or according the literature were eliminated, because riparian sites do not represent a form of disturbance that would threaten the integrity of the protected area. Thus, the inclusion of species associated with riparian disturbance as indicators could result in conservationists mistakenly concluding, based on bird monitoring results from riparian areas, that habitat degradation by humans was taking place. Species that were associated with both riparian sites and anthropogenically disturbed sites in the analyses and for which no specific association with riparian areas was mentioned in the literature were retained for further consideration, since we assumed that the response of these species was due to the disturbance of vegetation from flooding and not riparian habitats per se.

Results

We detected 244 species during the bird surveys (Appendix 1). Of these, 99 occurred at > 20% of sites and were included in the analyses, of which 20 species exhibited significant associations with ecosystem types, disturbance variables, and/or elevation across both years and years combined (Table 2).

Orange-billed sparrow, yellow-olive flycatcher, dusky antbird, blue ground dove, buff-throated saltator, and northern waterthrush were significantly associated with both riparian and anthropogenically disturbed sites (Table 2). Yellow-billed cacique was associated with riparian sites and not anthropogenically disturbed sites. Red-legged honeycreeper and brown jay were significantly associated with only anthropogenically disturbed sites.

Black-headed trogon, green shrike-vireo, rufous piha, and chestnut-colored woodpecker were associated with either one or both of the forested habitats within the protected area (sandy and acidic) yet were also associated with riparian and/or anthropogenically disturbed sites (Table 2). Keel-billed motmot was the only species associated with both closed-canopy forest types (sandy and acidic), but this relationship was only significant in our analyses in 2016 and both years combined.

Table 2 Species significantly associated with ecosystem type, disturbance, or elevation. Data are from point count surveys at the Cockscomb Basin Wildlife Sanctuary, Belize, 2015 and 2016

Species	*f*[1]	ECO[2]	DIT[3]	EVI[4]	CAN[5]	ELE[6]
Green shrike-vireo	0.68	SA	D			MH
Black-headed trogon	0.64	RS	D			
Orange-billed sparrow	0.57	R	D			
Collared trogon	0.53					MH
Rufous-tailed jacamar	0.48					LM
Rufous piha	0.48	SA	D			MH
Yellow-olive flycatcher	0.48	R	D			
Chestnut-colored woodpecker	0.46	SA	D			
Red-legged honeycreeper	0.45		D			
Dusky antbird	0.39	R	D	MH		L
Keel-billed motmot	0.32	SA*				
Blue ground dove	0.31	R	D			L
Buff-throated saltator	0.27	R	D	H		L
Yellow-billed cacique	0.25	R				L
Black-headed saltator	0.24					L
Barred antshrike	0.24	R		H		L
Northern waterthrush	0.24	R	D			
Golden-hooded tanager	0.21				L	
Brown jay	0.20		D	LH	L	
Social flycatcher	0.20					L

[1]Percentage of sites where species occurred

[2]Ecosystem: R = riparian, S = sandy, A = acidic

[3]Disturbance: D = disturbed

[4]EVI: L = low (4086–4601); M = moderate (4618–4937); H = high (4954–5698)

[5]Canopy height: L = low (17–26); M = moderate (30–33); H = high (27–29)

[6]Elevation: L = low (< 250 m); M = moderate (> 250–500 m); H = high (> 500 m)

*Only significant in 2016 and years combined

Buff-throated saltator and barred antshrike were associated with high value for EVI; dusky antbird was associated with medium and high values for EVI, and brown jay was associated with both high and low values for EVI (Table 2). Golden-hooded tanager and brown jay were associated with low canopy height.

Dusky antbird, blue ground dove, buff-throated saltator, yellow-billed cacique, black-headed saltator, barred antshrike, and social flycatcher were associated with low elevations; rufous-tailed jacamar was associated with low and medium elevations; green shrike-vireo, collared trogon, and rufous piha were associated with medium and high elevations (Table 2).

EVI did not differ among any of the ecosystem types, or between any of the ecosystem types and anthropogenically disturbed sites ($P > 0.05$). Canopy was taller at acidic sites compared to sandy and riparian sites ($P < 0.005$), and marginally lower at disturbed sites compared to acidic sites ($P < 0.053$), and did not differ between sandy, disturbed, or riparian sites ($P > 0.05$). Elevation was greater at acidic sites than sandy, disturbed, or riparian sites ($P < 0.005$), and was greater at sandy sites compared to riparian sites ($P = 0.0005$), and did not differ between sandy, disturbed, or riparian sites ($P > 0.05$).

