Animal Conservation

ZSL LET'S WORK FOR WILDLIFE

Animal Conservation. Print ISSN 1367-9430

Social network analysis reveals specialized trade in an Endangered songbird

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Keywords
aviculture; illegal wildlife trade; overexploitation; pet trade; social network analysis; threatened species; unsustainable harvest; Venezuela.

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Editor: Sadie Ryan
Associate Editor: Elina Rantanen

Received 05 October 2018; accepted 10 April 2019

doi:10.1111/acv.12514

Abstract

Unsustainable harvest is one of the most important threats to biodiversity, and birds are highly impacted, but avian markets remain poorly understood. When species value and corruption/criminality are high, the "parallel trafficking" hypothesis predicts that illegal animal items will move through networks used for other illicit products. Alternatively, when particular demands, logistical skills or access limits trade, "specialized trafficking" hypotheses predict that few, expert actors will control markets. Here, we use social network analysis of trade in an Endangered songbird, the Red Siskin *Spinus cucullatus*, originating in Venezuela, to examine the generality of the parallel trafficking hypothesis in a setting where corruption/criminality and species value are high. In spite of these circumstances, of 2575 Red Siskin (RS) records compiled from 2010 to 2017, we found just six reports consistent with parallel trafficking. Instead, we discovered an independent network of 15 actor types, and a trade structure consistent with specialized trafficking. Just two intermediary types (national vendors to intermediaries and to consumers) and one consumer type (national breeders) had the highest exposure to the flow of birds, and the most trade connectivity. Use of wild-caught over captive-bred birds was high (67% of records), as was use of natural-phenotype birds over hybrid or mutant-phenotype birds (65% of records). Geographically, Spain and Venezuela had the highest exposure to the flow of birds, but Brazil and Colombia had the most direct connections with other countries. The unexpected lack of evidence for parallel trafficking suggests that combined flows of illicit products are not inevitable, even in adverse settings. In a context where law enforcement may not be feasible, our results suggest that it may be possible to reduce unsustainable harvest using breeder connectivity in informational campaigns to stimulate peer-to-peer interactions and accelerate behavior change.

Introduction

Unsustainable use, or overexploitation, is one of the most important threats to global biodiversity (Lawson & Vines, 2014). The portion of this harvest entering illegal wildlife trade creates a black market valued at US$ 5–20 billion/year (Wyler & Sheikh, 2013), and legal trade may also have adverse impacts on targeted species (Santos, Satchabut & Vigo Trauco, 2011). Avian species are the third-most impacted taxonomic group (after mammals and reptiles), mostly due to global demand for cage birds (Bush, Baker & Macdonald, 2014), and overexploitation of birds can clearly contribute to the extinction of threatened bird species in the wild (Angulo *et al*., 2009). Although only 13% of passerines are affected by overexploitation, this order is so speciose that the illegal portion of trade alone has affected over 655 passerine songbird species traded internationally since 1970. The songbird trade particularly affects finches in the families Estrildidae, Fringillidae and Ploceidae (BirdLife International, 2015). The vulnerability of charismatic birds like the Javan Green Magpie *Cissa chinensis* (Nijman *et al*., 2017) and the Blue-headed Macaw *Primolius couloni* (Gastañaga *et al*., 2011) has been well-documented.

However, the operation of markets in these and other high-value species remains opaque (but see Alves, 2013; Chng *et al*., 2015; Su *et al*., 2015). Without a general understanding of who the actors in the market are and how they interact – the market "network structure" – implementing interventions to mitigate overharvest will be difficult, and monitoring efficacy impossible (Clifton & Rastogi, 2016; Milner-Gulland *et al*., 2018).

The songbird trade remains poorly documented, in part because most passerine species are not listed in the primary international instrument for regulating wildlife trade, the appendices of the Convention on the International Trade in Endangered Species (CITES; UNEP-WCMC, 2015). Monitoring mechanisms are rarely in place for species traded outside this instrument, whether they are traded legally or illegally (Challender & MacMillan, 2013). Research on the songbird trade to date has focused on identifying the number of species traded (Daut *et al*., 2015), estimating the number of individuals involved (Alves, 2013), evaluating the laundering of illegally caught wild birds in the captive-bred market (Nijman & Shepherd, 2015), and analyzing the effect of conservation interventions on trade (Cooney & Jepson, 2006). However, few studies have focused on understanding the factors structuring trade (Milner-Gulland *et al*., 2018). Worldwide, much of the songbird trade occurs openly, in street markets or pet shops (Nijman *et al*., 2017), but rare species may be traded through hidden networks of intermediaries and consumers, making them difficult to characterize, understand, and monitor.

Research in other taxa suggests that wildlife trade may sometimes be conducted via "parallel trafficking" (Clifton & Rastogi, 2016), or the movement of illegal animal trade items through the same networks used for illicit drugs, arms, slaves, and other contraband, by criminal and even terrorist groups (Ayling, 2012; Haas & Ferreira, 2015). Actors in these networks may exchange wildlife items directly for other illicit goods, may simply use the same transportation or personnel, or may use the relatively low-risk/high reward from wildlife trade to fund other illicit activities (Clifton & Rastogi, 2016). Factors favoring parallel trafficking include high unit value, high levels of societal corruption/criminality and globalization of communication and markets (Wright, 2011). However, although many cases of parallel trafficking involving mammals have been reported (Warchol, Zupan & Clack,2003), some question the generality of this phenomenon, particularly in birds (South & Wyatt, 2011; Duffy *et al*., 2015; Pires, Schneider & Herrera, 2016).

