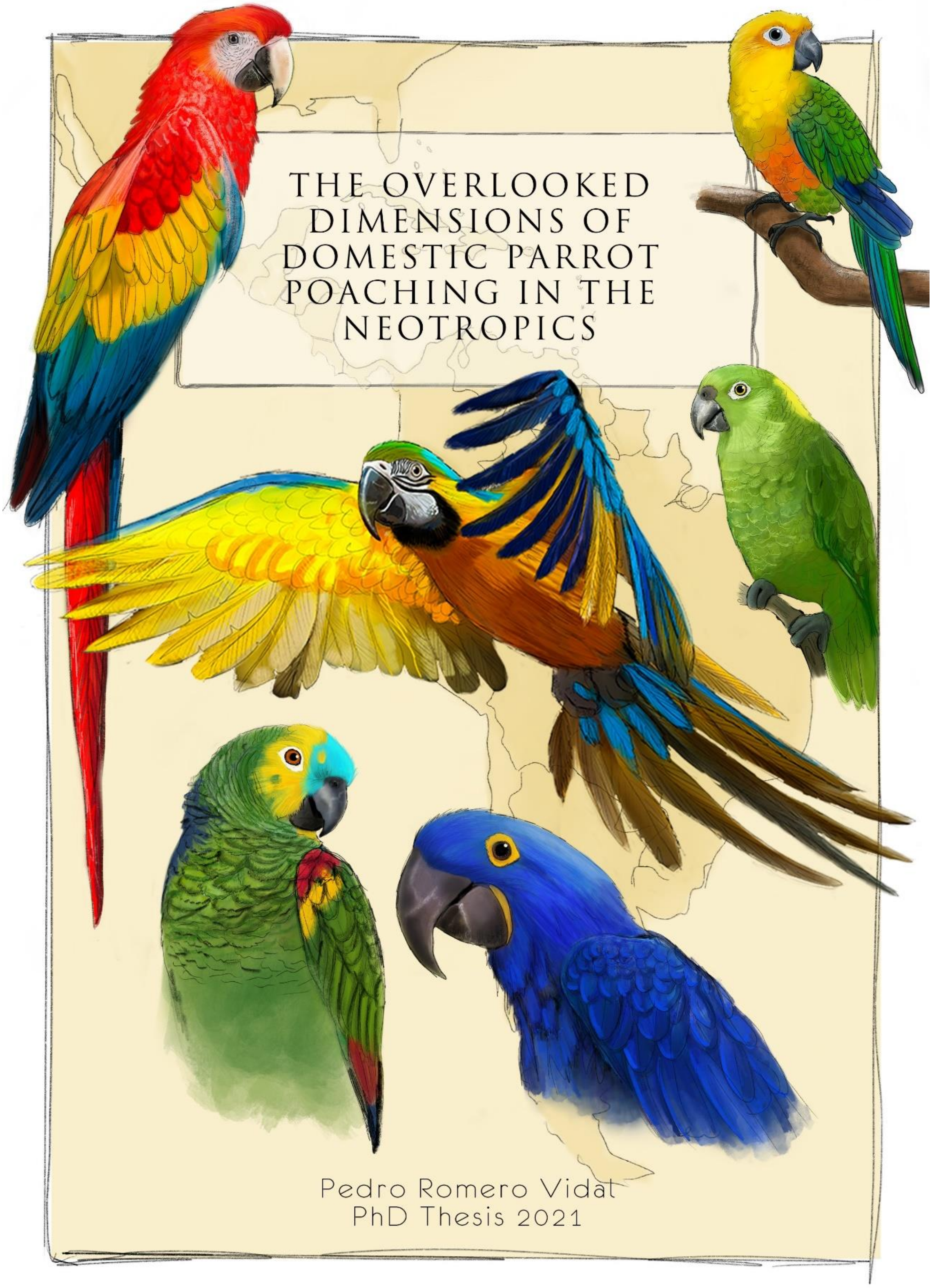

THE OVERLOOKED DIMENSIONS OF DOMESTIC PARROT POACHING IN THE NEOTROPICS

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The overlooked dimensions of domestic parrot poaching in the Neotropics

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Resumen

Los procesos de defaunación tienen importantes consecuencias ecológicas. Numerosos factores pueden propiciar dichos procesos de defaunación, incluyendo el cambio climático, la pérdida de hábitat o la persecución directa por el ser humano. El tráfico ilegal de fauna representa una de las causas más importantes de defaunación, constituyendo una seria amenaza para un gran número de especies de vertebrados en todo el mundo.

Los loros (Psittaciformes) constituyen uno de los grupos de aves más amenazados del planeta, encontrándose el 28% de sus especies bajo amenaza según los criterios de la IUCN. Entre las principales amenazas de este grupo se encuentran la pérdida de hábitat como efecto de la deforestación y la intensificación agrícola, y el tráfico ilegal de fauna. Si nos centramos en la región Neotropical, podemos ver que aquí el porcentaje de especies amenazadas es incluso superior, llegando a representar el 36%. Lo loros se han visto muy afectados por el tráfico ilegal de fauna debido características como son su atractivo plumaje, inteligencia y capacidad de imitar la voz humana, que los ha convertido en una popular mascota en todo el mundo.

Hasta fecha muy reciente la atención de la comunidad científica con respecto a la problemática del tráfico ilegal se había centrado fundamentalmente en el tráfico internacional, restando importancia al papel que podía desempeñar el tráfico ilegal a una escala más local. Un reciente estudio llevado a cabo con 196 poblaciones de loros Neotropicales comprobó que el tráfico ilegal a nivel doméstico constituía una de las principales amenazas. Además, diferentes estudios realizados en varios mercados de Sudamérica comprobaron que miles de individuos son vendidos al año para abastecer la demanda local de loros en estas zonas. Esto pone de manifiesto la importancia que este tipo de tráfico ilegal puede tener para la conservación de las especies de loros

Neotropicales. Sin embargo, muchos aspectos de esta actividad siguen estando poco estudiados.

Esta tesis aborda diferentes aspectos del tráfico ilegal de loros en el Neotrópico a nivel doméstico, pasados por alto hasta la fecha. Para ello, se ha llevado a cabo un exhaustivo trabajo de campo comprendiendo más de 40.000 km de recorrido en 12 países. Así mismo, se han utilizado nuevas herramientas estadísticas, como es la utilización del índice se selección de Savage, que han permitido arrojar luz sobre algunas de las cuestiones más controvertidas en referencia a esta importante amenaza para los loros.

A partir de los datos obtenidos en el mercado de Los Pozos en Bolivia, gracias a un exhaustivo seguimiento de 5 años por parte de un parabiólogo (una persona sin estudios en el campo de la biología, pero con amplia experiencia en la identificación de las especies de loros nativas) se pudieron obtener estimas muy fiables del número de loros vendidos anualmente en dicho mercado. Realizando un muestreo paralelo en las principales localidades del país que constituían lugares habituales de origen, se pudo estimar la proporción de individuos que son capturados y enviados al mercado, comprobando que solo un 20% son destinados a venta en dicho mercado mientras que el resto permanecen localmente o son vendidos sin llegar a entrar en el mercado. Esto permitió estimar que más de 370.000 individuos son capturados en Bolivia cada año, sobrepasando enormemente cualquier estima anterior referente a tráfico ilegal doméstico. Además, a través de las edades de los loros que estaban vivos o la edad a la que murieron, se pudo comprobar que la mediana se situaba entorno a los 2 años, poniendo de manifiesto el importante turnover existente.

En segundo lugar, se discute la hipótesis planteada por criminalistas ambientales, en la cual establecen que el tráfico doméstico de loros es una actividad oportunista focalizada en las especies más abundantes y no en aquellas más apreciadas. Utilizando datos de campo obtenidos en Colombia en un muestreo a gran escala, se arroja luz acerca de este aspecto en particular, comprobando que esta actividad se encuentra dirigida hacia aquellas especies más atractivas, que además adquieren un valor más alto en el mercado.

Utilizando datos obtenidos en dos muestreos realizados en Perú y Ecuador se analizan las rutas nacionales de comercio ilegal de loros a nivel local. Utilizando la misma metodología de campo, pero además calculando las distancias desde las localizaciones de todas las mascotas ilegales encontradas hasta el punto de su área nativa más cercano a través de carreteras, se analiza si existen diferencias en cuanto a las distancias a las que son movidos las especies en función de las preferencias de la gente. También se analiza si el tráfico se focaliza en mercados o a una escala más local, en las propias zonas dónde se extraen los individuos sin entrar a los mercados de fauna. Esto permitió comprobar como los individuos de aquellas especies más atractivas son desplazados hacia zonas más lejanas mucho más que los pertenecientes a especies menos apreciadas por la gente local, y que la mayor parte del tráfico ilegal ocurre a una escala más local, sin pasar a través de los mercados de fauna.

Otra de las cuestiones sin resolver es la importancia relativa que tienen la pérdida de hábitat y el tráfico ilegal doméstico como amenazas para los loros a nivel Neotropical. Utilizando como modelo Costa Rica, al ser unos de los paradigmas de conservación a nivel del Neotrópico, se analiza como estos dos factores afectan a las poblaciones de loros. Para ello se diseñaron recorridos sistemáticos por carretera, en los que se contabilizaron todos los loros de todas las especies encontradas, así como el grado de antropización del medio en el que se encontraban. De esta forma, y complementando estos datos con información obtenida de teledetección, se pudo comprobar que el hábitat no tenía un efecto significativo para las comunidades de loros de Costa Rica, pero si estaban afectadas por el tráfico ilegal, que era muy intenso y focalizado en ciertas especies, a pesar de la gran protección ambiental existente en el país.

destacando el importante papel que juega el tráfico ilegal incluso en zonas con una gran protección ambiental.

Utilizando como modelo de estudio República Dominicana, se evaluó el estado de las dos especies de loros nativos de observó que se encontraban en una situación crítica, residiendo la mayor parte de la población de ambas especies dentro de las ciudades, que actuaban como protección ante las amenazas a las que estaban expuestas. Estás dos especies se veían muy afectadas por el tráfico ilegal a nivel local, así como por la caza en ciertas zonas, lo que ha llevado sus poblaciones prácticamente a desparecer fuera del área de las ciudades. La pérdida de las funciones ecológicas que proporcionan algunas especies cuando desaparecen de los hábitats naturales y sólo persisten en las ciudades puede tener efectos inesperados a largo plazo en los ecosistemas. En este caso, varias zonas urbanas pueden ser pronto los últimos refugios para dos loros endémicos si continúa la sobreexplotación, en cuyo caso su ignorada función como dispersores de semillas se perdería por completo en la naturaleza. La extinción funcional de estas especies podría afectar fuertemente a las comunidades vegetales en un entorno insular donde las especies dispersoras de semillas son naturalmente escasas.

Por último, se aborda el riesgo potencial que el tráfico ilegal puede representar para el ser humano. Debido al gran volumen animales salvajes capturados y tenidos como mascota a nivel local, así como a lo extendido en todo el Neotrópico de esta actividad, se recalca el riesgo potencial que supone para la salud humana. Las escasas condiciones de higiene, el nulo seguimiento veterinario, el incremento de población en la región, así como el aumento de la conectividad entre zonas remotas y grandes ciudades son factores que convierten el Neotrópico en un riesgo para la aparición de zoonosis. Al encontrarse en esta región algunos de los hotspots de biodiversidad más importantes del planeta, la riqueza de especies de patógenos puede ser muy elevada. La intensa deforestación, combinada con el intenso tráfico doméstico de fauna que permite el contacto entre fauna salvaje y humanos y/u otros animales domésticos supone un riesgo importante para fenómenos de spillover, comprándose a los wetmarkets de algunas zonas de Asia.

1. Introduction

During the last century, human activities have induced profound changes on the global scale, reshaping ecosystems and even changing atmospheric composition (Lewis and Maslin, 2015). This has lead scientists to propose a new geological era, the Anthropocene (Crutzen 2002; Zalasiewicz et al. 2010; Zalasiewicz et al., 2011), characterized by a loss of biodiversity of such magnitude that can be compared with mass-extinction events registered in the past (Barnosky et al. 2011). Habitat loss and transformation, climate change, species introductions, pollution, and overharvesting are the main factors behind the decreasing population trends of thousands of species worldwide (Sala, 2000; Thomas, 2004; Fischer and Lindenmayer, 2007; Price and Gittleman, 2007; Bálint et al., 2011; Vilá et al. 2011; Ripple et al., 2016; Powers and Jetz, 2019; REF), being even responsible for recent most of the modern extinctions (Bellard et al., 2016; Turvey and Crees, 2019). Species loss is so pervasive that the term “defaunation” (Dirzo and Miranda, 1991) has been also coined, this time to describe the disappearance of animals from their habitats (the “empty forest syndrome”; Redford, 1992). Defaunation is a consequence of global change but also constitutes one main driver of biodiversity loss on its own, deeply reshaping ecosystems by altering ecological and evolutionary processes (Harrison et al., 2013; Dirzo et al., 2014; Bello et al., 2015; Young et al., 2016).

Direct prosecution and overharvesting constitute the main causes of defaunation worldwide (Harrison et al., 2013; Dirzo et al., 2014). Bushmeat and trophy hunting, species prosecution for being considered harmful or pests, and poaching for clothing, decorative purposes, pet market, and traditional medicine are the activities with the deepest impact on vertebrate species (Yimin and Wilcove, 2005; McAllister et al., 2009; Rosen and Smith., 2010; Williams et al., 2014). In particular, wildlife trade is considered one of the main causes of biodiversity loss (Maxwell et al., 2016) by extirpating hundreds of millions of wild individuals of several species each year around the world to supply international pet markets (Bush et al., 2014; Karesh et al., 2005). In 1975, CITES was established to regulate the legal trade of species and preserve source native populations which, in some cases, were experiencing severe declines associated with overharvesting (Ribeiro et al., 2019). CITES established a series of regulations, limiting or prohibiting the legal export of numerous species considered threatened by organizations such as the IUCN (). However, even though these regulations meant a significant reduction in the volume of internationally traded wild-caught animals (Phelps et al., 2010) through their replacement by captive-bred ones (Hierink et al., 2020), illegal trade is still important (Challender et al., 2015). In fact, the main importers of wild-caught animals in the past (the UE and the USA) have been replaced by new flourishing markets in Asia or the Arab countries, where most of the imports come from illegal channels. Today, the illegal wildlife trade constitutes one of the largest illegitimate business (Warchol, 2007; Wyler and Sheikh, 2008; Nellemann et al., 2016), and is responsible for the endangerment of many species.