Discussion

By sampling across a number of environmental gradients and analyzing these data using indicator species analyses, we generated associations between the abundance of individual species with sites differing with respect to disturbance. Two species, the red-legged honeycreeper and brown jay, were associated with only disturbed sites in our analyses. As such, the detection of either of these species at a site should indicate that it had been subject to anthropogenic disturbance. Both of these species are widely reported to use edge and open areas (Mills & Rogers, 1992; Saab & Petit, 1992), and although they are also reported to use forest occasionally (Howell & Webb, 1995; Jones, 2003; Vallely & Dyer, 2018), increases in their numbers at sites where they were previously recorded, or their occurrence at sites where they were previously absent, would be expected to indicate increased disturbance.

The association of six other species (orange-billed sparrow, yellow-olive flycatcher, dusky antbird, blue ground dove, buff-throated saltator, and northern waterthrush) with both disturbed sites and riparian sites could potentially indicate an association with disturbance useful for monitoring disturbance within non-riparian areas. Riparian areas resemble anthropogenically disturbed habitats by being similarly characterized by canopy and shrubby understory resulting from natural disturbance from periodic flooding. Of these species, the northern waterthrush was eliminated because it is specifically associated with rivers and small streams (Howell & Webb, 1995; Vallely & Dyer, 2018), and thus, its association with disturbance in our analyses was probably due to the disturbance created by the flooding and erosion caused by streamflow. Similarly, the orange-billed sparrow is reported to be a forest obligate (Howell & Webb, 1995; Jones, 2003). Its association with disturbance in our analyses is puzzling, but in any case, the conflict with these reference works suggests that this species is not a valid indicator for disturbance, and it was also eliminated from further consideration. Although the remaining species (yellow-olive flycatcher, dusky antbird, blue ground dove, and buff-throated saltator) are reported to occur in forest as well as open habitats, they appear to use forested habitats sparingly (Howell & Webb, 1995; Whitman et al., 1998; Jones, 2003; Vallely & Dyer, 2018), and were not associated with forested sites within the protected area in our analyses. Thus, their presence is likely to indicate increased disturbance.

Thus, we propose six species as indicators for anthropogenic disturbance based on our criteria of being associated in both years and years combined with anthropogenically disturbed sites, or anthropogenically disturbed and riparian sites with no explicit mention in the literature of an obligate association with riparian habitats, or association of remotely sensed measures of disturbance: yellow-olive flycatcher, red-legged honeycreeper, dusky antbird, blue ground dove, buff-throated saltator, and brown jay. We propose the keel-billed motmot as an indicator of undisturbed forest based on its significant association with forested sites in our analyses (albeit only in 2016 and both years combined). This obligate relationship was borne out in the literature (Howell & Webb, 1995; Jones, 2003; Vallely & Dyer, 2018).

Of the 11 species associated with distinct elevational zones, seven (dusky antbird, blue ground dove, buff-throated saltator, yellow-billed cacique, black-headed saltator, barred antshrike, and social flycatcher) were also associated with disturbed and/or riparian habitat in either our analyses or in the literature, which made them unsuitable for indicators of climate change because upward shifts in their elevation could be the result of either upward progression of habitat disturbance, or the upward shift of climatic conditions. Four species (green shrike-vireo, collared trogon, rufous-tailed jacamar, and rufous piha) were associated with low- and mid- and mid-to high-elevation sites within the CBWS, and were associated with both disturbed and undisturbed sites in our analyses, as well as in the literature (Howell & Webb, 1995; Jones, 2003; Vallely & Dyer, 2018; Whitman et al., 1998), so shifts in distribution due to climate change would be less likely to be confounded with upward shifts in habitat degradation, since they use both disturbed and undisturbed forest. Thus, these four species were retained for consideration as candidate indicators of climate change, since upward shifts in their elevational distribution could signify upward shifts in suitable bioclimatic conditions (Auer & King, 2014).