Alternatively, instead of being parallel, trade in songbirds may be "specialized," moving along networks dedicated to one or few species. Conditions favoring specialization include: (1) demand focused on products that require expertise to identify (e.g. hybrids, mutations or individuals trained for singing contests); (2) maintenance, transport and enforcement evasion requiring special knowledge, contacts or logistical capacities; or (3) geographically restricted access (Phelps, Biggs & Webb, 2016). Understanding exactly which trade type operates is important because each type requires contrasting interventions and monitoring strategies. For example, parallel trafficking may require coordinated law-enforcement and monitoring, with special safety protocols for wildlife professionals (Challender, Harrop & MacMillan, 2015). On the other hand, outreach and education focused on consumer behavior change can be effective if trade is mediated by demand for specialized products or by specialized actor roles (Olmedo, Sharif & Milner-Gulland, 2017). Furthermore, if specialization is mediated by limited access to the traded species, it may be more efficient to protect remaining populations with private reserves.

To understand the prevalence of parallel trafficking, here we examine trade in a high-value songbird in Venezuela, a setting where corruption and criminality are presently among the highest in the world (Botero, Agrast & Ponce, 2018). We employ social network analysis to evaluate the expectation that parallel trafficking should be the main vehicle for trade in this species, while considering varieties of specialization as alternatives (Table 1). We used data from the Red Siskin *Spinus cucullatus*, a Neotropical finch restricted to northern South America (Coats & Phelps, 1985; Sánchez-Mercado *et al*., 2018). This species was nearly eliminated from its historic range due to over-harvesting for the pet trade, and currently only a few populations survive in Venezuela, where the species is classified as Critically Endangered (BirdLife International, 2015). Demand for Red Siskin (RS) was originally driven by avicultural interest in RS hybridization with canaries to produce 'colorbred' red canary lines. However, more recently, interest in natural phenotypes and color mutations has increased (Birkhead, 2014). Today, many small captive populations of tens of individuals exist in a number of countries in the Americas, Europe and Australasia, but anecdotal evidence suggests that breeders still obtain wild-caught specimens for their captive flocks (Rivero Mendoza, 2004). All trade in this species is illegal in Venezuela (Supplementary Materials Data S1), but Venezuela is presently experiencing a breakdown in rule of law, with well-documented and robust traffic in other illicit goods (Transparency International, 2017). Between 2009 and 2016, Venezuela was included among the 20 countries with the most records of bird trafficking via airplanes, mostly to supply demand in the US, Europe and the Middle East (Utermohlen & Baine, 2015). As with other traded songbirds, RS are of high-value and are sourced internationally from both captive and wild populations, through poorly understood markets (Silva Souto *et al*., 2017). Thus, insights from RS may be applicable to other species, and an understanding of factors influencing trade network structure will be useful for designing efficient conservation interventions. Therefore, in addition to testing parallel vs. specialized trade hypotheses, we also aimed to: (1) estimate RS use scope, magnitude and value; (2) identify key actors, their roles and their interactions; and (3) understand trade routes.

Materials and methods

Study area and actor classification

We focused on northwestern Venezuela, where historical probability of RS occurrence is high (Sánchez-Mercado

Table 1. Hypotheses about the structure of Red Siskin (RS) trade in Venezuela

Trafficking hypothesis	Predictions	Indicators
Parallel	1) Intermediaries are dedicated criminals	1) Proportion of actor income earned from illicit activities
	2) Other illicit products are exchanged for RS, are transported with RS, or are handled by actors handling RS	2) Type of goods traded
Specialized, due to focal products requiring specialized knowledge	1) The prevalence of special products across the trade network is higher than specimens with an RS phenotype, particularly among intermediaries and consumers	1) Proportion of RS phenotype specimens used by each actor relative to hybrids and mutations
	2) The cost of captive bred specimens is similar or lower than wild-caught ones	2) Market value for each type of bird traded
	3) The cost of special products is higher than RS phenotype birds	
Specialized, due to the need for specialized contacts and logistical capacity for transport or enforcement evasion	The trade network is restricted by:	
	1) A small number of intermediaries involved in the flow of individuals and money	1) The highest BC values in are found in one or two intermediaries
	2) Few or no direct links between consumers and harvesters, with several linked intermediaries between them instead	2) Consumers have lower IDC values than intermediaries do
Specialized, due to restricted geographic availability of the product	Extraction occurs in a limited, specific geographic area	Percent of specimens originating from each location

et al., 2018). In Venezuela, RS may only be captured or held legally by those with scientific collection permits (Supplementary material Data S1). We defined as "trade" all parts of the RS exchange network: all take without permits of birds from protected or private lands by anyone other than wildlife authorities, and all exchange of birds and their products except by authorized entities (e.g., zoos, wildlife rescue centers). "Use" included all trade, as well as possession. In Venezuela, all use of RS is illegal, but for other countries the use of RS, as defined here, is not necessarily illegal (Supplementary Material S1).

Research on other taxa suggests that RS use may involve three main actor classes (Phelps *et al*., 2016): (1) "harvesters," or people who extract the species directly from its natural habitat; (2) "intermediaries," who transport specimens to markets and trade with other intermediaries or final consumers, and (3) "consumers," who possess RS and are the final link in the trade chain. We used these three categories to initially classify actors identified during sampling.

We used different approaches to identify actor types in each class. To identify harvesters, we used an indirect approach: guided by informants and prior research (Sánchez-Mercado *et al*., 2016, 2017), we identified 19 locations where bird (and in particular RS) trapping was reported (Locations are available upon request, but withheld here to avoid fueling additional illegal trade; Lindenmayer & Scheele, 2017). At each of the 19 locations, we located harvesters via introductions through mutual acquaintances or through conversations with local residents. We identified 51 harvesters, of which 44 were willing to be interviewed (Supplementary material Data S2 and S3). For intermediaries and consumers, we built a preliminary list of informants based on direct contacts by the authors, and on responses from Venezuelan ornithological and captive breeding societies. Then, using "snowball" sampling (a technique in which existing study subjects recruit future subjects from among their acquaintances; Voicu, 2011), we initially identified and contacted five consumers known to co-authors. These then contacted and recruited other consumers and intermediaries, and so on, until we identified 70 consumers and intermediaries in total, of which 64 were willing to be interviewed (Supplementary material Data S2 and S3).