Whereas the growing concern of conservationists and the implementation of international regulations seem to have induced an important reduction in the volume of international illegally traded individuals, the role of domestic illegal trade has been largely overlooked as a source of extinction risk for many species, with important gaps of knowledge regarding its magnitude, functioning, and characteristics. According to recent studies, illegal trade at the domestic level could widely overpass the volume of individuals moved during international trade (Gastañaga et al., 2011; Aloysius et al., 2020).

Parrots are among the bird orders with a highest percentage of threatened species worldwide (28%) according to the IUCN (Olah et al., 2016; Olah et al., 2019; IUCN 2020). The situation is even worse in certain areas such as the Neotropics, where more than 30% of the species are threatened (Olah et al. 2016). Parrots are affected by several anthropic disturbances such as habitat conversion to agricultural and pasture lands, climate change, urban development, the presence of invasive species, logging, hunting, and trapping (Wright et al., 2001, Bush et al., 2014, Olah et al., 2016; Vergara-Tabares et al., 2020). Their slow life-history strategy, or breeding site and feeding requirements increase the impact of these activities (White et al., 2005; Olah et al., 2016). Parrots as secondary cavity nesters are strongly affected by the removal of big trees or the systematic poaching of chicks or adults to supply pet markets (White et al., 2005; Wright et al., 2002). Nest poaching can be so intense in some areas that extraordinary measures are required to stop poachers from removing chicks of critically endangered species (Briceño-Linares et al, 2011). In this sense, the direct effects of illegal trade combined with habitat loss may be devastating for several species (Marín-Togo et al., 2012; Wright et al., 2019), pushing them toward an even more vulnerable situation.

Numbers of parrots legally exported from their native areas after CITES implementation round XXX million individuals (cites.org). Thanks to CITES and other international regulations (for example, the US and EU bans), international exports of wild-caught birds have been strongly reduced during the last decades (www.cites.org). For instance, the grey parrots (Psittacus erithacus and P. timneh) have been recently added to Appendix 1 of CITES to reduce the capture of wild individuals (Martin et al., 2018) and thus the international pet market is now supplied with captive-bred birds. However, illegal international trade still represents a serious threat for several species worldwide, although estimating numbers is difficult. CITES data show that at least 30,000 of parrots have been seized from 1975 to 2019, a figure surely represent a small percentage of the actual number of illegally traded animals.

Contrary to international illegal trade, the domestic illegal trade of parrots has been overlooked as a factor of endangerment until recent time. Studies conducted during the last decades in several Neotropical countries show the existence of an important domestic illegal trade in this area (Herrera and Hennessey, 2007; Gastañaga et al., 2011; Pires, 2012; Pires and Clarke 2012; Alves et al., 2013; Daut et al., 2015; Pires et al., 2016; Berkunsky et al., 2017; Wright et al. 2019; Sanchez-Mercado et al., 2020; Biddle et al., 2021), with thousands of individuals traded each year across wildlife markets. Other studies focused on regions such as Indonesia or Asia demonstrate the existence of similar patterns (Cottee-Jones et al., 2014; Burivalova et al., 2017; Aloysius et al., 2020; Indraswari et al., 2020), despite attention keeps focused on international illegal trade towards main importers such as China (Ngoc and Wyatt, 2013; Uprety et al., 2021). However, despite the growing number of studies dealing with domestic illegal trade, this topic remains largely ignored and focused on markets, which only account for a small percentage of the illegal trade.

The Neotropics constitute the second most biodiverse region in terms of parrots, holding almost half of the world species (Forshaw, 2011) and the highest percentage of species classified as endangered by the IUCN (Olah et al., 2016). The intense logging and habitat transformation experienced in this region, as well as the illegal poaching and hunting, have led to an important decrease in most parrot populations in the area (Marín-Togo et al., 2012; Berkunsky et al., 2017).

Despite the apparent reduction in illegal trade in the Neotropics after CITES regulations, domestic illegal trade still represents a serious threat for this group, affecting around 68% of parrot populations (Berkunsky et al., 2017). Studies conducted in the area estimate that between 80,000 and 90,000 native parrots may be sold annually at wildlife markets just in Peru (Gastañaga et al., 2011). However, these figures may be severely underestimating the illegal domestic trade as only a small proportion of poached individuals are shipped to the main wildlife markets located in big cities, as it happens with other taxa such as primates (Shanee et al., 2017), while the bulk is locally traded among neighbours.

The domestic illegal trade of parrots has been studied by wildlife criminalists using the CRAVED model, which considers that “hot products” sold by thieves are Concealable, Available, Valuable, Enjoyable, and Disposable. Using data from wildlife markets in Mexico (Pires & Clarke, 2012), Peru (Pires, 2015), and Bolivia (Pires, 2015; Pires and Petrossian, 2016), these researchers concluded that illegal domestic poaching is an opportunistic activity focused on the most abundant and widely distributed species. This result is important for parrot conservation because implies that illegal domestic trade would not affect rare or endangered species. However, the use of rough proxies of abundance in the wild and as pets may be biasing results and leading to wrong conclusions. In fact, dealing with the same dataset used in one of these studies (Pires and Clarke, 2012), Tella and Hiraldo (2014) obtained completely different results by simply changing their statistical approach, finding that valuable and less abundant species were the most demanded. Determining whether illegal trade is an opportunistic crime or is selective towards certain species constitutes a key factor for the conservation of Neotropical parrots.

Another issue related to previous studies about illegal domestic trade is their focus on markets (offer) instead of pets (demand) to evaluate its magnitude and routes. For instance, Pires et al. (2016) and Pires (2015) found that most parrots available on illicit markets were poached within a 250 km radius from the market, suggesting that parrots can be moved over long distances inside the country to be sold at wildlife markets. However, procedures used to estimate these distances can be underestimating the actual routes of species, especially those preferred by people, as shown by the presence of rare and threatened species in some wildlife markets, far from their native ranges. Morevover, markets often have exposed more common species, having expensive species hide to avoid that get confiscated by authorities.

Habitat loss and transformation are recognised as the main threat for parrots in the Neotropics (Berkunsky et al., 2017). The removal of big trees is considered critical for several species of parrots (Brightsmith, 2005; Berkusky & Reboreda, 2008), and so the extended idea is that Neotropical parrots are mainly threatened by habitat loss. However, several parrot species show high adaptability to human-modified landscapes, thriving well in areas such as agroecosystems or cities (Rodríguez-Pastor et al., 2012; Bucher and Aramburú, 2014; Ivanova and Symes, 2019; Aplin et al., 2021). As an example, Monk parakeets (*Myiopsitta monachus*) have expanded their native ranges using human-modified landscapes (Bucher and Aramburú, 2014) and the biggest breeding colonies of Burrowing parrots (*Cyanoliseus patagonus*) are located in highly transformed habitats (Masello & Quillfeldt, 2012), including cities (Tella et al., 2014). Besides, many endangered parrots are persecuted while foraging in crops (Barbosa et al., 2021), supporting their wide tolerance toward habitat perturbations. Other species are more sensitive to habitat changes, such as those with a reduced distribution range and/or highly specialized, as the Yellow-eared parrot (*Ognorhynchus icterotis*), which main driver of populations decrease seems to be habitat change (Collar 2000; Krabbe 2000). However, several parrot species are also affected by poaching (Collar, 2000). In Neotropics, there is a rooted tradition of having parrots as pets (Tella, 2011; Pires, 2012), animals being captured from the wild as chicks or adults. Poaching pressure can be of such magnitude that it can restrict the distribution range of some species to inaccessible areas for poachers, such as islands or nature reserves (Sagarin et al., 2007). In some cases, poaching pressure may even push human-tolerant parrots into urban environments (Davis et al., 2011; Tella et al., 2014; Davis et al, 2012). Cities may offer available and predictable food resources year-round while protecting from poaching, which is mainly conducted in rural areas. However, despite preserving urban populations of parrots, their ecological functions in the wild virtually disappear, which may have unknown consequences for the ecosystem health.

It is worth mentioning that besides the conservation implications of illegal trade, wild parrots kept in captivity may pose their owners into close contact with diseases. Zoonotic diseases have become extraordinarily popular during the last year, after the emergence of the COVID, but they have a long history mainly link to the illegal trade of animals (Webster, 2004; Woo et al., 2006; Chomel et al., 2007; Jones et al., 2008; Paige et al., 2014; Pernet et al., 2014; Kurpiers et al., 2016; Green et al., 2020). Thus, illegal wildlife trade can be harmful to the species involved but also to people and/or poultry due to their contact with animals caught in the wild without any kind of sanitary control (Chomel et al., 2007; Pavlin et al., 2009).

1.1 Captive breeding counteracts illegal trade as a major threat for parrots worldwide

Parrots (order Psittaciformes) have been appreciated as pets for millennia in their original ranges, and more recently by modern societies worldwide because of their colourful plumage and ability to mimic human speech (Grahl, 1990; Silva, 2018). These traits have led them to be among the most internationally traded vertebrates, with millions of individuals moved across countries in recent decades (Cardador et al., 2017). International wildlife trade has been regulated since 1975 by the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) to ensure that trade in wildlife species is managed for sustainability under scientific criteria (Rosser & Haywood, 2002). However, the paucity of reliable population and demographic data (Marsden & Royle 2015) caused a scarcity of studies on sustainable parrot harvesting (Beissinger & Bucher, 1992; Valle et al. 2018), and thus arbitrary exporting quotas, which may be responsible for the decline of several species. Grey (*Psittacus erithacus*) and Timneh (*P. timneh*) parrots constitute a clear example, as they have been recently (2017) included in the CITES Appendix I to halt the export of wild-caught individuals after becoming globally endangered due to international trade (Martin, 2018; Martin et al., 2018). Today, trade on all but four parrot species is regulated through their inclusion in CITES Appendix 1 or Appendix 2 (allowing non-commercial and commercial trade, respectively; www.cites.org) due to the potential risk that international trade may pose to their wild populations.

Both legal and illegal wildlife trade may have contributed to placing parrots among the most threatened avian orders (Olah et al., 2016; McClure & Rolek, 2020). In fact, recent studies have highlighted that the impact of the international and domestic illegal trade on some parrot populations may have been underestimated (Tella & Hiraldo, 2014; Ribeiro et al., 2019; Romero-Vidal et al., 2020). According to expert knowledge, 68% of Neotropical parrot populations are somehow threatened by illegal trade, mostly at the domestic scale (Berkunsky et al., 2017). Similar situations occur in certain areas of Asia and Oceania, where many parrots are illegally caught to supply local and neighboring countries´ wildlife markets (Indraswari et al., 2020; Aloysius et al., 2020). Nevertheless, the actual role played by illegal trade on a global scale remains unclear. Olah et al. (2016) analyzed threats faced by parrots using data from the assessment made by the IUCN in 2014, considering the use of parrot species as pets as a surrogate of trade. They found that pet use mainly focused on non-threatened species and thus suggested that trade did not constitute a significant global threat to parrots. However, these authors did not consider the dual wild-caught and captive-bred sources of parrots used as pets. The historic international trade has allowed the creation of captive reproductive stocks of many species (Grahl, 1990; Arndt, 1996), several of which are currently bred in captivity for their commercialization as pets worldwide (Silva, 2018). Indeed, the EU blanket ban on wild-caught birds in 2005 induced a fast replacement by captive-born individuals to supply the demand for pets (Cardador et al., 2019). As a consequence, the use of parrots as pets at a global scale might not pose a threat to their populations nowadays due to the large availability of captive-born parrots, whereas the illegal trade, mostly to supply the domestic demand for pets in source countries (Daut et al., 2015; Biddle et al., 2020; Romero-Vidal et al. 2020; Sánchez-Mercado et al., 2020), could constitute a serious threat for a significant number of species.

Here, we analyzed updated information provided by the IUCN Red List (IUCN, 2020) to disentangle the role played by illegal trade and their use as pets in the conservation status of the 402 extant parrot species at a global scale. Complementarily, we analyzed long-term changes in the international legal and illegal trade of wild-caught and captive-bred parrots, as well as information on which species –and how easily- are reproduced in captivity. Our results highlight that both domestic and international illegal trade, but not their use as pets (given the high availability of captive-bred species), are threatening parrots worldwide, while captive breeding is emerging as an important tool to halt illegal trade.

1.2 The hidden face of parrot poaching: local demand of pets largely outnumbers domestic and international trade on parrots

A quarter of all parrot species are threatened worldwide (Olah et al., 2019), with a higher proportion in certain areas as the Neotropics (Berkusnky et al., 2017; Olah et al. 2016). International trade and, to a lesser extent domestic trade, have been recognized as one of the main drivers of population decline for several parrot species (Berkunsky et al., 2017; Olah et al., 2019; Tella & Hiraldo, 2014). Despite the implementation of regulations on international trade (CITES, 1973), several species continuous to be affected by international illegal trade, increasing their risk of extinction (Martin et al., 2018, Ribeiro et al. 2020). However, recent studies highlighted the relevance that domestic trade have on parrot populations declines (Berkunsky et al., 2017; Aloysius et al., 2020; Romero-Vidal et al., 2020), which might be severely underestimated compared to international trade.

In the Neotropics, keeping parrots as pets is a cultural rooted tradition which is extended across several countries of South and Central America, as well as the Caribbean (González, 2003; Tella & Hiraldo, 2014; Luna et al., 2018; Romero-Vidal et al. 2020). Studies conducted in markets estimates that thousands of parrots are sold each year locally at numerous wildlife markets across countries (Herrera and Hennessey 2007; Gastañaga et al., 2011; Pires, 2015; Daut et al., 2015). In fact, the figures of total parrots domestically traded each year may be much higher considering that these surveys may covet only around 3% of the total numbers sold in markets (Gastañaga et al., 2011), and that markets represent only a fraction of the parrots poached in each country (Romero-Vidal et al., 2020).