The keel-billed motmot, in addition to being included on the Belize List of Critical Species (Meerman, 2005), is listed as "vulnerable" by the International Union for the Conservation of Nature, meaning it is likely to become endangered throughout its range unless conservation measures are undertaken. This species is considered to be rare throughout its Central American range, yet studies in Belize suggest that conservation areas in this country support a disproportionate number of this species and could represent a conservation stronghold (Miller & Miller, 1996). We encountered this species on 32% of our surveys over both years, suggesting it is indeed widely distributed in the Cockscomb Basin Wildlife Sanctuary (Table 3). The close association of this species with closed-canopy forest, its elevated conservation status, and its loud and distinctive vocalizations make it a particularly valuable target for continued monitoring. One potential disadvantage is that the call of the keel-billed motmot is similar to that of the broad-billed motmot (*E. playrhynchum*), consisting of single hoarse notes (Vallely & Dyer, 2018). This should not be a problem for monitoring in

Table 3 A preliminary list of indicator species for the Cockscomb Basin Wildlife Sanctuary, Belize, which includes widespread species exhibiting quantitative associations with disturbance or occupy specific elevational ranges

Species	Rationale for inclusion
Yellow-olive flycatcher	Indicates disturbance
Red-legged honeycreeper	Indicates disturbance
Dusky antbird	Indicates disturbance
Blue ground dove	Indicates disturbance
Buff-throated saltator	Indicates disturbance
Brown jay	Indicates disturbance
Keel-billed motmot	Indicates lack of disturbance/vulnerable resident
Green-shrike vireo	Indicates climate change
Rufous piha	Indicates climate change
Collared trogon	Indicates climate change

Belize, since the broad-billed motmot does not occur in Belize (Jones, 2003); however, this should be taken into consideration when considering the keel-billed motmot as an indicator in areas of sympatry.

Given the rich forest avifauna of Belize, the fact that only one species, the keel-billed motmot, was exclusively associated with forest was an unexpected result. This is despite surveying closed-canopy forests deep within one of the largest and most intact protected areas in Central America. We did detect species reported by others to be strongly associated with forest (e.g., wedge-billed and northern barred woodcreeper and scaly-throated foliage gleaner; Jones, 2003; Whitman et al., 1998), yet these species were not identified as indicator species for forest in our analyses. One potential explanation is that the disturbed areas we surveyed were relatively close to the protected area (< 3 km), and proximity to extensive forest is known to positively influence the abundance of forest-dependent species in non-forested habitats (Chandler et al., 2013). Alternatively, our use of unlimited-radius point counts may have included forest-dependent species in adjacent disturbed habitats, which would result in a species being associated in the analyses with disturbed habitats. We attempted to reduce this likelihood by locating point counts ≥ 100 m from different habitats. The fact that keel-billed motmot was identified as a forest-dependent species suggests that the detection of species from adjacent habitats did not entirely detract from our ability to identify them as forest associates; the vocalization of the keel-billed motmot is loud and detectible from a great distance (Howell & Webb, 1995; Vallely & Dyer, 2018). Alternatively, the logging history at the CBWS, and potentially the background disturbance dating even back to the Maya could have resulted in a tendency for forest-associated birds to also occur in anthropogenically disturbed sites (Whitman et al., 1998). Finally, the lack of associations with undisturbed forest could simply reflect our relatively modest sample of disturbed sites ($n = 13$).

Although the initial points were stratified among ecosystem type, EVI, canopy height, and elevation, disturbed areas outside the park were located at sites that were on average lower in elevation (121.1 m) than the rest of the park (195.5 m; $P = 0.03$). This is an artifact of the point of entry to the protected area and environs, which are on its southern and eastern margins, and elevations within the country generally increase as one progresses from the coastal plain in the east towards the mountainous interior to the west. This could be problematical if the species we selected as indicators of disturbance were restricted to sites at lower elevations, in which case disturbance could occur above their elevational range and not be indicated by their presence. Conversely, species associated with closed-canopy conditions could appear to be negatively associated with disturbance if disturbed areas occurred below their elevational range. This is unlikely, however, since the elevational ranges of these closed-canopy species all extend from sea level to at least 1500 m (Howell & Webb, 1995). Thus, both the disturbed and reference sites were well within their elevational range.