Interviews and online media monitoring

In November 2016 and from March to September 2017, ACU, LM, JMC, and LO conducted semi-structured interviews with the actors described above. In all cases, we obtained verbal informed consent from each subject, after explaining research objectives and assuring subjects that information would be used only for research and presented in aggregate, protecting participant identity (Buppert & McKeehan, 2013). We asked subjects about five main topics: (1) motivations for using RS; (2) knowledge of the trade network and other products (legal or illegal) exchanged, transported, or handled by actors handling RS; (3) techniques used for capture, housing, care, transport, and exchange; (4) number of use events in a given year (use rate); and (5)

number of contacts involved in buying, selling, and possessing RS. Because of the sensitivity of the question, we did not ask actors directly if they engaged in other illegal activities. Instead, we asked if they felt their activities carried risks, and assumed that the co-occurrence of RS trade with other illegal activities would result in a positive response. In these cases, we encouraged interviewees to provide additional details. We also asked about other economic activities, as well as each subject's gender, age, and socio-economic and educational level. Finally, we assessed his or her level of openness and comfort with the interview (Supplementary MaterialS2 and S3). We then classified each actor as one of 25 actor types based on Phelps *et al*. (2016; Supplementary Material S3, Table 2).

In addition to interviewing actors in the RS trade network, we also visited online media sites (Facebook.com and WhatsApp.com) to identify additional records of use events, actors, and information about the geographic distribution of supply and demand. We identified 24 public and closed Facebook groups using keywords in English, Spanish, and French (Supplementary Materials Data S2). In total, we compiled 723 online media use records (352 in Facebook and 371 in WhatsApp). For both, we defined "offers" as any announcement of RS or their products for sale, and "demand" events as any price inquiry or request for RS to purchase. We considered "possession" events any reference to pure RS, hybrids or mutations kept as pets without evidence of commercial transaction. Finally, we classified as "exchange" any barter event. We classified as "captive-bred" birds with closed rings or those explicitly identified as raised in captivity, as "wild" when explicitly described as such, and as "unknown" all others. Classification of individuals as natural RS phenotype, hybrid, or mutation was estimated based on images and post context.

Trade databases and summary statistics

We then generated two databases with information from interviews and online media monitoring. The "actor" database consisted of information from interviews, and contained actor-level information, including socio-economic status and motivations, experience, and evidence of participation in parallel trafficking. In this database, each participant was considered a unique record (109 records in total; Table S3). The "use" database combined information from Facebook, WhatsApp, and interviews, about specific instances of use (Table 2). Each record consisted of a combination of event date; type of use; number, sex, and developmental stage of birds involved; type of specimens involved; actors involved; and wild or captive origin. Trade records contained additional associated information, including the value and currency of the transaction, other goods bartered, etc.

We refined our typology of actors according to the type of specimens involved (RS, hybrids or mutations) and participant socio-economic status and motivations, including investments made and profit margin obtained. We identified 15 actor types involved in RS use, and were able to gather data on 10 of those types (Table 2; Supplementary material Data S3). We obtained anecdotal references to the remaining five types, but they could not be corroborated. We estimated the frequency of each actor type, though we were only able to describe socio-economic status and motivations for actors identified through interviews, because online media records did not contain this information. We also summarized socio-economic traits and motivation frequencies, and classified the proportion of monthly income that each actor type derived from RS trade profits. We finally recorded how much each actor spent monthly on activities related to RS use.

We then described RS use in three ways: (1) use volume (number of individuals used and their value), (2) actor network configuration (actor nodes and connections among them), and (3) trade routes (country nodes and connections). For these analyses, we first filtered the data, removing records in which the number of individual birds traded or their origin could not be determined. We calculated the total number of RS individuals used, as well as the number of individuals used in national and international markets, and the number of records of each transaction type (supply, demand, possession and exchange) for each actor type. However, because birds may be transferred among multiple actors, we could not distinguish when different events involved the same individual birds. Thus, our estimates should be interpreted as an index of use rather than an estimation of the absolute number of different individuals used. Finally, we summarized the US dollar value of national and international trade. We expressed values in US dollars using the mean currency conversion value during the monitoring period. We also calculated the mean value of RS, hybrids and mutations, as well as their standard error.

Social Network Analysis (SNA) and trading routes

Next, we analyzed networks using SNA as implemented in the R package *igraph* (Csardi & Nepusz, 2006). We represented our data as two directed, weighted networks of n nodes, one of actor types and one of countries. Nodes were connected by L observed fluxes (or "directed edges"), weighted by the number of individuals traded across nodes. For our models, we created two adjacent matrices describing these flows of trade in individual birds (L_{i}), among either actor type (L_{iACTOR}) or country nodes (L_{iCOUNTRY}).

We calculated three measures to describe network distribution for each matrix: "In-Degree Centrality" (IDC), "Out-Degree Centrality" (ODC) and "Betweenness Centrality" (BC) following Clifton & Rastogi (2016). IDC indicated the number of edges directed into each node, such that an actor type with a high IDC had higher exposure to the content flowing through the network (Freeman & White, 1991). ODC indicated the number of edges that a given node directed to others, so higher ODC may be interpreted as greater gregariousness. We also calculated BC, the number of instances in which a node served as the bridge linking the shortest path between two other nodes that were not otherwise connected directly. We did not use weights in our BC calculations because *igraph* treats edge weights as a measure of cost rather than strength, which was incorrect in the case

Table 2. Types of actors involved in using RS in Venezuela, adapted from Phelps *et al.* (2017), and records of use 2010–2017. Types with one or more records are indicated in bold