The aim of this study is to assess the real importance of illegal trade at the domestic level. Using data on Bolivia's main wildlife market surveys conducted daily for 5 years, combined with pet surveys throughout some of the most common localities of origin for parrots sold in the market, we tried to estimate the real volume of parrots illegally poached in the country to supply the local demand, which does not enter the common trade channels. Likewise, we compare these data with the historical legal and illegal exports of Bolivia after CITES (Convention on International Trade in Endangered Species of Wild Fauna and Flora) regulations, to see the importance of illegal trade at the domestic level compared to the international. Finally, using data on ages of the individuals observed during the pet surveys, we tried to estimate the turnover for native parrots kept as pets, using survival probabilities and informal interviews.

1.3 Opportunistic or Non-Random Wildlife Crime? Attractiveness rather than Abundance in the Wild Leads to Selective Parrot Poaching

Defaunation (defined as the global, local or functional extinction of animal populations or species from ecological communities) differs from extinction, as it includes both the disappearance of species as well as their declines in abundance, and has profound ecological consequences, ranging from local to global coextinctions of interacting species to the loss of ecological services critical for humanity (Young et al., 2016). Understanding the causes of defaunation is a growing priority for ecologists, wildlife managers, and conservation biologists, and is important to try to reduce its pace. The drivers of defaunation range from threats operating at global scales, such as climate change, to those that are mostly local, including direct harvest and habitat loss. However, after analyzing the information gathered by the IUCN for more than 8,000 threatened or near-threatened species, (Maxwell et al., 2016) concluded that by far the biggest drivers of biodiversity decline are overexploitation (the harvesting of species from the wild at rates that cannot be compensated for by reproduction or regrowth) and landscape conversion for food production. Moreover, wildlife overexploitation to meet local and global markets was ranked second of five key drivers of harmful ecosystem change by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES, 2019).

Wildlife trade is one of the main causes of overexploitation in some taxonomic groups (Young et al., 2016), given that some animal products (e.g., ivory and tiger bones) or groups of species (e.g., cage birds) are highly demanded across the world. Considering closely related species, consumers prefer some over others. For instance, buyers prefer multi-flowered species among traded orchids (Hinsley et al., 2015), while sale prices of traded songbirds are determined by their body size, coloration and song attractiveness (Su et al., 2015). Body size, coloration and the ability to imitate human speech are traits that make parrots highly valued pets (Silva, 2018), thus making them the most traded vertebrate taxa worldwide (Bush et al., 2014). The extent to which these consumer preferences determine poaching activities and their impacts are, however, poorly known. Poachers may supply species according to their availability in the wild or could selectively focus on the most demanded among closely related species. This is a key question with important conservation implications, as selective poaching could cause overexploitation and accelerate the defaunation and even extinction of the most demanded species.

The above question was assessed by wildlife criminologists using the CRAVED model. This model proposes that ‘‘hot products’’ sought by thieves are concealable, removable, available, valuable, enjoyable and disposable (Pires & Clarke, 2012) and was applied to data available on the parrot trade in Mexico (Cantú et al., 2007), Bolivia and Peru (Pires, 2015)). These authors concluded that parrot poaching was an opportunistic crime where more widely available species were poached in greater numbers than rare and threatened ones, thus lowering concerns for the conservation impacts of poaching on threatened species (Pires & Clarke, 2012; Pires, 2015). However, rough proxies of parrot abundances in the wild were used in these studies, including the number of years each species was allowed to be legally trapped (Pires & Clarke, 2012) or the detectability of species indicated in field guides (Pires, 2015). Moreover, these authors recognized that a multivariate approach could have let to different conclusions (Pires & Clarke, 2012). Indeed, new analyses (Tella & Hiraldo, 2014) challenged these conclusions when applying multivariate analyses to the same data (Cantú et al., 2007), showing that amazons and macaws, the most attractive species as reflected by their body size, coloration and ability to imitate human speech, were disproportionally more traded considering the number of years they were legally trapped, thus contributing to their population declines. Nevertheless, these results could be flawed due to the use of the only available proxies for estimating both wild parrot availability and poaching pressure. The number of years each species was allowed to be legally trapped should reflect their abundance in the wild, assuming that scarcer species were allowed to be trapped for fewer years (Pires & Clarke, 2012), although international markets, local economics, and political pressures could influence this. On the other hand, the use of seizures as a proxy of poaching pressure (Tella & Hiraldo, 2014) may have affected the results, given that seizures usually represent <10% of poaching volumes and are often biased towards certain species (Esmail et al., 2020). In fact, the proportion of amazons and macaws among all parrots seized in Costa Rica (50%) is significantly higher than among those actually poached and kept as household pets (33%), showing that seizures are biased to the most valuable and threatened species (authors' data, in prep.). Thus, a positive selection of amazons and macaws (Tella & Hiraldo, 2014) could at least partially result from seizure biases. Given the limitations of these proxies (Pires & Clarke, 2012; Pires, 2015; Tella & Hiraldo, 2014), reliable information on both the abundance of the species in the wild and poaching pressure is needed to properly test whether parrot poaching is selective or opportunistic (Tella & Hiraldo, 2014).

To disentangle if parrot poaching is a selective or opportunistic activity, we designed a large-scale survey in Colombia, where trapping and keeping native animals as pets is a rooted tradition punished by law since 1977 (Rodríguez & García, 2008). We simultaneously measured the relative abundance of 28 parrot species in the wild and as household poached pets. We then applied a selectivity index widely used in habitat selection studies, the Savage index, to ascertain if pet abundances mirrored wild abundances or, conversely, if some species were found as pets more than expected. Our results show a strong selection for more attractive parrot species to be kept as pets, despite their lower abundances in the wild. Positively selected species, but not those less abundant in the wild, were thus the most expensive. This selection has important consequences for the conservation of parrots and their ecosystem services, as well as for our understanding of overharvesting and defaunation, and the management of illegal trade in general.

1.4 Selective poaching as the main pet source in Peru and Ecuador: warns on the unsustainable domestic demand for preferred parrot species

Wildlife trade is considered a major threat for a wide array of species (Scheffers et al., 2019). Although the constitution of The Convention on International Trade in

Endangered Species of Wild Fauna and Flora (CITES) in 1973 has greatly contributed to the regulation of international wildlife trade to protect species from overexploitation (Challender and MacMillan, 2014), many species continue to be illegally traded, both globally and domestically (Rosen and Smith, 2010; Ribeiro et al. 2019).

Parrots (Psittaciformes) is the avian order with the largest percentage of species threatened with extinction (i.e., ca. 30% of the 402 extant species are classified as vulnerable, endangered, critically endangered, extinct in the wild or extinct; Olah et al. 2016; IUCN, 2020) and one of the most traded vertebrates worldwide as they are greatly appreciated as pets (Bush et al., 2014). International trade of almost all parrot species is regulated by CITES, and the wild bird trade bans of the United States (1992) and Europe (2005) have generated geographic redirections, but not changed the number of parrots internationally traded (Cardador et al., 2017). Though, the bulk of individuals moved worldwide belongs to rather common species and international illegal trade of endangered parrots, although persistent, is mainly restricted to movements of birds among neighboring countries (Ribeiro et al. 2019). More concerning is, however, the illegal domestic trade of parrots, which has been pointed to as having a larger impact on parrot populations than international trade (Gastañaga et al., 2011). In the Neotropics, expert knowledge indicated that 68% of the parrot populations are threatened by illegal domestic trade (Berkunsky et al., 2017), with tens of thousands of parrots annually sold at illicit markets in countries such as Bolivia, Peru or Brazil (Gastañaga et al., 2011; Herrera and Hennessey, 2007; Nóbrega-Alves et al., 2013). These figures are surely an underestimation of the actual extraction rates, as they do not account for the high mortality during capture, transport, and captivity before and after selling (González, 2003; Baños-Villalba et al., 2020). Moreover, surveys mostly focus on markets sited in large cities while there are no comprehensive field studies aimed at estimating the number of parrots removed for self-supply or sold by poachers on a more local scale, which could largely outnumber parrots sold in markets (Romero-Vidal et al., 2020).

Despite its conservation implications, little is known about the characteristics of the illegal domestic trade of parrots (Berkunsky et al., 2017). Pires et al. (2016) and Pires (2015a) found that most parrots available in illicit markets of Bolivia and Peru were poached within a radius of ca. 250 km, suggesting that traded birds can be moved over long distances. Most of these parrots belonged to species considered common in the wild (Pires 2015b), although ca. 10% were threatened species (Daut et al. 2015a). In Peru, for instance, the majority of individuals illegally traded in markets belonged to the few species for which the country has established harvest quotas for their legal exportation (Daut et al., 2015a), assuming their international trade is sustainable because they are common species. Overall, these results suggested that parrot poaching is focused on common species, with little impact on wild populations and threatened species (Pires 2015b). However, estimates of abundances in the wild –which are needed for assessing the true impact of poaching (Tella and Hiraldo, 2014)- are very rarely available. Recently, Romero et al. (2020) simultaneously evaluated the relative abundance of parrot species in the wild and their poaching pressure in Colombia, finding that the most attractive species (in terms of body size, coloration, and ability to imitate human speech) were poached much more frequently than expected attending to their availability. These results confirm parrot poaching as a selective pressure that might affect the population trends and conservation status of the most preferred species (Tella & Hiraldo 2014).

Here, we conducted a large-scale survey across Peru and Southern Ecuador to assess the role played by poaching and illegal markets as providers of parrot pets. We investigated whether parrot pets belong to abundant or specific, positively selected species and if birds were poached locally, transported from their distant range distributions, or bought at pet markets. In the case of transported pets, we reconstructed trade routes through the existing grid of roads. Attending to the selective poaching hypothesis (Tella and Hiraldo, 2014; Romero-Vidal et al., 2020), we predicted that: 1) parrot poaching is non-random but directed toward the most preferred species, mainly amazons and large macaws, 2) the most preferred species are transported at larger distances, far from their distribution ranges and pet markets, 3) positively-selected species are more valuable and scarcer in the wild, and thus more expensive. Finally, if selective poaching and domestic trade act at large spatial scales, 4) preferred species should have a more concerning global conservation status and a negative population trend (Tella and Hiraldo 2014).

1.5 Deforestation or overharvesting? Pet-keeping cultural burden rather than habitat transformation causes selective parrot defaunation in Costa Rica

Over the last century, the widespread and sustained increment in the human population has promoted the conversion of more than three-quarter of the terrestrial biosphere into anthropogenic biomes (Ellis and Ramankutty, 2008). This scenario of habitat transformation has exposed species to new pressures which, in many cases, have reduced their populations' sizes and increased their extinction risk (Newbold et al., 2015; Pimm, 2009; Tittensor et al., 2014). In an effort to reduce the biodiversity loss associated with habitat degradation and secure ecosystem services, most countries have created protected areas networks, which today cover 15% of the world’s terrestrial surface and 7% of the coastal and marine areas (UNEP-WCMC and IUCN, 2020). However, the percentage of protected areas effectively managed is much lower (5 and 1%, respectively; UNEP-WCMC and IUCN, 2020), and most of this territory is still experiencing intense pressure derived from human activities and has technical and practical limitations that make them fail in their attempt to address the global problem of biodiversity loss (Harrison, 2011).

Contrary to habitat transformation, which is so conspicuous that it can be tracked through remote sensing technologies, defaunation (i.e., the process of species and population extinctions, range contractions, and local population declines of animals) is a largely cryptic phenomenon that can even occur in large, apparently well-conserved areas (Dirzo et al., 2014; Harrison, 2011; Harrison et al., 2013). Studies focused on marine ecosystems have shown that overexploitation (i.e., the harvesting of species from the wild at rates that cannot be compensated for by reproduction or regrowth) is behind the collapse of seafood fisheries (e.g., Merino et al., 2012; Worm et al., 2007b). Maxwell et al., (2016) have recently painted a starker picture, in which overexploitation emerges, together with habitat loss, as the biggest driver of biodiversity decline worldwide. Particularly concerning is defaunation associated with poaching (i.e., the illegal hunting or capturing of wild animals for bushmeat or trade), which is known to be threatening the persistence of not only high-profiled species, such as rhinoceroses or elephants (Di Minin et al., 2015), but also many lesser-known species (UNODC, 2016). A few studies have associated animal abundances and defaunation in the wild with the extraction rate of species targeted by poaching (e.g. Bulte and Horan, 2003; Rist et al., 2009; Tilker et al., 2019), but assessing its actual magnitude is difficult due to the intrinsic nature of the information that requires intensive surveys and because most declining species are also affected by other factors, with unknown interactions and feedbacks among them (Maxwell et al., 2016). For instance, habitat transformation may directly drive animal populations declines by reducing habitat quality, but also indirectly by facilitating illegal hunting (Laurance et al., 2006) or captures for trade (Rist et al., 2009). In a vicious circle, defaunation greatly contributes to the loss of important ecological interactions and processes further increasing habitat degradation and population declines (refs).

Parrots (Order Psittaciformes) have been largely coveted as pets due to their colorful plumage and their ability to imitate human speech. Thus, they have been internationally traded by millions worldwide (Beissinger 2001; Cardador et al., 2017), strongly contributing to the decline of many species in their native ranges (Collar and Juniper, 1992; Tella and Hiraldo, 2014). Although this trade has been largely reduced after international bans (Cardador et al., 2017; 2019), illegal poaching remains still highly active in several countries, mainly the Neotropics. There, 37% of parrot species are threatened primarily by their capture for the local pet trade (Olah et al., 2016; Berkunsky et al., 2017), with organized networks dedicated to this activity (Herrera and Hennessey, 2007; Gastañaga et al., 2011; Alvarado-Martínez, 2012; Alves et al., 2013). As parrots provide key mutualistic services through dispersal processes (endozoochorous and estomatochorous seed dispersal, secondary dispersal, pollination, and other functions; Blanco et al., 2016; 2018; Sebastián-González et al., 2019), species extinction or even rarefaction as a consequence of defaunation by poaching for the pet trade may have long-term consequences for the ecosystems where they live.