The enhanced vegetation index (EVI) appeared to be an ambiguous measure of disturbance in this study. Importantly, EVI values did not differ between disturbed and undisturbed sites ($P < 0.05$). Furthermore, species associated with disturbed and riparian areas were associated with both low and high values of EVI. Our remotely sensed metric of canopy height seemed more promising, as canopy height was marginally lower at anthropogenically disturbed sites compared to forest sites on acidic soils, although canopy height did not differ between disturbed sites and forested sites on sandy soils. Furthermore, only one of two species associated with low canopy height was also associated with disturbed sites in our study (brown jay), although the other species (golden-hooded tanager) was associated with disturbance according to the literature (Howell & Webb, 1995; Vallely & Dyer, 2018). The relatively coarse resolution of the EVI data (250 m) is one possible explanation for its apparent lack of association with disturbance; however, the resolution of the remotely sensed canopy measures we employed were coarser than our EVI measurements (1 km^2), yet these coarser values of canopy did differ between disturbed and undisturbed sites. Although the resolution of the remotely sensed data may have been a cause of weak associations between birds and environmental variables, they still appear to have been useful in these analyses, and the results were borne out by reference to published references on these bird species. As more refined remote-sensing data become available, their use will refine our ability to better identify indicator species.

The process of selecting indicator species can be undertaken based on consultation with experienced ecologists (Andreasen et al., 2001); however, we decided to employ a quantitative approach as recommended by Carignan and Villard (2002), specifically the approach recommended by Siddig et al. (2016) in which species associations with disturbance were quantitatively evaluated following the approach of Dufrêne and Legendre (1997). Although this approach has the desirable attribute of objectivity, the approach is still susceptible to methodological and sampling considerations. For example, the analyses we employed required that we use discrete habitat categories for “anthropogenic disturbance.” Although the sites we selected in agroforestry and recently logged areas clearly represented a disturbed condition, the contrast with forested sites within the protected area was abrupt, such that species associated with disturbance might only be present once a given site has already been affected (Andreasen et al., 2001). Furthermore, the undisturbed reference forested sites within the protected area were heterogeneous, both with respect to their site history (e.g., logging history) as well as their structural characteristics (e.g., similar canopy height in disturbed sites and forested sites on sandy soils). The variation among our forested sites in structure, combined with the relatively wide tolerances of birds at our sites to forest conditions, resulted in overlap in habitat associations of nearly all forest species between anthropogenically disturbed and reference forested sites. Analyzing the data along a continuous gradient of disturbance would have been an alternative approach; however given the disturbance history of the CBWS and the relatively broad habitat tolerances of forest birds at our sites, it seems likely the results would have been similar to those of Whitman et al. (1998), who reported no effect of selective logging on forest birds within the Rio Bravo Conservation Area 70 km to the north of the CBWS.

One potential limitation of our study is that our surveys took place during a 3-month period that corresponded with the onset of the dry season in Belize, and the temperate winter. Some Neotropical resident birds are known to shift among habitats or along elevational gradients between the wet and dry seasons (Stiles, 1985), so the elevational and habitat associations we report may not represent their distribution throughout the entire year. However, none of the species we recommend as potential monitoring targets are elevational migrants, except the green shrike vireo and collard trogon (Stiles 1985). For these two species, observers should be mindful if surveys are conducted outside of the survey dates we used the elevational associations we report may not be applicable. Our surveys also included Neotropical-Nearctic migrants that are only present during the temperate winter; however, since these species are subject to the jurisdiction of international treaties (e.g., the Migratory Bird Treaty Act) and some of them are considered to be vulnerable to forest destruction or degradation (Petit et al., 1992; Robbins et al., 1992; Gómez-Montes & Bayley, 2010), this may be a justification for conducting surveys when they are present.

A number of authors have noted that indicator species analyses might be biased in the absence of correction for heterogenous detection probabilities due to differences among observers (Quinn et al., 2011). The analytical methods used to correct point count data for detectability are generally not applicable to extensive, multi-species surveys such as ours, however (Johnson, 2008). Nevertheless, we were able to minimize the influence of observers to some extent by recruiting only highly trained observers (Kepler & Scott, 1981), rotating observers among survey points (Bibby et al., 1992), and recording each point count and reviewing the recordings prior to data entry. There remains the possibility that the associations of bird species with the various strata could have been influenced by differences in detectability among habitats (Urban et al., 2012); however, the associations we observed were consistent with the literature, and for the species, we suggest as an indicator of undisturbed forest conditions, the keel-billed motmot, its vocalizations are very loud and less likely to be influenced by habitat structure.