Actor	Type	Description	Records	Market (%)	Trade items (%)	RS origin (%)	Profit (%)
Harvester	**Opportunistic (op)**	Harvesters who trapped RS on demand, searching intensively (+20 h/week), but for whom RS trade was not a primary income source	24	National 100 International 0	RS 100 H 0 M 0	Wild 100 Captive 0	*N* = 13 Scant 8 Some 69 Half 15 Most 8
	By-catch (bc)	Harvesters aiming to trap other species, investing moderate search effort (12 h/week)	0	-	-	-	-
	Specialist commercial (sc)	Harvesters with explicit commercial goals and with significant avicultural skills, focused on RS	154	National 100 International 0	RS 100 H 0 M 0	Wild 100 Captive 0	*N* = 2 Scant 0 Some 0 Half 0 Most 100
	Local guide (lg)	Local residents hired to guide non-resident harvesters, providing logistical support, but not directly involved in trapping	0	-	-	-	-
	Recreational (rc)	Local residents who trap birds for enjoyment, frequently releasing birds after a few days	0	-	-	-	-
Intermediary	**Vendor to consumers (vc_n, vc_i)**	Seller without breeding or trapping skills, focused on commercial transactions with birds, who traded directly with consumers	485	National 17 International 83	RS 61 H 10 M 29	Wild 16 Captive 84	*N* = 3 Scant 0 Some 0 Half 33 Most 67
	Vendor to intermediaries (vi_n, vi_i)	Seller without breeding or trapping skills, focused on commercial transactions with birds, who traded directly with other intermediaries	64	National 81 International 19	RS 100 H 0 M 0	Wild 88 Captive 13	*N* = 5 Scant 0 Some 20 Half 60 Most 20
	Logistician (lo)	Aggregator of birds at interim locations, from different sources, who had animal health care skills but no captive breeding skills	3	-	RS 100 H 0 M 0	Wild 100 Captive 0	*N* = 4 Scant 0 Some 25 Half 0 Most 75
	Launderer (la_n, la_i)	Intermediaries with captive breeding skills who insinuated the offspring of wild-caught birds into legal captive breeding markets. They were members of or had contacts with avicultural clubs, to obtain closed rings	54	National 13 International 87	RS 100 H 0 M 0	Wild 83 Captive 17	*N* = 2 Scant 0 Some 50 Half 0 Most 50

Table 2 Continued.

Actor	Type	Description	Records	Market (%)	Trade items (%)	RS origin (%)	Profit (%)
	Processor (pr)	Intermediaries with captive breeding skills involved in producing hybrids or mutations from wild-caught RS. They generally believed that "fresh blood" from the wild was essential to produce robust hybrids	12	National 100 International 0	RS 100 H 0 M 0	Wild 100 Captive 0	*N* = 1 Scant 0 Some 0 Half 100 Most 0
	Third party (tp)	Intermediaries involved in transporting wild-caught birds from extraction localities to main cities. They do not have trapping or captive breeding skills are not involved with trapping	20	National 100 International 0	RS 100 H 0 M 0	Wild 100 Captive 0	*N* = 0
	Smuggler (sm)	Intermediaries that exported wild birds or helped intermediaries to evade detection with bribes	0	-	-	-	-
	Government colluder (gc)	Government employees directly involved in the illegal bird trade or indirectly supporting other intermediaries	0	-	-	-	-
Consumer	**Breeder (br_n, br_i)**	Hobbyists from avicultural clubs and societies who sought RS for captive breeding, but also sometimes sold them to others	83	National 51 International 49	RS 100 H 0 M 0	Wild 39 Captive 61	*N* = 5 Scant 0 Some 60 Half 20 Most 20
	Owner (ow_n, ow_i)	Consumers without breeding skills who kept RS as pets, and were not necessarily connected to avicultural clubs	321	National 97 International 3	RS 31 H 55 M 14	Wild 9 Captive 91	*N* = 1 Scant 0 Some 100 Half 0 Most 0

RS, pure Red Siskin; H, Hybrid; M, Mutation.

Profits indicate the proportion of income derived from Red Siskin trade: Scant (very little); Some (25% or less); Half (26% to 50%) or Most (51% or more). *N* indicates the number of actors who shared financial information in interviews.

of our trade network. An actor with high BC was likely to experience a greater flow of birds through the network if trade tended to follow the shortest path, and were actors whose removal from a network had the highest likelihood of disrupting network cohesiveness (Hinsley *et al*., 2016). We used the function *edge.betweenness.community* of *igraph* to identify cohesive groups of nodes, or "modules" that had more connections within them than to other nodes, which we represented using a hierarchical map or rooted tree (Csardi & Nepusz, 2006). We quantified the modularity score Q, which ranged from -1 to 1, and measured how strong the division was: the more positive the value of Q, the more significant the grouping. By definition, the entire network (as one community) had $Q = 0$.

Results

Trade and use volume, value and actors

Of 2575 Red Siskin (RS) use records compiled from 2010–2017, we recorded just six records in which actors were reportedly also involved in other illegal activities. We were unable to corroborate these reports, which consisted of members of the military trafficking in illicit goods. We furthermore detected no instances of RS or their products being exchanged for or traded alongside illicit non-monetary goods, except for other illegal bird species (mainly psittacids, exotics, and seedeaters), which were also traded by three actor types (logisticians, vendors, and launderers; Supplementary material Data S2).

In total, our records corresponded to a use index of 368 individuals/year. Among the 1113 records concerning trade, 773 involved captive-bred birds, 296 involved wild birds, and 44 involved birds of unknown origin. Some trade records involved more than one bird, such that the cases involving wild birds consisted of a total of 491 RS that were removed from the wild (190 adult females, and 301 adult males), suggesting an annual extraction rate of at least 70 individuals/year in western Venezuela. Across all records, 67% pertained to use of wild-caught birds. However, not all actors used wild-caught individuals in the same proportion. As expected, the focus on wild-caught RS was high among harvesters (100% of records involved wild birds), and although it was also high among intermediaries (83–100%), it was lower for final consumers, particularly owners (9%; Table 2).