Costa Rica represents a model of how to make compatible economic development with nature conservation (Sánchez-Azofeifa et al., 2001). During the last decades, Costa Rica has been at the forefront of tropical forest conservation, protecting one-quarter of its land under a National Park network or as public or private reserves (Robalino and Villalobos, 2015), which are today its major touristic destinations (Rivera, 2002). However, despite the strong environmental law restrictions that the country holds in the present (Quesada-Mateo and Solís-Rivera, 1990), consequences of past deforestation and habitat degradation are still visible. Indeed, well-conserved areas (protected and unprotected ones) are usually surrounded by deforested and human-modified lands (Sanchez-Azofeifa et al., 2001; Moran et al., 2019) from which human activities, mainly poaching, can permeate (Hansen and de Fries, 2007). Here, we evaluated for the first time, using large-scale field surveys and remote sensing data, the role played by habitat degradation and defaunation by poaching for the local pet trade on parrot communities in Costa Rica, a country that seriously promotes and invests in environmental conservation. Our results suggest that habitat degradation has a reduced effect on the presence, abundance, and richness of parrots. The illegal capture and maintenance of individuals in captivity as pets, however, are high, geographically widespread, and focused mainly on the rarest species (in terms of their abundance in the wild), such as Ara and Amazona species, which were the most seized species.

Nevertheless, and despite the strong legal environmental restrictions of the country, the deep cultural roots of keeping wild parrots as pets seems to still be the main factor threatening this taxonomic group and the long-term persistence of their ecological services.

1.6 Cities may save some threatened species but not their ecological functions

Urbanization is one of the most rapidly growing, prevalent and lasting causes of habitat change (Seto et al. 2012) and is resulting in the loss of biodiversity through local extinction processes worldwide (McKinney, 2006; Grimm et al. 2008; Sol et al., 2014). However, wildlife responses to urbanization are highly variable: while most species are unable to occupy these new habitats, including endemic and threatened species (González-Oreja 2010), others are able to persist or colonize even the most populated cities (Chace & Walsh, 2006; Kark et al., 2007; Carrete & Tella 2011; Sol et al., 2014). Paradoxically, some species achieve much higher densities in urban than in natural habitats and thus, cities arise as conservation hotspots (Mason 2010; Rebolo-Ifrán et al. 2017). Cities have also been known to host some threatened species, thus becoming key refuges to guarantee their persistence. As recent examples, 22% of the known occurrences of threatened plants in the USA fall within the 40 largest cities (Schwartz et al. 2002), a third of 54 cities sampled by Aronson et al. (2014) contained globally threatened birds, and Australian cities support more threatened plant and animal species than all other non-urban areas on a unit-area basis (Ives et al. 2015). Thus, the conservation of some threatened species is an additional motivation to make urban environments compatible with the persistence of wildlife (Miller & Hobbs, 2002; Dearborn & Kark, 2010).

From a species-based conservation point of view, the fact that cities may help some species avoid regional or even global extinctions (Ives et al. 2016; Gibson & Yong 2017) is a welcomed insight for conservationists and policymakers. However, little attention has been paid to the ecological consequences of the restriction of species to urban environments as their final refuges. Particularly, the loss of ecological functions and ecosystem services provided by species when they disappear from natural habitats to only persist in urban environments may have long-term, unexpected effects on ecosystems. We aim to draw attention to this likely phenomenon using two species of threatened parrots as an example.

Parrots (Psittaciformes) are among the most threatened bird orders with 28% of the c. 400 species of the world classified as threatened by the IUCN Red List (Olah et al., 2016). Habitat loss, through logging and the spread of agriculture, is one of the main threats to parrots worldwide (Olah et al. 2016). However, some parrot traits (such as their high inter-individual variability in behavior associated with their relatively large brain sizes, Carrete & Tella 2011) allow them to successfully colonize and thrive in urban habitats, where they make use of the new food and nesting resources provided by cities (e.g., Fitzsimons et al. 2003; Davies et al. 2011; Tella et al. 2014). On the other hand, parrots are highly valued as pets given their attractive coloration and ability to imitate human speech. This societal demand drives an intense domestic and international trade that contributes to the rarity in the wild of many parrot species (Tella & Hiraldo 2014, Annorbah et al. 2016, Berkunsky et al. 2017), but also to the establishment of urban parrot populations both within their native and foreign distribution ranges due to the escape or deliberated release of caged parrots (Abellán et al. 2017; Cardador et al. 2017, Mori et al. 2017). This has created a dilemma: while many wild parrot populations are vanishing due to habitat loss and harvesting for the pet trade, some exotic urban populations are flourishing worldwide to the point that their conservation value could overcome concerns about their potential negative impacts as invasive species (Gibson & Yong 2017). Conservation efforts focused on some urban parrot populations may save those species from extinction (Gigson & Yong 2017), but not their ecological functions in their native ecosystems, which remain poorly understood. Parrots have been traditionally considered as pure plant antagonists, as they consume fruits, seeds, flowers and other non-reproductive tissues of their food plants. Recent works, however, have suggested that several parrot species also act as plant mutualists through pollination, seed dispersal, and plant healing (Blanco et al. 2018). While the role of parrots as seed dispersers has been largely overlooked (Tella et al. 2015, Blanco et al. 2016), long-distance seed dispersal by parrots has been shown to be key in some ecosystems (Blanco et al. 2015; Tella et al. 2016a, 2016b; Baños-Villalba et al. 2017). Parrots may even shape vegetal landscapes by influencing the spatial distribution and demography of their food plants and vegetal communities (Blanco et al. 2015, Baños-Villalba et al. 2017, Speziale et al. 2018), and plant-parrot mutualistic interactions may lead to an increase in the robustness of parrot communities when facing the loss of plant species (Montesinos-Navarro et al. 2017). All of these ecological functions may be lost when human persecution causes the disappearance of parrots in the wild, with remaining population confined to urban refuges.

Here, we used as a model the two threatened Caribbean parrot species endemic to Hispaniola Island: the Hispaniolan parakeet (*Psittacara chloropterus*) and the Hispaniolan amazon (*Amazona ventralis*) (Figure 1). These species are listed by the IUCN Red List as Vulnerable due to their population declines associated with habitat loss, hunting and poaching for the pet trade (BirdLife International, 2016a, 2016b). In fact, these species are known to be trapped and hunted since the Spanish colonization of the island (Wiley & Kirwan 2013). We therefore hypothesized that 1) past and current human persecution of parrots may cause a contraction of wild populations to predator-free (considering humans as predators through hunting and trapping for the pet trade) urban refuges (Rebolo-Ifrán et al. 2017), and 2) that these parrot species may act as legitimate seed dispersers of several plant species (Blanco et al. 2018), an ecological function thus far overlooked that might be definitively lost if these species continue to disappear in the wild. For testing these hypotheses, we conducted a large-scale field survey to estimate parrot abundances in natural, rural and urban habitats, obtained information from local people to know whether hunting and trapping are still threating these species, and assessed their potential role as seed dispersers.

1.7 The widespread poaching of wild pets as an overlooked risk of zoonosis in the Neotropics

Zoonoses (i.e., infectious diseases that originate from animals and infect people) are responsible for more than 2,7 million human deaths every year (Grebeyes et al., 2014) and have catastrophic socioeconomic consequences (Narrod et al., 2012). Most of these diseases have infected humans for years, but growing population size, global connectivity, and habitat disruptions are collectively increasing the chances for the emergence of novel infectious diseases (Morse et al., 2012). Stop zoonotic diseases to become epidemic or pandemic is a war that humanity is not prepared to fight (Fineberg, 2014; Wood et al, 2012), .as seems to be demonstrating by recent MERS-CoV, EVD and SARS-CoV2 outbreaks (Brolin et al., 2016; Dudas et al., 2018; Lee & Hsueh, 2020; Wang et al., 2021), despite the origin of the last one remains controversial (Segreto & Deigin, 2020). Thus, efforts should be devoted to identifying potential scenarios or activities that facilitate diseases to jump from animals to humans to increase monitoring and manage them (Gibb et al., 2020).

The strongest predictor of human infectious disease richness known to date is wildlife richness (Dunn et al., 2010). However, this correlation may not necessarily imply direct causation, as the increment in animal-human contacts is the determinant in the emergence of zoonoses. The exponential growth of the human population has led to major ecological changes and drastic wildlife habitat reduction, and many examples of the emergence or re-emergence of zoonoses related to human encroachment on wildlife habitats exist (Greger, 2007; Jones et al., 2013; Hassell et al., 2017; White & Razgour, 2020). Among the human disturbances on wildlife habitats, wildlife trade plays a pivotal role (Bell et al., 2004; Chomel et al., 2007; Cantlay et al., 2017). Most discussions on the risk of wildlife trade for human health have been focused on the importance of wet markets and bushmeat consumption (Webster, 2004; Woo et al., 2006; Field, 2009; Karesh & Noble, 2009). Nevertheless, keeping wild animals as pets is also a potential source of diseases (Jones et al., 2008; Green et al., 2020).

Different measures have been implemented to reduce this risk on an international scale (Morse et al., 2012; Daszak et al., 2020). For instance, Europe banned in 2005 the importation of wild-caught birds to reduce the probability of transmitting Avian Flu after finding a lethal strain in the UK. Despite its sanitary risks, the international trade of wild-caught animals has associated a significant mortality rate (Thomsen et al., 1992) that may change the constitution of the original pool of captured individuals (Carrete et al., 2012; Baños-Villalba et al., 2020), removing sick or weak ones and thus reducing the number of potential diseases (mainly rare and thus unknown ones) introduced in the new areas (Colautti et al., 2004). More concerning, however, is the tradition of poaching and keeping wild, native animals as pets, which is very extended in several Asian and Latin American countries (Berkunsky et al., 2017; Gastañaga et al., 2011; Edmunds et al., 2011; Tella & Hiraldo, 2014; Luna et al., 2018; Aloysius et al., 2020). The confinement of wild individuals captured within their distribution ranges should cause a much lower mortality of infected individuals than international trade, and thus should increase the probability of putting into contact a diseased animal with a human or domestic animal that might become infected (spillover). Indeed, the most important recent outbreaks are coming from Asian local markets, where animals are locally traded in completely antihygienic conditions and without sanitary controls (Woo et al., 2006; Edmunds et al., 2011). Moreover, wild birds in Asian markets are sold together with poultry, increasing the risk of cross-transmission (Dinh et al., 2006; Wang et al., 2006; Ward et al., 2008), so it is not strange than most HPAI (Highly Pathogenic Avian Influenza) virus outbreaks, for example, were associated with these sources (Olsen et al., 2006). Here, we use information from a large-scale survey of household poached pets across the Neotropics to alert on how the widespread tradition of keeping wild animals as pets can be setting the scene for the appearance of zoonotic outbreaks.

1.8 Objectives

The aim of this thesis is to disentangle the overlooked aspects of domestic parrot poaching in the Neotropics. In the first place, we analyze the danger that illegal trade represents for the conservation of parrots worldwide, highlighting the relevance of illegal domestic trade (chapter 1). After this global assessment, we focus on the Neotropics to clarify some of the most important issues regarding illegal domestic trade: i) estimate more accurate figures of number of parrots traded and the annual turnover at the domestic level (chapter 2), ii) analyse if parrot poaching in the Neotropics is an opportunistic activity (Pires and Clarke, 2012; Pires, 2015; REF) or driven by people preferences (chapter 3), iii) assess the local dimension of domestic trade and determine trade routes and distances where parrots can be moved at the domestic level, and if these distances are influenced by the selection of these species according to people preferences (chapter 4), iv) determine the impact of habitat transformation on parrot communities compared to illegal poaching (chapter 5) and v) provide evidences of the ecological consequences which disappearance of parrots from their native areas due to overharvesting can bring to ecosystems, as a consequence of the loss of their ecological functions (chapter 6). Finally, we call attention on the potential risk which domestic illegal trade have for human health in the Neotropics, given the characteristics of this activity that make it an ideal scenario for zoonoses spillover.

2.Methods

2.1 Study area

This thesis is conducted in the Neotropical region, including South America, Central America and the Caribbean. The Neotropics comprises a wide variety of biomes and ecoregions such seasonally dry forests, grasslands and shrublands, deserts, mountain yungas and lowland rainforests (Olson et al., 2001), constituting one of the most species-richest region on the globe (Olson et al., 2001; Loyola et al., 2009; Ulloa et al., 2017; Antonelli et al., 2018). The complex topography and habitat diversity derived from it is in big part responsible for the high parrot-species richness of this region (Forshaw, 2011), constituting the second one (first is represented by Australasia) where parrots have radiated more extensively (Davies et al., 2007). On this study, we focus on most of the biomes and ecoregions present on the Neotropics, analysing different aspects of the domestic illegal trade on all the species of parrots present on them. In total, 22 study areas were selected in 12 different countries, comprising more than 40,000 Km of large-scale road surveys, covering a wide variety of habitats on different biomes and ecoregions (Figure 2.1.1). In this sense, this thesis represents the most exhaustive study on parrot poaching at the Neotropical scale.