In this paper, we used quantitative analyses to identify indicator species for anthropogenic disturbance and climate change, for a total of 11 monitoring targets from the 244 species encountered. Monitoring based on fewer indicator species can increase the pool of potential participants in monitoring, can reduce the costs or challenges with training, and by reducing the problems with misidentification can increase the overall quality of monitoring datasets. Naturally, the adoption of an indicator species approach should not be construed to mean that monitoring the entire avian community is not useful, and efforts to increase bird identification capacity is an important and worthy endeavor. A necessary step in applying these findings is to aggregate survey data to quantify changes in indicator species over time and space in a form that can be interpreted in relation to changes in environmental conditions, and a variety of approaches exist differing in their complexity and other attributes (Andreasen et al., 2001). Nevertheless, the selection or adoption of any of these approaches for interpreting monitoring data requires robust sampling and analyses, which was the objective of this project, and which we believe has been achieved. The list of avian indicators we present can be used to assess the ecological integrity of humid forests in the region and evaluate responses to habitat disturbance and climate change. It also simplifies monitoring, which allows observers with less training to generate more reliable data.

Appendix 1 Bird species detected on point count surveys on at 114 sample sites within the Cockscomb Basin Wildlife Sanctuary during 2015 and 2016

Species		% Sites detected
White-breasted wood-wren	*Henicorhina leucosticta*	1.00
Lesser greenlet	*Pachysylvia decurtata*	1.00
Short-billed pigeon	*Patagioenas nigrirostris*	1.00
Yellow-bellied flycatcher	*Empidonax flaviventris*	0.99
Magnolia warbler	*Setophaga magnolia*	0.99
Wood thrush	*Hylocichla mustelina*	0.96
Kentucky warbler	*Geothlypis formosa*	0.95
Long-billed hermit	*Phaethornis longirostris*	0.95
Tawny-crowned greenlet	*Tunchiornis ochraceiceps*	0.95
Spot-breasted wren	*Pheugopedius maculipectus*	0.94
Rufous-tailed hummingbird	*Amazilia tzacatl*	0.94
Pale-billed woodpecker	*Campephilus guatemalensis*	0.93
Slaty-tailed trogon	*Trogon massena*	0.92
Black-faced antthrush	*Formicarius analis*	0.90
Bright-rumped attila	*Attila spadiceus*	0.90
Ivory-billed woodcreeper	*Xiphorhynchus flavigaster*	0.90
Gartered trogon	*Trogon caligatus*	0.89
Stripe-throated hermit	*Phaethornis striigularis*	0.89
Red-capped manakin	*Ceratopipra mentalis*	0.88
Dot-winged antwren	*Microrhopias quixensis*	0.88
Northern schiffornis	*Schiffornis veraepacis*	0.88
Keel-billed toucan	*Ramphastos sulfuratus*	0.87
Long-billed gnatwren	*Ramphocaenus melanurus*	0.85
Northern bentbill	*Oncostoma cinereigulare*	0.84
Olive-backed euphonia	*Euphonia gouldi*	0.84
Great tinamou	*Tinamus major*	0.83
Red-crowned ant tanager	*Habia rubica*	0.82
Red-throated ant tanager	*Habia fuscicauda*	0.82
Mealy parrot	*Amazona farinosa*	0.81
Blue-black grosbeak	*Cyanocompsa cyanoides*	0.81
Chestnut-sided warbler	*Setophaga pensylvanica*	0.80

Species		% Sites detected
Blue-crowned motmot	*Momotus momota*	0.80
Hooded warbler	*Setophaga citrina*	0.79
Black-cheeked woodpecker	*Melanerpes pucherani*	0.79
Slaty-breasted tinamou	*Crypturellus boucardi*	0.78
American redstart	*Setophaga ruticilla*	0.77
White-bellied emerald	*Amazilia candida*	0.77
Stub-tailed spadebill	*Platyrinchus cancrominus*	0.75
Brown-hooded parrot	*Pyrilia haematotis*	0.75
Gray catbird	*Dumetella carolinensis*	0.74
Gray-chested dove	*Leptotila cassinii*	0.72
Black-faced grosbeak	*Caryothraustes poliogaster*	0.72
Buff-throated foliage gleaner	*Automolus ochrolaemus*	0.71
Scaled pigeon	*Patagioenas speciosa*	0.68
Green shrike vireo	*Vireolanius pulchellus*	0.68
Ochre-bellied flycatcher	*Mionectes oleagineus*	0.68
White-crowned parrot	*Pionus senilis*	0.67
Squirrel cuckoo	*Piaya cayana*	0.65
Black-headed trogon	*Trogon melanocephalus*	0.64
White-collared manakin	*Manacus candei*	0.63
Wedge-billed woodcreeper	*Glyphorynchus spirurus*	0.57
Rufous mourner	*Rhytipterna holerythra*	0.57
Orange-billed sparrow	*Arremon aurantiirostris*	0.57
Dusky-capped flycatcher	*Myiarchus tuberculifer*	0.57
Plain xenops	*Xenops minutus*	0.56
Tropical gnatcatcher	*Polioptila plumbea*	0.56
Red-lored parrot	*Amazona autumnalis*	0.55
Collared trogon	*Trogon collaris*	0.53
Black-and-white warbler	*Mniotilta varia*	0.51
Yellow-olive flycatcher	*Tolmomyias sulphurescens*	0.48