Individuals with the RS phenotype were the focus of most use. On average, just 16% (142 records of 881 use event records with information about specimen phenotype) corresponded to mutations and 19% to hybrids (167), while 65% were RS (572 records), although again this varied greatly by actor type. As expected, harvesters (both opportunistic and specialist commercial, *op* and *sc,* respectively) focused exclusively on RS in domestic markets. Intermediaries also focused more on RS than mutants or hybrids; third parties (*tp*), processors (*pr*), vendors to intermediaries (*vi*) and logisticians (*lo*) also traded RS exclusively, although vendors to consumers (*vc*) also traded mutants and, to a lesser extent, hybrids (Table 2). Among consumers, breeders (*br*) focused exclusively on RS (mainly in international markets; see below), but owners (*ow*) were quite different, with hybrids the most used (55% of records), followed by RS (31%) and mutations (14%; Table 2).

We detected no instances of trade profits being used to fund illicit activities. The total value of the RS trade detected was US$37,499 (±SE $168) in records spanning 2010–2017, although many interview subjects declined to give information about the value of their RS transactions (Table 2). Because of this, we were also unable to estimate the portion of trade value in the hands of each actor class, nor compare wholesale to retail prices for RS. Mutations cost significantly more than natural RS phenotypes (mutations $69 ± SE 7; RS $40 ± 5; chi-squared = 7.7543, P-value = 0.005), as well as hybrids (chi-squared = 5.022, P-value = 0.03), but there was no difference between hybrids and natural RS phenotypes (hybrids $45 ± 21; chi-squared = 0.30973, P-value = 0.5778). Also, we found no difference between the mean retail price of captive-bred ($45 ± 3) vs. wild-caught birds ($48 ± 12; chi-square = 0.069, df = 1, P-value = 0.793). Opportunistic harvesters (*op*) reported being motivated in part by the prospect of additional income, while specialist commercial harvesters (*sc*) were motivated more by an interest in improving their breeding skills. Reported motivations for by-catch harvesters (*bc*) varied from additional income to improvement of breeding skills (Supplementary material Data S3). Most harvesters were adult males over 30 years old with low education levels, except for specialist commercial harvesters, of whom two of the six identified were career professionals.

Similarly, we found few intermediaries motivated by other illicit activities. Most intermediaries were adult males (> 27 years) with at least primary school education. The main motivation expressed by processor (*pr*), launderer (*la*), logistician (*lo*) and vendors to intermediaries (*vi*) was an interest in improving their breeding skills. Although smuggler (*sm*) and government colluder (*gc*) intermediaries were together mentioned six times by our informants, we were not able to confirm their existence or obtain records of their trade activities. Breeders (*br*) clearly indicated that profit was not an important motive, and invested money to purchase birds, although they did sometimes sell them. They were mostly professional males, up to 46 years of age. Finally, we uncovered limited information on the profile and motivations of owners (*ow*, Supplementary material Data S3), though this typology accounted for hundreds of records, mostly from online media (Table 2).

Trade network structure

Our actor network had 17 nodes, connected by 34 edges (Fig. 1a). International owners (ow_i), vendors to consumers (vc_i) and launderers (la_i) handled the highest proportion of individuals (Table 3). National vendors to intermediaries (vi_n) and to consumers (vc_n) as well as breeders (br_n) had the most direct connections, with the highest IDC values, and also the highest BC values (Table 3). Harvesters had the highest ODC values, consistent with their expected role as

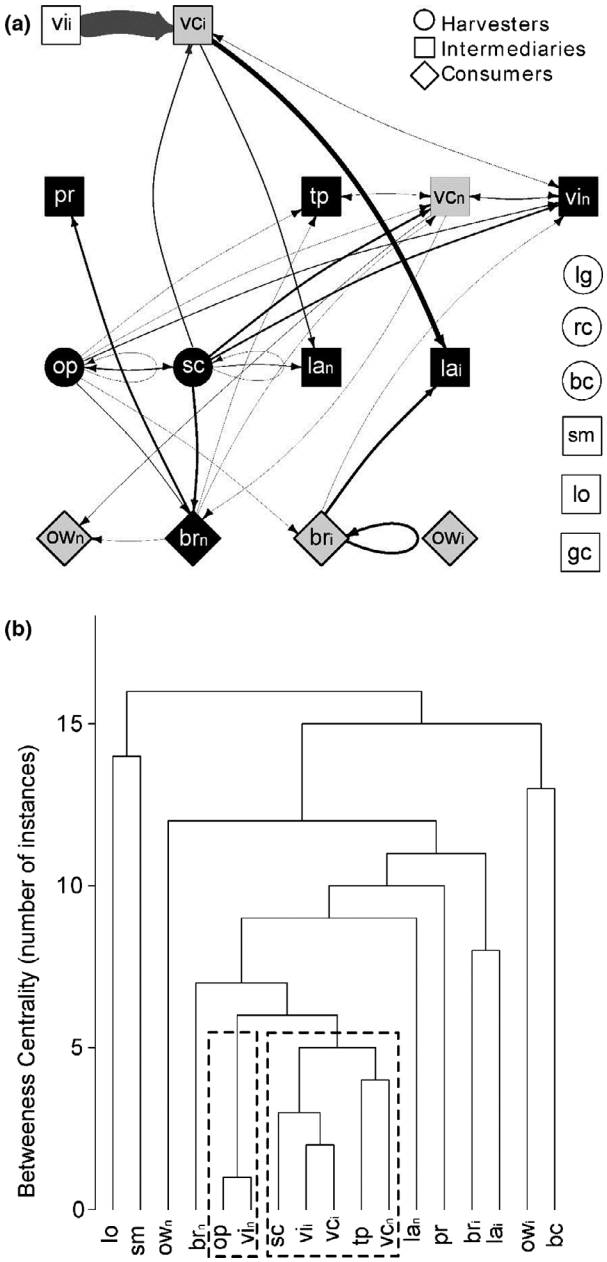

Figure 1 Red Siskin actor network analysis. Subscripts indicate international (i) or national (n) trade, and abbreviations are as in Table 2 as follows: Opportunistic (op), By-catch (bc), Specialist commercial (sc), Local guide (lg), Recreational (rc), Vendor to consumers (vc_n, vc_i), Vendor to intermediaries (vi_n, vi_i), Logistician (lo), Launderer (la_n, la_i), Processor (pr), Third party (tp), Smuggler (sm), Government colluder (gc), Breeder (br_n, br_i), Owner (ow_n, ow_i); (a) Flow of Red Siskins across actors. Harvesters are represented as circles, intermediaries as squares and consumers as diamonds. Flows are represented by lines and direction by arrows. Line thickness is proportional to number of individuals traded. Actor color indicates the proportion of wild-caught Red Siskins traded, either 50% or more (black), or less than 50% (gray). Actors in white had no information about trade activity. (b) Dendrogram of the actor network. Dotted boxes represent modules of densely connected actor types.