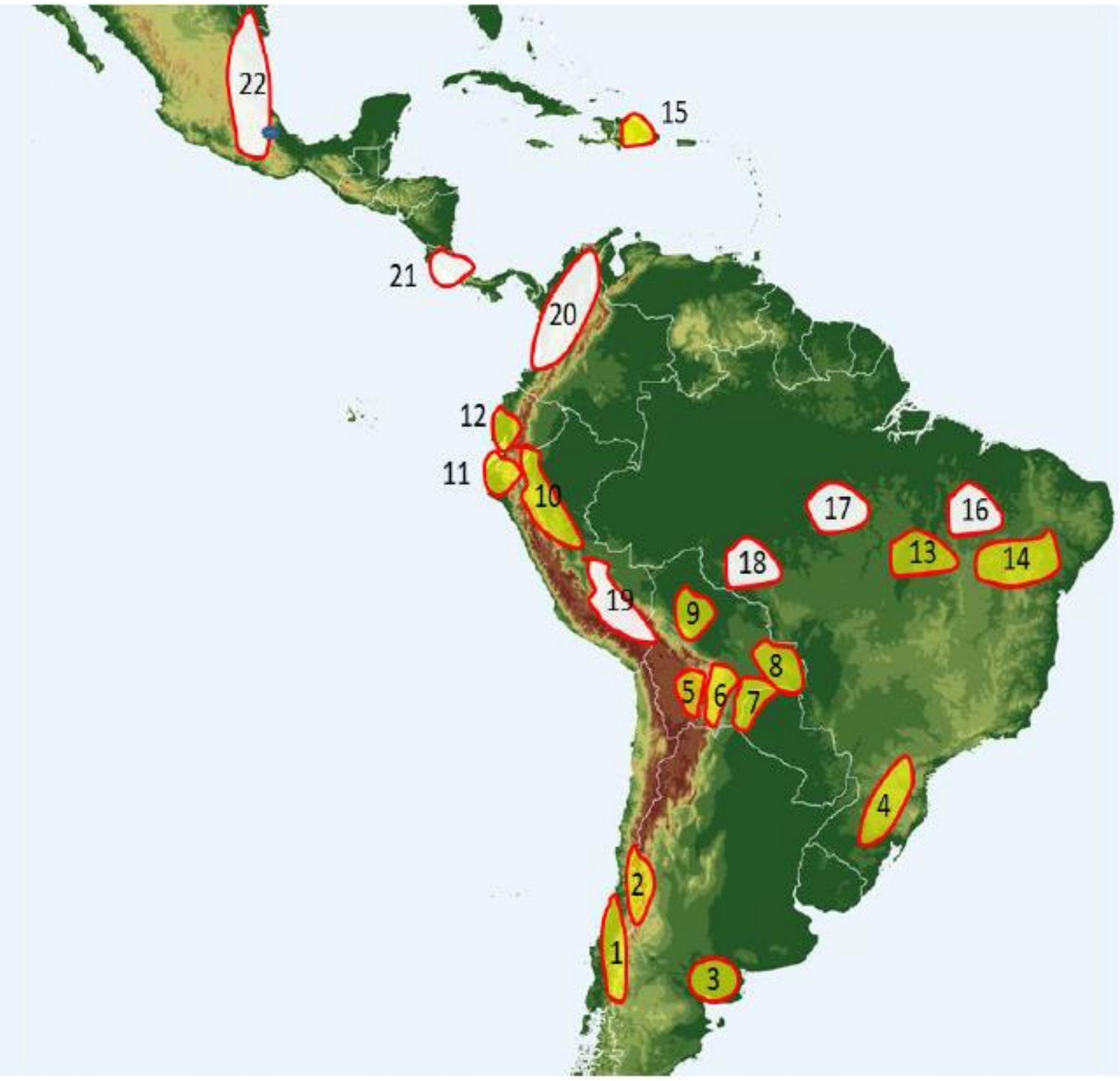


Figure 2.1.1. Areas already surveyed (yellow) and proposed to be surveyed through this project (white) to assess the effects of habitat alterations and poaching on parrots. The areas and their main biomes are: 1) Andean Araucaria araucana forests, Argentina-Chile, 2) Valdivian lowland forests, Chile, 3) Pampa grasslands, Argentina, 4) Araucaria angustifolia forests, Mata Atlantica, Brazil, 5) inter-Andean dry forests, Bolivia, 6) Chaco Serrano, Bolivia, 7) Chaco, lowland dry forests, 8) Chiquitania forests and Pantanal, Bolivia, 9) Beni, Amazonian flooded savannahs, Bolivia, 10) Andean forests, Perú and Ecuador, 11) Tumbesian dry forests, Perú, 12) coastal dry forests, Ecuador, 13) Cerrado, Brazil, 14) Caatinga, Brazil, 15) Caribbean rain, dry and pine forests, Dominican Republic, 16) ecotone Cerrado – forested Caatinga, Brazil, 17) ecotone Amazonian forests – Cerrado, 18) ecotone Amazonian forests – dry forests, 19) Andean and sub-

Andean forests, Perú, 20) Choco, dry and mountain forests, Colombia, 21) rain and dry forests, Costa Rica, and 22) dry and mountain forests, México.

With the exception of the first chapter, which has a global approach focused on all the regions with psittacine species, different areas of the Neotropics were selected to test the different hypothesis proposed on the thesis. The selection of the areas was taken based on the particular characteristics and data quality to solve these questions.

2.2 Methods: Captive breeding counteracts illegal trade as a major threat for parrots worldwide

We used the IUCN Red List (IUCN, 2020) to score the following variables for each parrot species: 1) conservation status (0: Least Concern, LC; 1: Near Threatened, NT; 2: Vulnerable, VU; 3: Endangered, EN; 4: Critically Endangered, CR; 5: Extinct in the Wild, EW); 2) whether they are threatened (1) or not (0) by international or domestic illegal trade; 3) whether they are used (1) or not (0) as pets and/or for display; and 4) the regions where they are distributed (Neotropical, Afrotropical, Indomalaysia, and Australasia). International and domestic illegal trade were combined in the variable “illegal trade.”

We also recorded whether and how common each species is bred in captivity, scoring species as 0 (breeding never achieved in captivity until 2020), 1 (exclusively bred in zoos, ex-situ conservation programs, and/or by a few private aviculturists; species not easily available in the pet market), 2 (regularly bred in captivity by aviculturists specialized in particular species; the supply of captive-bred individuals is mostly demanded by other specialized aviculturists), 3 (commonly bred in captivity; captive-bred individuals available to the general public through web pages and pet-shops), and 4 (widely bred in captivity, color mutations often well established after captive-breeding selection; widely available to the general public in pet shops). Information was obtained from Arndt (1996) and Silva (2018), and completed by asking experienced parrot breeders and checking the exports of captive-bred parrots reported by CITES (www.cites.org). The CITES Database (www.cites.org) was consulted to obtain the number of live individuals of wild-caught and captive-bred parrots legally exported across the world from 1975 to 2019, and the number of individuals illegally traded and seized in the same period.

We overlapped the the range distribution map (BirdLife International and Handbook of the Birds of the World, 2019) of each parrot to count the number of species of each class of conservation status and type of illegal trade within square grids of ca. 90km2 (0.1º x 0.1º) distributed over the globe. Using this same approach, we also calculated the number of species divided (scaled) by the maximum number of parrot species in each grid. We then evaluated the existence of hotspots of threatened parrots and parrot species threatened by illegal trade through the Gi* spatial statistic (Getis & Ord 1992; Ord & Getis 1995). Then, we performed an ordinal logistic regression (package MASS, Venables & Ripley, 2002) to assess whether the conservation status of parrots (ranked from 0 to 4) was related to their illegal trade and use as pets/display. The region was included as a fixed factor to control for potential common regional threats (Olah et al., 2016). We used Generalized Linear Models (GLM) to test if species used for pet/display (binomial error distribution, logistic link function) were more frequently reproduced in captivity. We also explored the relationship between illegal trade and captive breeding (GLM: binomial error distribution, logistic link function). The temporal trends in the number of legally traded wild-caught and captive-bred parrots (number of individuals and species) and seizures were analyzed using Generalized Additive Models (GAM). Additional methodological and statistical details, as well as the dataset analyzed, are provided in Supplementary Material.

2.3 Methods: The hidden face of parrot poaching: local demand of pets largely outnumbers domestic and international trade on parrots

Market surveys in Los Pozos market, located in Santa Cruz de la Sierra (-17.77225, -63.17938), were conducted by a contracted parabiologist (person with a wide knowledge on wildlife but without formal training on biology) during a five-years period (2004-2009). The parabiologist have been working on the pet trade for over 10 years, so he was able to identify most of the species, being provided with a digital camara for verification of difficult species. Data on number of individuals traded, species they belonged, and place of origin was collected daily from the people who brought the parrots to sell in the market.

Pet surveys were carried out in 150 municipalities corresponding to the most common places of origin for parrots at the market, covering different biomes in the country (Pires et al. 2016). Driving across these areas we noted every pet observed exposed on the outside of the houses. In addition, we performed informal interviews with local people, asking questions to obtain information about the pet age, obtention method and whether they keep them as household pets, sell them locally, or alternatively send them to Santa Cruz market for sale. Moreover, we asked if they have had more native parrots as pets in recent time and what happened to them, whether they know somebody in the area who has or had and if they “ancestors” have or had. We discarded systematic surveys using questionnaires (Young et al., 2018) due to the illegal nature of parrot trade and that most of the people will be reluctant to answer questions on this matter. Instead, we pretended to be tourist interested on birds, so people did not distrust us, freely answering all questions posed (see Luna et al., 2018; Romero-Vidal et al., 2020).

Data on legal and illegal trade was extracted from the CTES Trade Database (www.cites.org; see supplementary for search terms).

2.3.1 Statistical analyses

Data of informal interviews on parrots age alive at the moment of the surveys and age of the individuals that owners had in the past and already were lost (i.e., died, escaped or were sold) were used to estimate turnover rates of pets. We estimate survival probabilities for the species which data was enough to estimate the survival curves (Amazona aestiva, Ara rubrogenys, Brotogeris chirir, Eupsittula aurea, Psittacara mitratus and Thectocercus acuticaudatus) using the survival package in R (Therneau T (2020). A Package for Survival Analysis in R. R package version 3.2-7, https://CRAN.R-project.org/package=survival.). At last, we estimate the number of pets per family, as a method to refine in the calculation of the annual domestic trade figures.

2.4 Methods: Opportunistic or Non-Random Wildlife Crime? Attractiveness rather than Abundance in the Wild Leads to Selective Parrot Poaching

2.4.1. Study Area

Colombia, with a surface area of 1.1 million km2 and 45.4 million people (DANE, 2020), is one of the most biodiverse countries on Earth (Myers et al., 2008). Differences in elevation and latitude produce large climatic variations across the country, which are responsible for the high diversity of habitats. Colombia can be divided into five continental regions (Andean, Caribbean, Pacific, Orinoco, and Amazon), with remarkable biogeographic, socio-cultural, economic, and demographic differences (Sánchez-Cuervo et al., 2012). Using satellite maps, we designed an a priori road itinerary (4,232 km in total) to cover the main biomes of the Andean, Caribbean, and Pacific regions across a wide altitudinal range (4 – 3,520 m.a.s.l., Figure 2.4.1.1).

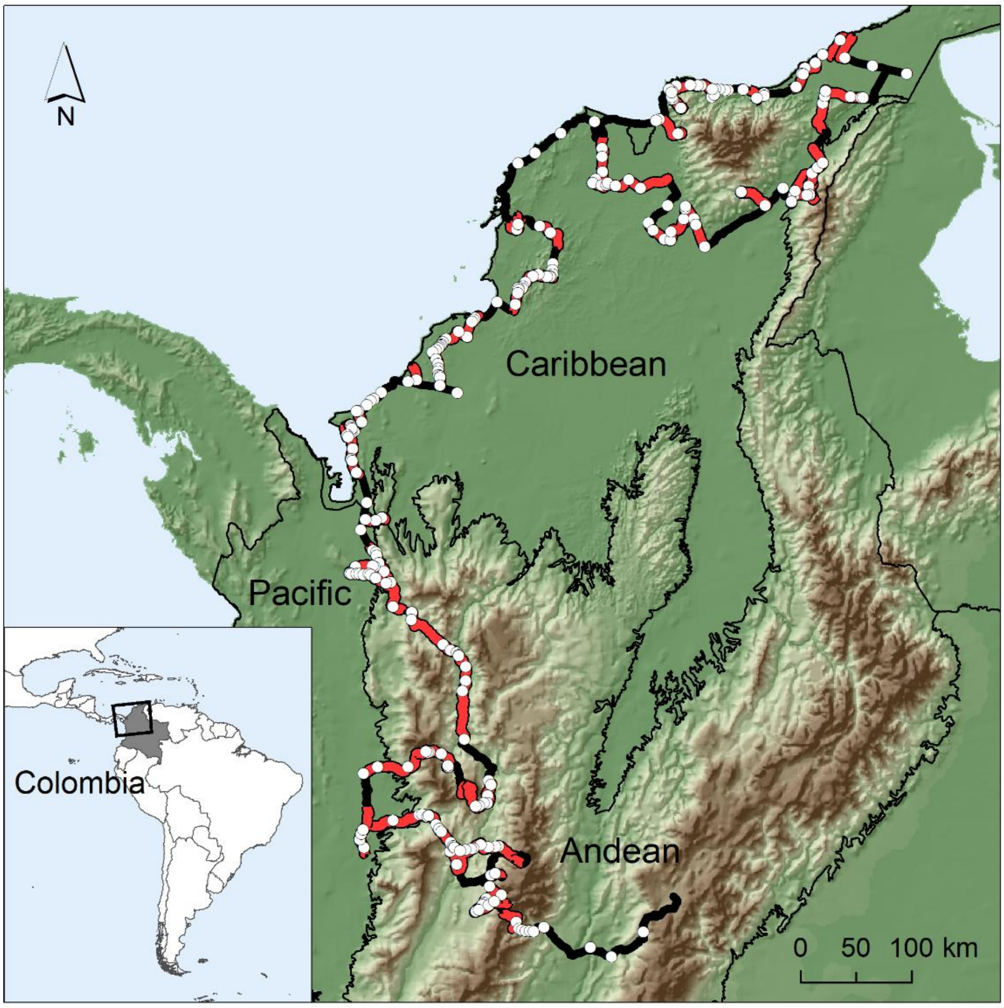


Figure 2.4.1.1. Study area showing the itinerary (black line) crossing the Andean, Pacific and Caribbean regions of Colombia, the roadside parrot surveys (in red), and the localities where poached pets were recorded (white dots).

The itinerary (Figure 2.4.1.1) was designed to cover the spatial distribution of many parrot species (35 species in total, see (Rodríguez-Mahecha & Hernández-Camacho, 2002) and to visit villages where we looked for poached pets (see below), thus maximizing the chances of finding a large variety of poached and wild parrot species at a large geographic scale.