Species		% Sites detected
Rufous piha	*Lipaugus unirufus*	0.48
Rufous-tailed jacamar	*Galbula ruficauda*	0.48
Sulphur-rumped flycatcher	*Myiobius sulphureipygius*	0.47
Chestnut-colored woodpecker	*Celeus castaneus*	0.46
Red-legged honeycreeper	*Cyanerpes cyaneus*	0.45
Summer tanager	*Piranga rubra*	0.45
Chestnut-headed oropendola	*Psarocolius wagleri*	0.45
Little tinamou	*Crypturellus soui*	0.41
Masked tityra	*Tityra semifasciata*	0.40
Dusky antbird	*Cercomacra tyrannina*	0.39
Crested guan	*Penelope purpurascens*	0.39
Sepia-capped flycatcher	*Leptopogon amaurocephalus*	0.39
Tawny-winged woodcreeper	*Dendrocincla anabatina*	0.39
Collared aracari	*Pteroglossus torquatus*	0.39
Greenish elaenia	*Myiopagis viridicata*	0.38
Worm-eating warbler	*Helmitheros vermivorum*	0.34
Smoky-brown woodpecker	*Picoides fumigatus*	0.33
Gray-headed dove	*Leptotila plumbeiceps*	0.33
Keel-billed motmot	*Electron carinatum*	0.32
Olive-throated parakeet	*Eupsittula nana*	0.32
Yellow-bellied tyrannulet	*Ornithion semiflavum*	0.32
Blue ground dove	*Claravis pretiosa*	0.31
Black-throated shrike tanager	*Lanio aurantius*	0.30
Great crested flycatcher	*Myiarchus crinitus*	0.29
Scarlet macaw	*Ara macao*	0.28
Buff-throated saltator	*Saltator maximus*	0.27
Eye-ringed flatbill	*Rhynchocyclus brevirostris*	0.26
Yellow-billed cacique	*Amblycercus holosericeus*	0.25
Barred antshrike	*Thamnophilus doliatus*	0.24

Species		% Sites detected
Black-headed saltator	*Saltator atriceps*	0.24
White-throated thrush	*Turdus assimilis*	0.24
Bananaquit	*Coereba flaveola*	0.24
Northern waterthrush	*Parkesia noveboracensis*	0.24
Montezuma oropendola	*Psarocolius montezuma*	0.24
Red-eyed vireo	*Vireo olivaceus*	0.21
Golden-hooded tanager	*Tangara larvata*	0.21
Olivaceous woodcreeper	*Sittasomus griseicapillus*	0.21
Brown jay	*Psilorhinus morio*	0.20
Social flycatcher	*Myiozetetes similis*	0.20
White-necked jacobin	*Florisuga mellivora*	0.19
Black-throated green warbler	*Setophaga virens*	0.19
Melodious blackbird	*Dives dives*	0.18
Barred forest falcon	*Micrastur ruficollis*	0.18
Ruddy woodcreeper	*Dendrocincla homochroa*	0.18
Clay-colored thrush	*Turdus grayi*	0.18
Great kiskadee	*Pitangus sulphuratus*	0.18
Baltimore oriole	*Icterus galbula*	0.17
Ruddy quail-dove	*Geotrygon montana*	0.17
White hawk	*Pseudastur albicollis*	0.17
Green honeycreeper	*Chlorophanes spiza*	0.15
Crimson-collared tanager	*Ramphocelus sanguinolentus*	0.15
Piratic flycatcher	*Legatus leucophaius*	0.15
Collared forest falcon	*Micrastur semitorquatus*	0.15
Tennessee warbler	*Leiothlypis peregrina*	0.14
Black-cowled oriole	*Icterus prosthemelas*	0.13
Violet sabrewing	*Campylopterus hemileucurus*	0.13
Yellow-throated euphonia	*Euphonia hirundinacea*	0.13
Rose-throated becard	*Pachyramphus aglaiae*	0.13
Plain chachalaca	*Ortalis vetula*	0.13
Yellow-green vireo	*Vireo flavoviridis*	0.13
White-whiskered puffbird	*Malacoptila panamensis*	0.12