RS suppliers. National owners (ow_n) had high IDC and low ODC values, suggesting that they acted as RS consumers. In contrast, international breeders (br_i) had high ODC but low IDC values, suggesting that they acted more like suppliers than consumers, while national breeders (br_n) acted in both ways to an equal degree. The two modules identified had a Q value close to 0 (0.033) suggesting that they were not strongly isolated (Fig. 1b). The first module was dominated by vendors to consumers in Venezuela (vc_n), who were more densely connected with third party intermediaries (*tp*), specialist commercial harvesters (*sc*), and international vendors to consumers (*vc*) and intermediaries (vi_i). The second module was dominated by vendors to intermediaries in Venezuela (vi_n) who were more directly connected with opportunistic harvesters (*op*). Finally, breeders in Venezuela (br_n) interacted with both modules (Fig. 1b).

Red Siskin trade routes

Geographically speaking, internationally Spain and Venezuela most influenced the flow of individuals, with the highest BC values. Brazil, Colombia and Mexico had high IDC but very low ODC, suggesting they acted as consumers, while Venezuela, USA and Spain had high ODC but very low IDC, suggesting they acted as suppliers (Table 3). The country network had a much higher value of Q (0.37), suggesting greater isolation of the three modules identified (Fig. 2b). The first module was dominated by Venezuela (accounting for 51% of transactions) which traded RS with countries in the Americas (United States, Curacao, Aruba, Cuba, Colombia), Europe (Spain, Portugal and Ireland) and Asia (China). The second module connected Vietnam and Indonesia, the latter of which surprisingly also provided RS to Brazil. A third module revealed trading between Mexico and Argentina, and weakly related them to Brazil (Fig. 2b).

At the national level, the source of RS for most trade records was, as expected, the western region of Venezuela (71% of records, including locations in Lara, Trujillo and Zulia states). The central region was the main destination for Venezuelan trade records (56% of records, mainly to the capital city of Caracas).

Discussion

Drivers, scope and magnitude of Red Siskin use and trade

We found almost no evidence to support the hypothesis that trade in RS originating in western Venezuela is driven by parallel trafficking. Even though we confirmed that RS were high value (with trading for amounts per bird that nearly an order of magnitude higher than the monthly minimum wage at the time), of more than two thousand RS use records obtained from 2010–2017, none involved the exchange of birds for illicit goods, or were conducted via networks or actors involved in the trade of such goods. Only six records were reported to involve actors connected with government collusion or smuggling. Among all actors interviewed

Table 3. Network analysis for the flow of RS between 2010 and 2017 among a) actors (L_{iACTOR}) and b) countries ($L_{iCOUNTRY}$). Values indicate Betweenness Centrality (BC), In-Degree Centrality (IDC), Out-Degree Centrality (ODC), and the number of birds sought or offered by each actor. Units for BC and IDC/ODC are number of edges and number of instances, respectively. Abbreviation of actor types as in Table 2. Subscripts indicate international (i) or national (n). Highest BC and IDC/ODC values in bold

(a) L_{iACTOR}

	Harvesters		Intermediaries									Consumers			
	op	sc	Vc_n	vc_i	Vi_n	vi_i	lo	la_n	la_i	pr	tp	br_n	br_i	ow_n	ow_i
BC	1	1	**20**	16	**30**	0	0	0	0	0	0	**18**	1	3	0
IDC	2	2	**5**	3	**5**	0	0	3	2	1	3	**4**	2	1	0
ODC	**8**	**8**	3	3	3	1	0	0	0	0	1	4	3	0	0
Birds sought	6	0	66	217	58	0	0	74	96	84	12	32	86	22	418
Birds offered	46	49	76	771	64	0	0	0	198	0	12	89	26	0	0
Total birds	52	49	142	988	122	0	0	74	294	84	24	121	112	22	418

(b) $L_{iCOUNTRY}$

	Argentina	Belgium	Brazil	China	Colombia	Cuba	Curacao/Aruba	Europe	France	Indonesia	Ireland	Italy	Mexico	Portugal	Spain	USA	Venezuela	Vietnam
BC	8	0	0	0	**12**	0	0	0	0	0	0	0	0	0	**35**	0	**29**	0
IDC	2	0	**4**	2	3	1	1	1	0	0	1	0	2	1	**5**	2	3	1
ODC	3	0	1	0	1	0	0	0	0	2	2	0	1	1	**5**	3	**8**	0

involved in RS trade nationally, most (65%) received <50% of their income from RS trade (Table 2). Instead, the majority of their incomes came from other legal activities, primarily professional and entrepreneurial activities.

Rather, our data were more consistent with hypotheses of specialization in RS use and trade. Some evidence pointed to specialization due to a need for expert contacts and logistical capacity for transport or enforcement evasion. Market channels were concentrated: the highest BC values were observed in just a handful of Venezuelan intermediary actor types (Tables 1 and 3). Of the eight intermediary types identified, just two (Vc_n and Vi_n) maintained the connections required to control flow of birds through the network (Table 3), and consumers had few direct connections with harvesters (Fig. 1a,b). Furthermore, distinct geographic modules emerged, with a high Q scores (Fig. 2b), indicating that flow between country groupings was limited. Evidence for specialization due to focal products requiring specialized knowledge was more mixed. Supporting this hypothesis was the fact that prices for captive-bred and wild-caught specimens were similar, and the price of mutations was higher than natural-phenotype birds. However, on the other hand, natural-phenotype and hybrid birds had similar prices, and special products were not more prevalent overall across the trade network than natural-phenotype birds – although there was one exception: special products were markedly favored by owners (*ow*), with just 31% of records involving natural-phenotype birds.