2.4.2. Wild Parrot Surveys

We estimated the abundance of parrots in the wild through roadside car surveys, a method adequate for parrots as it allows coverage of large areas, thus increasing the probability of detecting individuals of species occurring at very low densities or spatially aggregated (Tella et al., 2013; Blanco et al., 2015; Tella et al., 2016; Baños-Villalba et al., 2017; Denés et al., 2018; Luna et al., 2018; Blanco et al., 2020). Within the designed itinerary, we selected 2,221 km of low-transit and unpaved roads to record all parrots detected (Figure 2.4.1.1). The beginning and the end of each habitat patch (categorized as pristine natural, degraded natural, mixed, agricultural and urban; see below) was GPS-recorded to the nearest 10 m, and the length of the transect varied between 0.1 and 28.88 Km (mean = 2.88, SD = 3.63, N = 754). Roadside surveys covered the three different regions surveyed (total rounded lengths: Andean: 839 km, Caribbean: 1002.4 km, Pacific: 379.6 km) and habitats with different degrees of human-induced transformations (see Tella et al., 2013): pristine natural habitats: 31.4 km; degraded natural habitats, where subtle transformations like selective logging were perceived: 577.5 km; natural habitats mixed with agriculture: 1085.6 km; agriculture: 114.2 km; and rural areas with human settlements: 412.4 km. Surveys were performed only once at each road transect to avoid pseudo-replication and double counting.

Surveys were conducted in 2019, during a relatively short period (29th April to 22th May) at the beginning of the wet season, thus avoiding potential spatial biases in parrot abundances due to large seasonal changes. This period mostly coincided with the end of the breeding season, as indicated by the presence of juveniles of several parrot species in the wild, by the full-grown stage of the poached chicks, and by comments of local poachers and pet owners. According to local people, in 2019 the parrot breeding season was earlier due to weather.

Similar to other roadside parrot surveys (Tella et al., 2013; Blanco et al., 2015; Tella et al., 2016; Baños-Villalba et al., 2017; Denés et al., 2018; Luna et al., 2018; Blanco et al., 2020), the driver and two experienced observers drove a 4x4 vehicle at low speed (10-40 km/h) from dawn to dusk (aprox. 6 AM – 6 PM), avoiding rain and hot middays (from 10:00 to 14:00), when parrot activity decays (Wirminghaus et al., 2001; Salinas-Melgoza & Renton, 2006), briefly stopping when needed to identify species and to count the number of individuals in flocks. Observers were familiar with parrot species after previous field-work in Colombia and surrounding countries, so they were able to visually and aurally identify them. Distances of detection (i.e., the perpendicular distance from parrots to the road when they were detected) were recorded to compare two estimates of parrot abundance (see below). Detection distance was estimated visually for short distances or using a laser rangefinder incorporated into binoculars for large distances (Leica Geovid 10x42 HD-R, range: 8-1500 m). In the case of loose flocks, we measured the distance to the closest individual. In some instances, when individuals were heard but not seen and thus flock size could not be estimated, we used the median flock size recorded for the species for analyses. This allowed us to include non-visual contacts, especially of rare and more secretive species, whose omission could result in an underestimation of their relative abundances. All roadside surveys and parrots were recorded using the ObsMapp application for smartphones, which uploads the observations to the citizen science platform Observation (www.observation.org). Therefore, all records, exact location, and associated information can be viewed and downloaded (looking for the observer Pedro Romero Vidal, dates: April 29 – May 22, 2019) to be used by other researchers in the future (Tella et al,. 2020).

Several methodologies are available to estimate wild parrot abundances, all of them carrying different assumptions, pros and cons, and the adequate method will depend on the objectives of the study (Tella et al., 2016). For this work, we used the relative abundance of each species, measured as the total number of individuals recorded divided by the total of km surveyed (indiv./km, Tella et al., 2016). This estimate of abundance has been used in other species- and community-based parrot studies (Tella et al., 2013; Blanco et al., 2015; Tella et al., 2016; Baños-Villalba et al., 2017; Denés et al., 2018; Luna et al., 2018; Blanco et al., 2020), with the constraint that it does not account for differences in detectability among species as it is done by distance-sampling methods (Denés et al., 2018). However, density estimates through distance sampling are not suitable for our study because: 1) they cannot be obtained for rare species with a low number of contacts (Denés et al., 2018), and thus we could only model densities for 11 of the 28 study species assuming a minimum of 10 contacts per species is enough (but see Tella et al., 2016 for the recommendation of using larger numbers of contacts for robust modelling), 2) detection distances cannot be obtained for flocks detected through vocalizations but not sighted, and thus their exclusion would underestimate densities, particularly of the smaller species, and 3) the densities obtained (indiv./km2) can not be used as units of resource available when applying a poaching selectivity index (see below), while using the total number of individuals recorded allows it. Nonetheless, previous studies on two different parrot communities (Blanco et al., 2015; Baños-Villalba et al., 2017) showed that relative abundances (indiv./km) were strongly correlated to detectability-corrected density estimates (indiv./km2). We measured detection distances for assessing whether it is also the case in this study. We calculated detectability-corrected estimates of parrot densities using the software Distance (Thomas et al., 2019) for 11 species for which densities could be modeled. We assumed that detection decreases monotonically with distance from the road transect (Tella et al., 2016) and modeled this process using the half-normal detection function (Blanco et al., 2015). As densities cannot be calculated using non-visual records, we recalculated the relative abundances of these 11 species excluding non-visual records to make results comparable (Table 2.4.1.1). Relative abundances resulted strongly correlated to density estimates (estimate: 0.80, SE= 0.15, t= 5.47, p = 0.0004, adjusted R2: 0.74; Figure 2.4.1.2). These results add further support to the idea that relative abundances of parrots obtained through roadside transects are good proxies of their actual abundance, especially when the high variability in abundance among species overcomes sources of sampling error such as differences in detectability (Tella et al., 2016).

Table 2.4.1.1. Detectability-corrected estimates of density (individuals/km2) obtained through distance sampling and relative abundances (individuals/km) for parrot species with at least 10 visual detections (i.e., sightings of individuals or groups of individuals). Total count refers to the total number of individuals observed during surveys. w indicates the maximum perpendicular detection distance from the survey line for each species.

Species	**Detections**	**Total Count**	**Density (ind/km²)**	***w* (m)**	**Relative Abundance (ind/km)**
Amazona amazonica	24	93	0.2881	200	0.0422
Amazona autumnalis	10	46	0.0307	307	0.0209
Amazona ochrocephala	43	106	0.2214	348	0.0481
Ara ararauna	16	60	0.0570	757	0.0272
Ara severus	15	30	0.0395	365	0.0136
Brotogeris jugularis	260	1678	3.9032	420	0.7620
Eupsittula pertinax	168	1669	2.7928	235	0.7579
Forpus passerinus	10	15	0.1546	45	0.0068
Pionus chalcopterus	14	115	0.0621	650	0.0522
Pionus menstruus	76	356	0.8029	397	0.1617
Psittacara wagleri	19	322	0.9090	270	0.1462

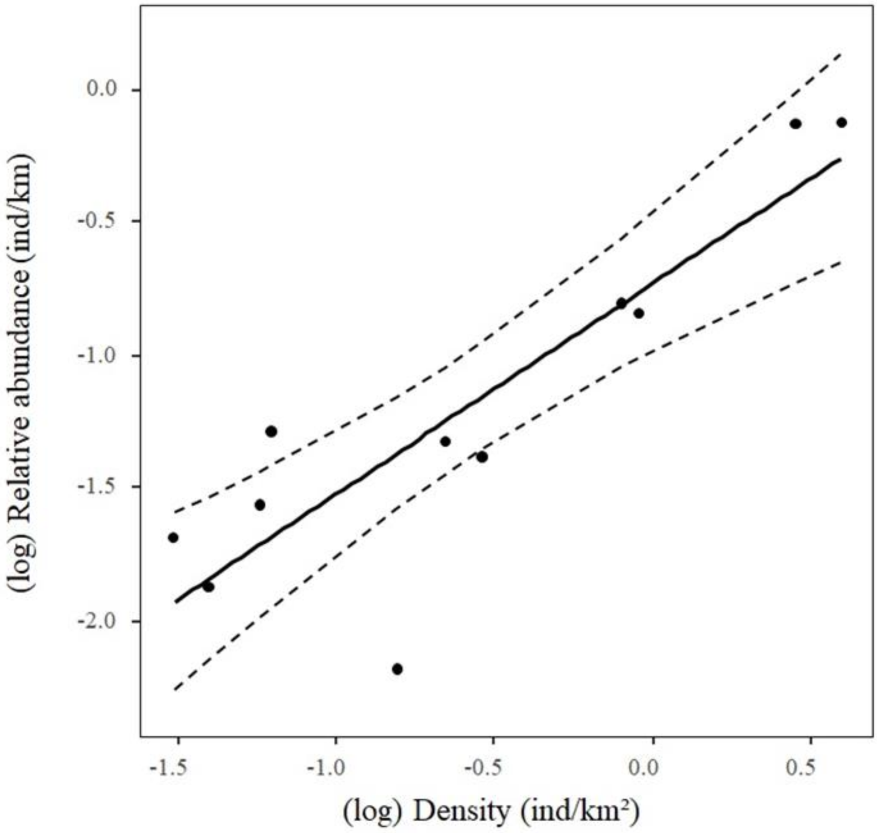


Figure 2.4.1.2. Relationship between detectability-corrected estimates of density and relative abundances of 11 parrot species. The regression line (solid) and 95% confidence interval (dashed lines) are plotted.

2.4.3. Poached Parrot Surveys

As a direct measure of domestic poaching pressure, we recorded the number of all wild and exotic pets, and how many of them were poached native parrots, in 282 villages crossed by our itinerary (Figure 2.4.1.1). We did not conduct systematic surveys using questionnaires (Young et al, 2018), as answers to questions related to illegal activities that are prosecuted in the country would be unreliable (Luna et al., 2018). Nonetheless, most people did not hide their pets, nor were they afraid to keep them illegally. Therefore, we recorded many visible pets while driving and walking through streets or entering public establishments, such as shops, hotels or gas stations. We combined these direct observations with informal conversations (Luna et al., 2018) with randomly chosen local people (N = 358), indicating our interest to see and take pictures of their pets. In about half of the cases (55.6%), people told us they had pets at home, and in 62% of cases provided us with information about other people who poached or owned pets. We then confirmed this information by visiting their homes, taking pictures of the pets (Figure 2.4.1.3) and, at the same time, engaging in informal conversation to obtain additional information, such as the price they paid for the parrot and its ability to imitate human speech (see below). We could not obtain prices from all species, as in many cases the owners did not buy the pets but poached themselves. Pet owners confirmed that all native parrots were poached, with no evidence of attempts to breed them in captivity (contrary to a few exotic, small parrot species). All informants and pet owners shared the information with us freely and were kept anonymous.

Figure 2.4.1.3. Some pet parrots observed in public spaces such as streets (a-c) or within homes (d-f). Pictures also illustrate species positively (a: scarlet macaw Ara macao, b: yellow-crowned amazon Amazona ochrocephala, c: blue-and-yellow macaw Ara ararauna, d: blue-crowned parakeet Thectocercus acuticaudatus) and negatively selected by people as pets (e: brown-throated parakeet Eupsittula pertinax, f: orange-chinned parakeet Brotogeris jugularis). Pictures: P. Romero-Vidal and J.L. Tella.

2.4.4. Parrot Attractiveness

The attractiveness of each parrot species was rated based on its body size (obtained from Forshaw, 2010), coloration, and ability to imitate human speech (Pires & Clarke, 2012; Tella & Hiraldo, 2014). Parrot coloration was described as the proportion of the body (bright body) and head (bright head) covered by bright colors (i.e., other than the dominant green or brown coloration), scored from 0 to 2 following (Pires & Clarke, 2012), and the total number of colors (N colors) observed when the bird is perched, using plates in (Thomas et al., 2010). The ability of each individual pet to imitate human speech was ranked into five categories using the information provided by local pet owners (0: individuals not able to make imitations, 0.5: individuals able to whistle or imitate one or two words, 1: individuals able to imitate several words but poorly pronounced, 1.5: individuals able to imitate several words, with good pronunciation, and 2: individuals able to imitate human speech, using a wide repertoire of words and making up short sentences, singing songs, imitating other domestic animals or sounds such as telephone, TV, radio, etc.). Scores from different individual pets were averaged within species to obtain a rank describing the ability of each species to speak. However, the opinion of local pet owners could be biased by their experience, which is usually limited to their own pets. Therefore, we asked the same question to five people from USA, France, Germany and Spain with > 20 years of experience breeding and keeping a large variety of parrot species in captivity. The average scores provided by these experts correlated well with those provided by local pet owners (Spearman rank correlation = 0.85, $p < 0.0001$, Figure 2.4.1.4), thus validating the use of local knowledge for measuring the mimicry ability of different parrot species.

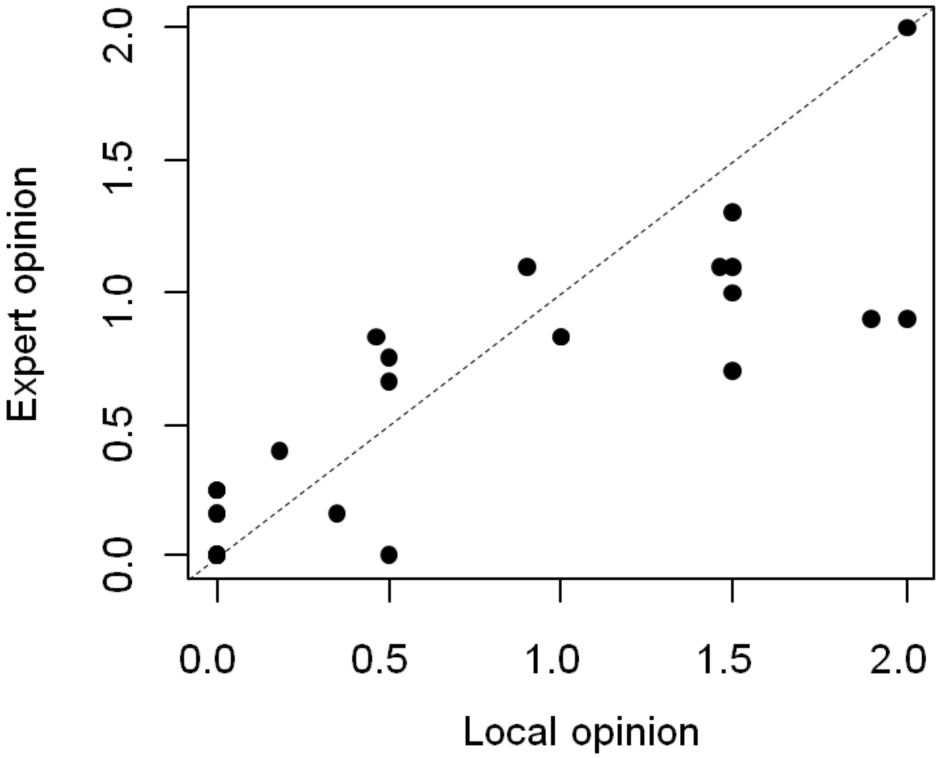


Figure 2.4.1.4. Scatterplot of the averaged opinion on the ability of different parrot species from Colombia to imitate human speech (0 = lowest, 2 = highest) provided by international experts and by local pet owners. Each dot represents a species, and the dashed line represents the theoretic perfect correlation.