Species		% Sites detected
Laughing falcon	*Herpetotheres cachinnans*	0.11
Yellow-throated vireo	*Vireo flavifrons*	0.11
White-necked puffbird	*Notharchus hyperrhynchus*	0.11
Vermiculated screech owl	*Megascops guatemalae*	0.11
Great antshrike	*Taraba major*	0.11
Variable seedeater	*Sporophila corvina*	0.11
Yellow-bellied elaenia	*Elaenia flavogaster*	0.11
Gray-headed kite	*Leptodon cayanensis*	0.11
Roadside hawk	*Rupornis magnirostris*	0.11
Ruddy crake	*Laterallus ruber*	0.10
Boat-billed flycatcher	*Megarynchus pitangua*	0.10
Scarlet-rumped tanager	*Ramphocelus passerinii*	0.10
Common tody-flycatcher	*Todirostrum cinereum*	0.10
Ovenbird	*Seiurus aurocapilla*	0.09
Grayish saltator	*Saltator coerulescens*	0.09
Lineated woodpecker	*Dryocopus lineatus*	0.09
Royal flycatcher	*Onychorhynchus coronatus*	0.09
Blue-gray gnatcatcher	*Polioptila caerulea*	0.08
Central american pygmy owl	*Glaucidium griseiceps*	0.08
White-eyed vireo	*Vireo griseus*	0.08
Pale-vented pigeon	*Patagioenas cayennensis*	0.08
Wilson's warbler	*Cardellina pusilla*	0.08
Yellow-tailed oriole	*Icterus mesomelas*	0.08
Rufous-breasted spinetail	*Synallaxis erythrothorax*	0.08
Streak-headed woodcreeper	*Lepidocolaptes souleyetii*	0.07
Tropical kingbird	*Tyrannus melancholicus*	0.07
Emerald toucanet	*Aulacorhynchus prasinus*	0.07
Northern barred woodcreeper	*Dendrocolaptes sanctithomae*	0.07
Band-tailed barbthroat	*Threnetes ruckeri*	0.07

Species		% Sites detected
Tropical pewee	*Contopus cinereus*	0.06
Yellow-throated warbler	*Setophaga dominica*	0.06
Golden-fronted woodpecker	*Melanerpes aurifrons*	0.06
Great curassow	*Crax rubra*	0.06
Nightingale wren	*Microcerculus philomela*	0.06
Slate-headed tody-flycatcher	*Poecilotriccus sylvia*	0.06
Sulfur-bellied flycatcher	*Myiodynastes luteiventris*	0.06
Tody motmot	*Hylomanes momotula*	0.06
Common yellowthroat	*Geothlypis trichas*	0.05
Green-backed sparrow	*Arremonops chloronotus*	0.05
Louisiana waterthrush	*Parkesia motacilla*	0.05
Philadelphia vireo	*Vireo philadelphicus*	0.05
Gray hawk	*Buteo plagiatus*	0.05
Turkey vulture	*Cathartes aura*	0.05
Cinnamon becard	*Pachyramphus cinnamomeus*	0.04
Gray-headed tanager	*Eucometis penicillata*	0.04
Band-backed wren	*Campylorhynchus zonatus*	0.04
White-collared seedeater	*Sporophila torqueola*	0.04
Golden-olive woodpecker	*Colaptes rubiginosus*	0.04
Lesser swallow-tailed swift	*Panyptila cayennensis*	0.04
Gray-throated chat	*Granatellus sallaei*	0.04
Great black hawk	*Buteogallus urubitinga*	0.04
Blue-winged warbler	*Vermivora cyanoptera*	0.03
Common pauraque	*Nyctidromus albicollis*	0.03
Ringed kingfisher	*Megaceryle torquata*	0.03
Scaly-breasted hummingbird	*Phaeochroa cuvierii*	0.03
Speckled mourner	*Laniocera rufescens*	0.03
Spotted wood quail	*Odontophorus guttatus*	0.03
Yellow warbler	*Setophaga petechia*	0.03
Indigo bunting	*Passerina cyanea*	0.03
Mangrove vireo	*Vireo pallens*	0.03