The proportion of records involving captive-bred birds also increased toward the end of the chain of trade actors: records of breeders (*br*), vendors to consumers (*vc*) and owners (*ow*) involved 61%, 84% and 91% captive birds respectively (Table 2). Anecdotal evidence suggests that breeders (*br*) are primarily located in countries other than Venezuela, where operations are small hobby aviaries producing dozens of birds each year. These operations may play an important role in supplying international markets; indeed, in contrast with assumptions of prior authors (Rivero Mendoza, 2004), we found that breeders (*br*) were not only consumers, but served as intermediaries as well, also selling birds. The similarity in cost of wild-caught and captive bred individuals that we documented in Venezuela may indicate that breeding is not yet a cost-efficient way to meet market demand within Venezuela, in spite of a preference for captive-bred birds. Future research on captive breeding operations will be useful for better understanding the role of aviculture in RS conservation, as will research on the effect of limited supply, on wholesale vs. retail prices, and on how behavioral differences may affect the preference for wild vs. captive-reared birds.

Finally, the magnitude of trade uncovered was sufficient to constitute an important threat. Our use index estimated that 324 Red Siskin individuals used annually, with at least 70 different individuals extracted from the wild per year in western Venezuela alone. On one hand, these numbers were small compared with documented trade in other passerine species. For example, 6381 individuals of the Oriental White-eye *Zosterops palpebrosus* were sold in Taiwanese pet

shops in 2012 alone (Su *et al*., 2015), while at least 10 972 individuals of the Yellow-bellied Seedeater *Sicalis nigricollis* were sold in just four street markets in Recife, Brazil in 2011 (Silva Regueira & Bernard, 2012). On the other hand, however, compared to the estimated number of remaining wild individuals for each of these species, the trade of RS was proportionally high; for example, *Z. palpebrosus* is still considered abundant in the wild (BirdLife International, 2015), while only a few thousand RS are estimated to persist in the wild in Venezuela (Rodríguez-Clark *et al*., 2015). Moreover, because trade in RS occurred mainly through a closed network of actors, it is likely that our results significantly underestimate the actual use of RS.

Research biases and needs

Although our work has clarified the structure of the RS trade network, gaps in our understanding remain. Our data had geographic, linguistic and temporal sampling biases, which could have affected results in two main ways: (1) causing an underestimate of trade magnitude, and (2) detecting a smaller range of actor types and trade routes than actually existed. These biases were due in part to the fact that our actor profiles were based on interviews only with Spanish-speaking people living in Venezuela, and our search of trade records was limited to Spanish, English, Portuguese and French, omitting important consumer languages like German, Dutch (Birkhead, 2014), and many languages from Southeast Asia. Indeed, we may have found only the tip of the Red Siskin trade iceberg in southeast Asia. At least 157 captive-bred RS individuals were offered by internet vendors based in Indonesia to disparate countries like Vietnam, Brazil and Spain. Currently, Indonesia is sixth in the top 10 countries providing native wild birds to US, Europe and the Middle East (Utermohlen & Baine, 2015), but its role as a transit country in the bird trade has not been well-documented. Clearly, greater monitoring effort will be necessary to better understand trade in Asia, as well as Europe, which appears to be the main market destination for Red Siskins from Venezuela (Fig. 2a).

Furthermore, interviewees reporting on illicit behavior may have underreported their activities if they did not trust us. However, the accuracy of our estimates of trade magnitude was likely reduced more by source sampling bias than by interviewee confidence. The high level of impunity for environmental crimes in South America in general, and in Venezuela in particular, along with relaxed demeanors of interviewees during interviews, suggested that our sources were indeed confident in sharing accurate trade information about RS (particularly on impersonal platforms like social networks). Nonetheless, under-reporting was still expected, due to poor recall among interviewees, to limitations on following up with all sources detected, or to limitations in distinguishing when different trade/use events involved the same individual birds. Furthermore, we were unable to distinguish wild-caught from captive-bred individuals with absolute certainty, and instead had to reply on interviewee information. Even using information about closed rings was not a perfect indicator of legal status, as CITES regulations distinguish between captive-*born* birds (hatched to wild-caught parents, which are illegal) and captive-*bred* birds (hatched to parents that are themselves captive bred- or -born; Nijman & Shepherd, 2015). Laundering may occur when captive-born individuals are declared as captive-bred, perpetuating use of wild-caught adults.