2.4.5. Statistical Analyses

We used the Savage selectivity index (Manly et al., 2007) to assess whether parrot species are poached proportionally to their abundances in the wild. This index is widely used in resource selection studies (e.g. Rebolo-Ifrán et al., 2017) and allows us to infer the statistical significance of selection (Manly et al., 2007). We used the number of parrots of each species recorded in the wild as units of resource availability and numbers recorded as pets as units of the resource used. The Savage selectivity index was calculated for each species as W = Ui /pi, where Ui is the proportion of a given species (among all poached parrots) recorded as a pet (i.e., used) and pi is the proportion of that species (among all wild parrots) recorded in the wild (i.e., available). A few species were so scarce that we did not record a single individual in the wild (Table 2) despite their known presence in the study area (Rodríguez-Mahecha & Hernández-Camacho, 2002) and finding them locally as pets. In those cases, as the availability of a used resource cannot be zero (Manly et al., 2007), we conservatively considered that at least one wild individual was recorded to allow calculating the Savage index. The Savage index theoretically varies from zero (full negative selection) to infinite (full positive selection), with one being the expected value by chance (i.e., used in proportion to its availability; Manly et al., 2007). The statistical significance of this index is obtained by comparing the statistic (wi -1)2/sewi2 with the corresponding critical value of a χ2 distribution with one degree of freedom (Manly et al., 2007), the null hypothesis being that species are poached in proportion to their availability in the wild. The standard error of the index (sewi) is calculated as √[(1-pi)/(u+ * pi)], where u+ is the total number of poached parrots recorded. Statistical significance was obtained after applying the Bonferroni correction for multiple tests. We did not calculate the Savage index for four species (Table 2.4.1.2) since they are unable to survive in captivity more than a few days or weeks (Silva, 2018) and thus they are rarely poached. However, results including these species were nearly identical (Spearman correlation, r = 1, p < 0.0001, n = 24).

We used Principal Component Analysis (PCA) to obtain a composite variable that describes the attractiveness of each parrot species as a function of its color, body size, and ability to speak. Variables, which were positively correlated (Pearson correlations: 0.50-0.94, all p<0.0001), were scaled before analysis. Bartlett's test of sphericity was computed to establish the validity of the data set. Eigenvalues >1 were used to assess the number of factors to extract.

We used Generalized Linear Models (GLM) to test whether the preference of people for certain species (measured through the Savage index; log-transformed; normal error distribution and identity link function) was related to their attractiveness. We then assessed whether preferred or rare species were the most valuable in monetary terms by relating the Savage indexes and abundances of species in the wild (ind./km) to their price (log-transformed; normal error distribution and identity link function). We used the average prices of species provided by pet owners (local currency transformed to US$, Table 2.4.1.2). All statistical analyses were performed in the R v.3.6.1 statistical platform (R Development Core Team, 2019).

2.5 Methods: Selective poaching as the main pet source in Peru and Ecuador: warns on the unsustainable domestic demand for preferred parrot species.

2.5.1 Study area.

The study area covers Peru and Southern Ecuador (Figure 2.5.1.1). Both countries are crossed by the Andes, which separates the Pacific coastal region from the Amazonian region and creates a wide diversity of biomes. Thus, these countries are considered as the most biodiverse areas in the world (Myers et al., 2000), holding ca. 15% of the extant parrot species (IUCN 2020).

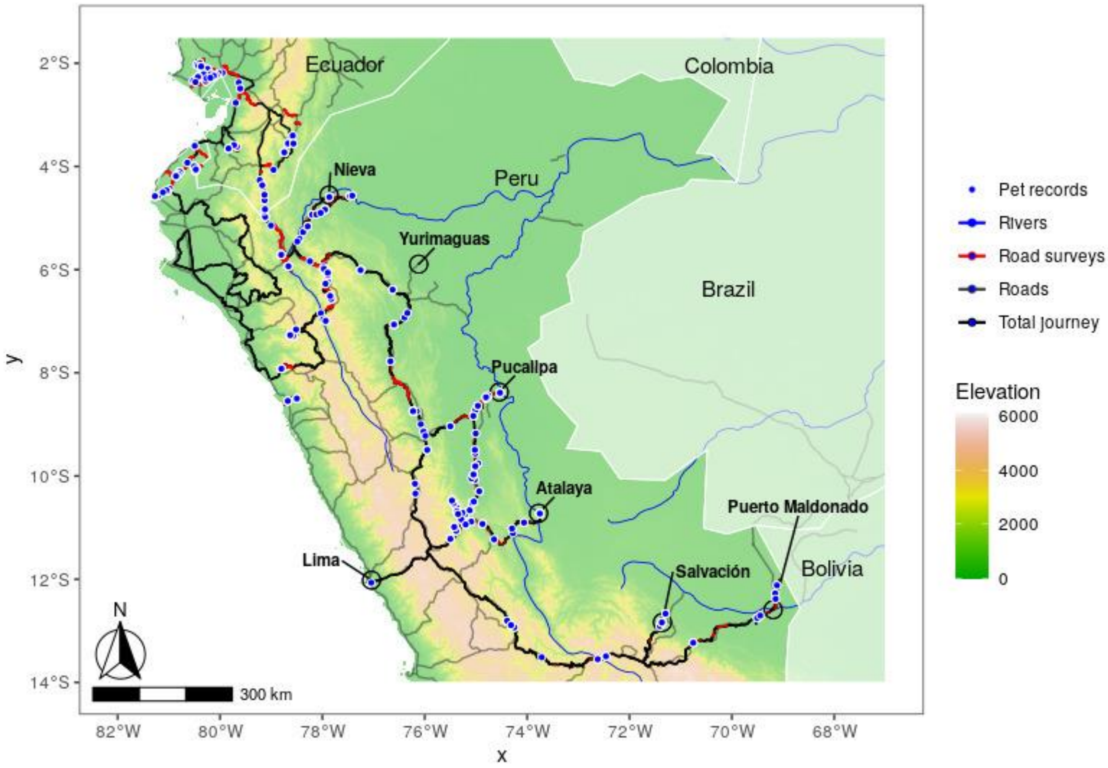


Figure 2.5.1.1. Study area showing the routes (black lines), roadside surveys (red lines), and locations where household pets were recorded (blue dots). Other main roads (not used during our surveys) and rivers used to transport poached parrots are shown in grey and blue, respectively. Cities with pet markets visited during the study are included.

2.5.2 Parrot abundance in the wild

Following Romero-Vidal et al. (2020), we conducted large-scale road surveys to estimate relative parrot abundances in the wild, covering ca 3000 km between 29 November and 17 December of 2014 and 2003.8 km between 7 and 31 October 2018 (Figure 2.5.1.1). This methodology allows the sampling of large areas to increase the likelihood of recording parrots showing patchy distributions and/or low densities (Dénes et al., 2018). The number of individuals recorded using this method strongly correlates with density estimates accounting for differences in detectability among species (i.e., distance-sampling procedures; Romero-Vidal et al., 2020). Road surveys were designed a priori using recent satellite images, selecting unpaved and low-transited roads to cover the main biomes and habitats potentially inhabited by parrots (Romero-Vidal et al., 2020). Car surveys were conducted during early mornings and afternoons by four persons driving at a low speed (20-40 km/h) and stopping, when needed, to identify the species and count the number of individuals. When parrots were only aurally detected, we used the average flock size recorded for the species for analyses (Romero-Vidal et al., 2020).

2.5.3 Abundance of poached parrots

We surveyed villages crossed during our road surveys to record the presence of pets, often visible from the streets or exposed in public establishments, and randomly ask people whether they had or knew others who had parrots as pets. This methodology proved to be useful to estimate poaching pressure in most Neotropical areas, where this activity is not actively prosecuted and thus animals are not hidden (Luna et al., 2018; Romero-Vidal et al., 2020). We georeferenced the location of each pet and asked owners how and where it was obtained. If the individual was bought, we asked its price and where it was obtained (markets or other people).

2.5.4 Distances to distribution ranges and markets

We measured the shortest distances by paved and unpaved roads (https://portal.mtc.gob.pe/estadisticas/descarga.html, https://geonode.wfp.org/layers/ogcserver.gis.wfp.org%3Ageonode%3Aecu_trs_roads_osm) from each parrot pet to the closest point of its native distribution range (Birdlife International; http://datazone.birdlife.org/species/requestdis) and, when parrots were bought, we also obtained the distance to the market of origin. When the information of the market was not available (n=X individuals), we considered that the bird was bought in the closest market. Calculations were performed using QGIS 3.4.12 and ArcGIS 10.3.1. Conservatively, the distance to the distribution range was set as 0 km for parrots poached within its distribution range. The main Amazonian and coastal markets were identified from previous studies (Gastañaga et al., 2011; Shanee et al. 2017) and during our surveys (Figure 2.5.1.1).

2.5.4 Conservation status and legal trade

We used the latest IUCN Red List (IUCN, 2020) to extract and score the global conservation status (0: Least Concern, 1: Near Threatened, 2: Vulnerable, 3: Endangered) and population trend (1: decreasing, 2: stable, 3: decreasing) of each species recorded. We obtained the species with harvest quotas for their legal international trade from Salinas (2014), actualizing taxonomic changes (IUCN, 2020) such as the split of Psittacara mitratus into three species (Arndt, 2006).

2.5.5 Statistical analyses

The Savage selectivity index (hereafter, selectivity index SI, Manly et al., 2007) was calculated for each species recorded as pet and/or present in our road census to test poaching selection, using the number of individuals recorded in the wild as the available resource and the number of individuals recorded as pets as the used resource (Romero-Vidal et al., 2020). Values of SI close to 1 indicate the use of the resource proportional to its availability, while values below 1 indicate a negative selection, and above 1 a positive selection (Manly et al., 2017). Statistical significance of SI was calculated after applying Bonferroni correction for multiple tests (see Romero-Vidal et al., 2020 for details). We tested differences in SI between amazons (genus Amazona), large macaws (genus Ara), and the remaining species using a Kruskal-Wallis test and posthoc pairwise Wilcoxon rank-sum exact tests (applying Bonferroni correction), and between species with and without legal harvest quotas using a Mann-Whitney test. We modeled the probability of a pet being moved and, when moved, its distance from its distribution range (log-transformed) to its SI using generalized linear mixed models (binomial error distribution and logit link function, and normal error distribution and identity link function, respectively; random term: species). We used generalized linear models (GLM) to assess whether SI was related to species price (transformed to US$; normal error distribution and identity link function) and to its conservation status (rank: 0-4) and population trends (rank: 1-3) (multinomial error distribution, cumprobit link function). We related the proportion of individuals bought in markets per species to its SI (GLM: binomial error distribution and logit link function). Model fit was checked using DhARMA (Hartig 2020). Statistical analyses were performed in R 3.5.2 (R Core Team 2018).

2.6 Methods: Deforestation or overharvesting? Pet-keeping cultural burden rather than habitat transformation causes selective parrot defaunation in Costa Rica

2.6.1 Study area and species

Costa Rica is a relatively small country (ca. 51,000 km2) that holds ca. 4-5% of all known plant and bird species in the world (Sanchez-Azofeifa et al., 2001; MINAE, 1992). This high biodiversity arises due to the complex interaction between soils, topography, microclimates, and its special geographic location between North and South America (Sanchez-Azofeifa et al., 2001). Costa Rica is divided into five main biomes, namely: Tropical humid Caribbean (THC), Tropical humid Pacific (THP), Tropical Dry Forest (TDF), Midlands (M), and Highlands (H; Garrigues and Dean, 2013). Although Costa Rica has experienced an important deforestation process during the XIX century for farming and wood extraction (Gaupp, 1992; Lutz et al., 1993; Sanchez-Azofeifa et al., 2001), by the year 2000 reforestation rates were higher than deforestation rates (Keenan et al., 2015), and the country has been slowly gaining forest cover since then (Chacón-Cascante et al., 2012; Algeet-Abarquero et al., 2015).

The parrot community in Costa Rica is composed of 18 species (Forshaw, 2010), two of them considered as Globally Endangered (Ara ambiguous and Amazona auropalliata), one Vulnerable (Touit costaricensis), and two Near Threatened (Amazona guatemalae, Eupsittula nana). The other parrot species present in the country are classified as of Least Concern (Amazona albifrons, Amazona autumnalis, Eupsittula canicularis, Eupsittula pertinax, Psittacara finschi, Brotogeris jugularis, Pyrilia haematotis, Pionus senilis, Pionus menstruus, Ara macao, Bolborhynchus lineola, Pyrrhura hoffmanni) according to the UICN categories (IUCN, 2019).