Species		% Sites detected
Orchard oriole	*Icterus spurius*	0.03
Russett antshrike	*Thamnistes anabatinus*	0.03
Shining honeycreeper	*Cyanerpes lucidus*	0.03
Yellow-bellied sapsucker	*Sphyrapicus varius*	0.03
Acadian flycatcher	*Empidonax virescens*	0.02
Amazon kingfisher	*Chloroceryle amazona*	0.02
Blue-gray tanager	*Thraupis episcopus*	0.02
Cassin’s kingbird	*Tyrannus vociferans*	0.02
Couch’s kingbird	*Tyrannus couchii*	0.02
Double-toothed kite	*Harpagus bidentatus*	0.02
Gray-crowned yellowthroat	*Geothlypis poliocephala*	0.02
Hepatic tanager	*Piranga flava*	0.02
House wren	*Troglodytes aedon*	0.02
Northern parula	*Setophaga americana*	0.02
Plumbeous kite	*Ictinia plumbea*	0.02
Prothonotary warbler	*Protonotaria citrea*	0.02
Tree swallow	*Tachycineta bicolor*	0.02
Violet-crowned woodnymph	*Thalurania colombica*	0.02
Wedge-tailed sabrewing	*Campylopterus pampa*	0.02
White-winged tanager	*Piranga leucoptera*	0.02
Yellow-faced grassquit	*Tiaris olivaceus*	0.02
Blue-black grassquit	*Volatinia jacarina*	0.02
Rose-breasted grosbeak	*Pheucticus ludovicianus*	0.02
Stripe-tailed hummingbird	*Eupherusa eximia*	0.02
White-winged becard	*Pachyramphus polychopterus*	0.02
Barn swallow	*Hirundo rustica*	0.01
Bat falcon	*Falco rufigularis*	0.01
Bicolored hawk	*Accipiter bicolor*	0.01
Black phoebe	*Sayornis nigricans*	0.01
Black-crested coquette	*Lophornis helenae*	0.01
Black-crowned tityra	*Tityra inquisitor*	0.01
Black-headed siskin	*Spinus notata*	0.01

Species		% Sites detected
Brewster's warbler	*Vermivora chrysoptera x cyanoptera*	0.01
Broad-winged hawk	*Buteo platypterus*	0.01
Bronzed cowbird	*Molothrus aeneus*	0.01
Brown-crested flycatcher	*Myiarchus tyrannulus*	0.01
Crane hawk	*Geranospiza caerulescens*	0.01
Crested eagle	*Morphnus guianensis*	0.01
Eastern wood peewee	*Contopus virens*	0.01
Grace's warbler	*Setophaga graciae*	0.01
Gray-collared becard	*Pachyramphus major*	0.01
Gray-necked wood rail	*Aramides cajaneus*	0.01
Great-tailed grackle	*Quiscalus mexicanus*	0.01
Green jay	*Cyanocorax yncas*	0.01
King vulture	*Sarcoramphus papa*	0.01
Least flycatcher	*Empidonax minimus*	0.01
Northern rough-winged swallow	*Stelgidopteryx serripennis*	0.01
Olive-sided flycatcher	*Contopus cooperi*	0.01
Painted bunting	*Passerina ciris*	0.01
Plain antvireo	*Dysithamnus mentalis*	0.01
Plumbeous vireo	*Vireo plumbeus*	0.01
Rose-throated tanager	*Piranga roseogularis*	0.01
Ruddy ground dove	*Columbina talpacoti*	0.01
Scaly-throated foliage gleaner	*Anabacerthia variegaticeps*	0.01
Scarlet tanager	*Piranga olivacea*	0.01
Striped cuckoo	*Tapera naevia*	0.01
Swainson's thrush	*Catharus ustulatus*	0.01
Thick-billed seed-finch	*Oryzoborus funereus*	0.01
White-tipped dove	*Leptotila verreauxi*	0.01
Yellow-backed oriole	*Icterus chrysater*	0.01
Yellow-billed cuckoo	*Coccyzus americanus*	0.01
Yellow-breasted chat	*Icteria virens*	0.01
Yellow-winged tanager	*Thraupis abbas*	0.01

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Declarations

Ethics approval This research was conducted under University of Massachusetts Institutional Animal Care and Use Committee (IACUC) protocol no. 2013–0073.

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