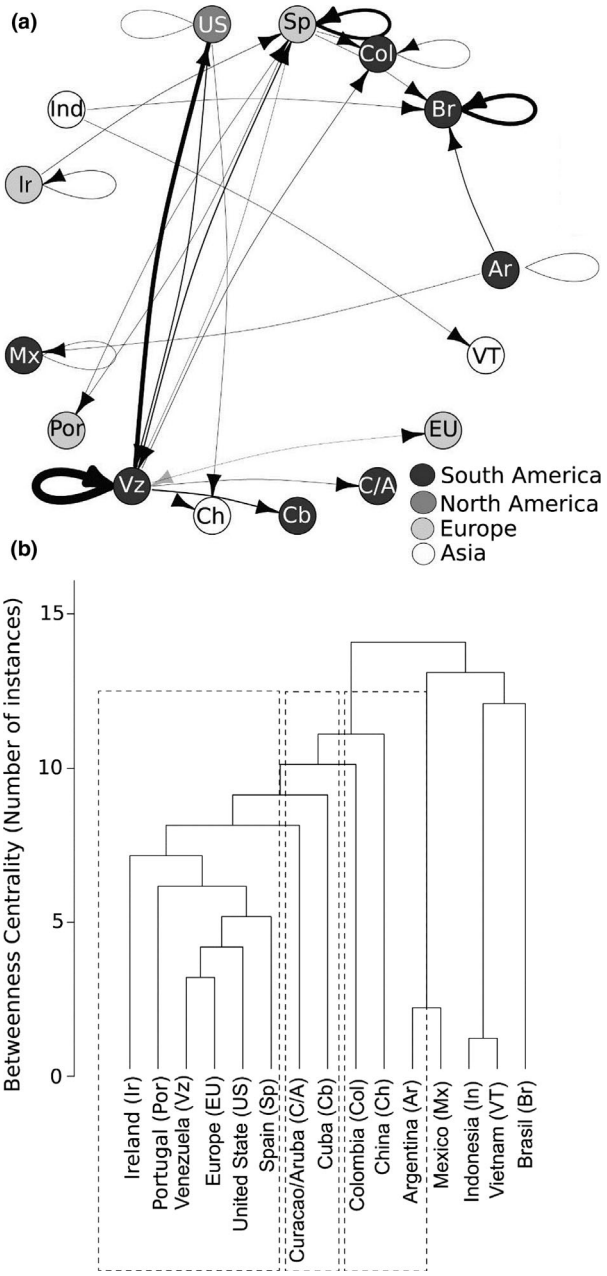

Figure 2 Red Siskin trade routes. Circles represent geographic regions. Subscripts as in Figure 1. (a) Flow of Red Siskins across countries. Flows are represented by lines and direction by arrows. Line thickness is proportional to number of individuals traded. (b) Dendrogram of the country network. Dotted boxes represent modules of densely connected countries.

Detectability of actor types was also likely reduced by low complementarity among and incompleteness of sources. More than 70% of records for 17 of the 19 actor types identified came from just one source (interviews), while social media was the only source that produced records of two other actor types, international vendors to consumers (vc_i) and international owners (ow_i). Moreover, our sources, which were largely local for interviews, were by definition incomplete, as an important portion of intermediaries may operate overseas. They were therefore only able to provide us part of the picture, biased toward the start and away from the end of the chain of trade actors. For example, it is not clear how international owners (ow_i) obtained birds and to whom launderers (*la*) sold them (Fig. 1a). Three actor types for which we documented little or no trade activity (government colluder *gc*, smuggler *sm* and logistician *lo*; Table 2) may be key for filling these gaps, and this incomplete picture may be due to biases in the search process. For example, our search of trade records did not include all relevant international sources, like cage bird clubs and aviculturist societies.

Opportunities for intervention

Although future parallel trafficking in Red Siskins in Venezuela may yet be uncovered, the present study makes clear that an important amount of RS trade operates through a specialized network. The standard strategy to reduce trade in the face of parallel trafficking is to disrupt the network by removing actors with the highest degree of betweenness, using law enforcement either to enforce trade bans or conduct surveillance (Challender & MacMillan, 2013). The weakness of this approach (beyond its failure to address underlying trade drivers), is that such enforcement would be a challenge to implement presently, given the broad geographic activity of the actors, the veiled nature of vendor operations, and the present breakdown of rule of law in Venezuela (Botero *et al*., 2018). Furthermore, this approach does not take into account the typically high resilience of wildlife trafficking networks, whether absorbing and therefore withstanding disruption, or adapting to changes arising from that disruption (Ayling, 2012). Given current conditions, such interventions could even foster a parallel trade that was not previously strong.

Rather, the discovery of a specialized network opens the opportunity of using an "induction" approach to mitigating the impact of RS trade. Induction takes advantage of the capacity of one actor type to connect with most of the network, to stimulate peer-to-peer interaction and create cascades of information to accelerate behavior change (Valente, 2012). Globally, there appear to be few breeders successfully reproducing RS in captivity, and this small group may enjoy respect among aviculturists. Breeders furthermore appear motivated more by the challenge of breeding this species than by profits. Breeders could therefore be "seeds" in a campaign to promote more sustainable uses (captive-bred over wild-caught RS, with closed rings to reduce laundering, etc) as a way to reduce the demand of wild-caught RS. "Seed" members recruit new members in their social networks, who subsequently encourage additional people to participate, and so on (Arvelo *et al*., 2017). Although there are some examples of successful captive-breeding programs to supply markets for endangered species (e.g., Vall-llosera & Cassey, 2017), there is still a high risk of such programs being used to launder wild-caught individuals (Nijman *et al*., 2018), In any case, other alternatives, such as campaigns to reduce harvest pressures, still require an in-depth understanding of demand, including consumer preferences and willingness to accept substitutes, the social dynamics of consumption, and the key attributes of species in demand (e.g., wild vs. farmed) as well as the social functions they perform (Challender *et al*., 2015).

The present study is one of the few network analyses conducted for trade in any bird species (Reino *et al*., 2017), and our framework for evaluating the relative importance of structural and contextual factors driving specialized trade that could be widely applied to other networks of specialized trade in endangered birds. In particular, this approach allowed us to focus on identifying the actors who may be open to changing their demand behavior, which is arguably more influential in wildlife trade than enforcement or other regulation (Challender *et al*., 2015). Future work will include the use of models such as the theory of planned behavior (Zain, 2012) to identify and prioritize the underlying factors that influence the behavior to be changed, and use this information to develop effective interventions targeted at the key actors identified (Saypanya *et al*., 2013).

Acknowledgements

Funds for this research were provided by the Neotropical Bird Conservation Fund, Provita, the Instituto Venezolano de Investigaciones Científicas, a Round Up for Conservation Grant from Smithsonian's Friends of the National Zoo, and a donation from Mr. James Sillers. We are grateful to the anonymous participants in this research for their cooperation, and to A. Blanco-Dávila, D. Romero, L. Torres, P. Caldera, J. Rojas, A. Navas Espinoza and J. Escudero for their support during field work. We thank Michael Fidler for information about international breeders, and J. Ott, Matthew Silk, and an anonymous reviewer for insightful comments on earlier versions of this manuscript.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Legal framework governing Red Siskin use.

Data S2. Internet monitoring and detailed interview methods.

Data S3. Actor classification.