2.6.2. Road surveys

We performed a countrywide road survey to census parrots and assess the degree of habitat transformation of the different biomes present in Costa Rica. This method has been largely used to monitor this and other taxonomic groups as it allows to cover large areas to increase the probability of detecting individuals of species present at low densities and/or spatially aggregated (Carrete et al., 2009; Grilli et al., 2012; Tella et al., 2013; 2016a, 2016b; Blanco et al., 2015; Montesinos-Navarro et al., 2017; Baños-Villalba et al., 2017; Dénes et al., 2018; Luna et al., 2018). We used a network of unpaved roads (when possible) to conduct the surveys to avoid traffic noise and facilitate hearing detection, and to ensure a constant slow driving speed (10-25 km/h; Luna et al., 2018). This network of roads covered all biomes present in the country, crossing 15 National Parks (Guanacaste, Santa Rosa, Palo Verde, Carara, Tortuguero, Braulio Carrillo, Los Quetzales, Tapantí-Macio Cerro de la Muerte, Corcovado, Braulio Carrillo, Volcán Arenal, Diriá, Barra Honda, Rincón de la Vieja, Barbilla, Volcán Poas) and 6 Wildlife Reserves (Caño Negro, Barra del Colorado, Lomas Barbudal, Golfo Dulce, Humedal Nacional Terraba Sierpe, Gandoca-Manzanillo), as well as unprotected areas with different degrees of habitat transformation. During the road surveys, we GPS-located all parrots detected, stopping the car when needed to identify the species or count individuals. Road surveys were completed between 10th April and 1st May of 2018, at the beginning of the wet season, by 3 experienced observers (the driver and two observers), from dawn to dusk. We avoided adverse weather conditions (e.g., rain, fog) and the central hours of the day (from 10:00 to 14:00), when parrot activity, and thus their detectability, decays (Salinas-Melgoza and Renton, 2006; Wirminghaus et al., 2001). Surveys were performed once for each road transect to reduce pseudoreplication and double counting.

During road surveys, we also GPS-recorded the beginning and the end of each habitat patch and categorized them by biomes and into five main categories representing an increasing degree of habitat transformation, namely: natural (i.e., highly preserved habitat, primary forest with the presence of large trees); degraded (i.e., secondary forests or primary forest where subtle transformations like selective logging are perceived); natural habitats mixed with agriculture (i.e., mosaic-type habitat, alternating crops and livestock areas with pristine or degraded patches); agriculture; and rural habitats with human settlements. This field-based habitat information is a rude estimate representative of the actual degree of habitat degradation of a patch when transformations are occurring in real-time (Carrete et al., 2009).

2.6.3. Habitat characteristics and parrot communities

We related the presence, abundance, and richness of parrots to habitat characteristics using two complementary approaches. First, we used patches across transects as sample units, assessing habitat features based on road transect information. Then, as parrot communities can be affected by habitat characteristics operating at different scales and not easily captured by our field-based habitat categorization, we complementarily used all geo-referenced points where we had detected at least one parrot to calculate point-level presence, abundances, and richness.

Absence points (i.e., pseudo-absences) were generated by randomly selecting them over each transect where we did not detect any parrot, using an excluding distance of 250m from presence points. Each absence point was characterized by the same time (i.e., the hour of the day) as the closest presence point. To balance the sampling effort, the number of absence points (n = 743 points, distributed over all transects) was proportional to the number of presence points in each transect. Then, we calculated the distance of each point to the nearest protected area (obtained from Sistema Nacional de Información Territorial of Costa Rica, http://www.snitcr.go.cr) and village (obtained from Centro Nacional de Información Geoambiental del Ministerio de Ambiente y Energía, https://www.repositorio.una.ac.cr), as well as the percentage of forest and crops and an index of the human footprint (see Venter et al., 2016 for details) within a radius of 1, 5 and 10 km around each one. Forest cover was obtained from the Global Forest Change project (updated to 2017; Hansen et al., 2013), a dataset characterizing vegetation taller than 5m height and elaborated from time-series analysis of Landsat images taken between 2000 and 2017. Cropland cover was obtained from MODIS land cover maps (MCD12Q1 V6 product, LC_Type 3 scheme) elaborated by the NASA EOSDIS Land Processes Distributed Active Archive Center (LP DAAC). Using this land cover dataset, we selected and merged into a unique cropland category the following classes: herbaceous annuals, shrublands, and broadleaf croplands. It is worth noting that this map reliable classifies as croplands large areas of continuous cultures (monocultures), but fails when dealing with small agricultural patches interspersed with natural vegetation. Human footprint (hereafter HF, downloaded from https://datadryad.org/resource/) is an index created from global data layers indicating human population pressure (population density), human land use and infrastructures (built-up areas, night-time lights, land use/land cover), and human access (coastlines, roads, railroads, navigable rivers).

We used Generalized Linear Mixed Models (GLMM) to relate parrot presence (binomial error distribution, logit link function), abundance and richness (Conway-Maxwell-Poisson error distribution; log link function) to the degree of habitat transformation (continuous variable, from pristine (1) to rural (5); linear and quadratic forms) using patch-level data. We did not correct our parrot abundance data employing the distance sampling model (Blanco et al., 2015; Baños-Villalba et al., 2017; Luna et al., 2018) due to the low number of contacts per habitat for most of the species, which arose unreliable habitat-specific detectability models (Dénes et al., 2018; Luna et al., 2018). However, the high correlation observed in previous studies between raw data and abundances estimated through distance-sampling models allows us to rely on our field estimations. Abundance and richness obtained at the patch-level (the number of individuals/km and the number of species/km, respectively) were rounded for modeling purposes. When their values were > 0 but < 0.5, we equaled them to 1 to not consider as 0 those patches were individuals or species, although scarce, were certainly present. Models included the transect as a random term and the biome and the hour of the day (morning: before 10 am, midday: between 10 am and 3 pm, and afternoon: between 3 pm and 7 pm) as controlling variables (fixed factors; Tella et al., 2013; Luna et al., 2018).

We used Generalized Linear Models (GLM) to complementarily explore factors driving the presence (binomial error distribution, logit link function), abundance (negative binomial error distribution; log link function) and richness (Conway-Maxwell-Poisson error distribution; log link function) of parrots using a point-level approach and three spatial scales (1, 5 and 10km around point counts). Models included distance to protected areas and villages, forest and crop cover, and HF as explanatory variables, and the biome and the hour of the day as controlling variables (fixed factors). In this set of models, we also added a spatial autocovariance (AC) term to account for the potential spatial autocorrelation in the data. AC was computed using the autocov_dist function (spdep library; Bivand et al., 2011) and the weighted average distance of all neighboring samples, indicating the degree of spatial clustering among the dependent variables.

All models were run using the package glmmTMB to correct for zero-inflation (Mollie et al., 2017) and their fit was evaluated using the package DHARMa (Hartig 2018). DHARMa employed a simulation-based approach to creating standardized residuals (values between 0 and 1) for fitted (generalized) linear (mixed) models and test the significance of the dispersion parameter, zero-inflation, and goodness-of-fit of the model (H0: fitted model suits well for the data). Model selection for both patch- and point-level analyses was performed using the Akaike Information Criterion corrected for small sample sizes, AICc (Burnham and Anderson, 2002). Within each set of models (which includes the null model), we calculated the ΔAICc (as the difference between the AICc of model i and that of the best model) and the Akaike weight (w) of each model. Models within 2 AICc units of the best one were considered as alternatives and used for model averaging (MuMIn package; Barton, 2019), dismissing those showing convergence problems. We considered that a given effect received no, weak or strong support when the 95% confidence interval (CI) strongly overlapped zero, barely overlapped zero, or did not overlap zero, respectively.

Finally, we used hierarchical partitioning (Chevan and Sutherland, 1991) to examine the independent effect of the variables included in averaged models on the presence, abundance, and richness of parrots. Hierarchical partitioning is a multiple-regression technique in which all possible models are jointly considered to provide a measure of the effect of each variable that is largely independent of the effects of others (Mac Nally, 2000). Hierarchical partitioning and associated randomization tests were implemented using the hier.part package (Nally and Walsh, 2004). As this package has not implemented the negative binomial and Conway-Maxwell-Poisson distributions, for abundance and richness we used the Poisson family. We evaluated competing models based on the R2 dev statistic, determining the significance of the effects through randomization tests (999 randomizations).

2.6.4. Poaching pressure on parrot species

We recorded the number of parrots found kept as pets in the villages crossed during our road surveys as a direct measure of local domestic poaching pressure on parrots. Systematic surveys using questionnaires (Young et al., 2018) were not feasible as most people could distrust to answer questions related to illegal activities which are prosecuted in the country. Thus, we performed informal conversations (Luna et al., 2018) with randomly chosen local people, showing them our interest to see and take pictures of their pets. Most people told us they had pets at home and, in most of the cases, they gave us information about other people owning pets (number and species). We then confirmed this information by visiting these houses, taking pictures of the pets (Figure 2.6.4.1). All informants and pet owners shared the information with us with total freedom and were kept anonymous. We combined this informal data with records of pets observed while driving and walking through streets or acceding to public establishments such as shops, hotels, or gas stations.

We used the Savage selectivity index to properly understand whether poaching pressure was focused on particular species or it was an opportunistic activity extracting individuals of the commonest taxa (Savage 1931; Manly et al., 2007; Caro et al., 2011). The Savage index varies from zero (full negative selection) to infinite (full positive selection), with one being the expected value by chance (i.e., used in proportion to its availability). The statistical significance of the index was obtained following Romero-Vidal et al. (2020), applying the Bonferroni correction for multiple tests. The Savage selectivity index was first calculated considering the abundance of each species as pets and in the wild (Romero-Vidal et al., 2020) to test the null hypothesis that species are poached in proportion to their availability in the wild. Then, we recalculated this index including seizures carried out by the Costa Rican environmental police from 2011 to 2017 and pet data as a measure of availability to test whether seizures were skewed toward certain species over others or proportional to what people have at home.

Finally, we assessed whether the existence of environmental vigilance close to protected areas may help to reduce parrot poaching. For this purpose, we related through GLM the abundance and richness of pets at each location (Conway-Maxwell-Poisson error distribution, log link function) as well as the proportion of these individuals that were exposed (i.e., which were easily observable from the street or road, not hidden inside the houses; binomial error distribution, logit link function) and their mean Savage selectivity index (normal error distribution, identity link function) to the distance to protected areas and the mean annual number of tourists visiting them (foreign, local and total number of tourists). Due to the dispersed, extended, and diffuse nature of most of these locations, we were not able to correct pet abundance and richness by the number of inhabitants. Models were built following the procedures explained before.

2.7 Methods: Cities may save some threatened species but not their ecological functions

2.7.1 Study area and species

The Dominican Republic is located in the central area of the Caribbean Sea, covering two thirds of La Hispaniola Island (the rest corresponding to Haiti). Since Spanish colonization in 1492, the island habitats have transformed to farmland, with agriculture currently covering 48.7% of its surface area (World Bank, 2014), although habitat degradation was higher in past decades and centuries (Olivo, 2007). Despite the habitat loss and fragmentation, this country still holds the largest variety of ecosystems in the Caribbean region, due to its mountainous relief (altitude ranging from 0 to 3,098 m.a.s.l.), climate variability, and a large surface area (25,472 km2) covered by 119 protected areas (c. 50% of the country). The main ecosystems can be broadly grouped as tropical rainforests in the northern lowlands, coniferous forests in the central mountains, and tropical dry forests in the southern lowlands. By 2001, 65% of the population (8.7 million people) lived in urban areas, with the capital (Santo Domingo) holding 3.5 million people and an urban population growth rate that reached 2.3% between 2000 and 2005 (http://www.nationsencyclopedia.com/Americas/Dominican-Republic-POPULATION.html). The Dominican Republic constitutes the core area for the two endemic Hispaniolan parrot species (P. chloropterus and A. ventralis), which are considered near extinction in Haiti (BirdLife International, 2016a, 2016b). A third, Near Threatened species endemic to Jamaica, the Jamaican parakeet (Eupsittula nana) (BirdLife International, 2016c), has been reported in the Dominican Republic, but its status as a native or alternatively human-mediated introduced species remains uncertain (Latta et al. 2006).

2.7.2 Estimating habitat-related parrot abundances

Habitat use by parrots was assessed through large-scale roadside surveys, conducted under permits from the Ministry of the Environment of the Dominican Republic. Among different methods available to estimate parrot abundance, roadside surveys are recommended given that they allow to sample large areas and thus increase the likelihood of recording parrots, as they usually show low densities and aggregated distributions resulting from their highly-mobile and flocking behavior (Dénes et al. 2018). This methodology has previously allowed the assessment of parrot abundances (Grilli et al. 2012; Blanco et al., 2015; Tella et al. 2016a; Baños-Villalba et al., 2017), of their foraging behavior (Tella et al. 2016b, Montesinos-Navarro et al. 2017), and of the effects of habitat loss and fragmentation in a variety of raptor and parrot species in different Neotropical biomes (Carrete et al., 2009; Tella et al., 2013). One of the authors (AL) travelled throughout the country in June 2016, gathering information on the distribution of habitats across the island. Thereafter, using recent satellite maps, we selected a network of secondary, mostly unpaved roads to be surveyed, which covered natural habitats as well as agricultural land and urbanized areas throughout the country. We included roads that crossed 12 protected areas (including the National Parks del Este, Jaragua, Bahoruco, Sierra de Neiva and Cordillera Central), where natural ecosystems of the island are still well preserved. The road network was plotted on paper maps and uploaded on a portable GPS. We conducted the field survey from June 6 to June 21, 2017, at the end of the parrots' breeding season (Latta et al. 2006), with 2,143.5 km surveyed (Figure 2). Surveys were conducted in the morning and afternoon by 3-4 persons driving a car at low speed (10-25 km/h). Habitats crossed through the roadside transects were grouped into the main island habitats: 1) coniferous forests, 2) tropical rainforests, 3) tropical dry forests, 4) farmland, 5) small villages, and 6) large cities. We recorded every time the habitat changed from one type to another to measure the length (in km) of the habitat crossed by the transect (sub-transect). For each sub-transect we also recorded the number of observed parrots of each species. We briefly stopped the car every time parrots were detected to record the species, number of individuals, their activity, the distance at which they were detected (detection distance) using a laser rangefinder (Leica Geovid 10x42, range: 10-1,300 m), and to geo-reference the site. All roadside transects were surveyed only once.

The estimation of parrot densities through distance sampling modelling (Blanco et al., 2015; Baños-Villalba et al., 2017) was not possible due to the scarcity of the species and thus the very low number of contacts we obtained for both species of parrots in most habitats (see Results), then precluding obtaining reliable habitat-specific detectability functions (see Dénes et al. 20187 for distance sampling modelling requirements). The number of contacts and associated detection distances of parrots were also low for distance sampling modeling when pooling habitats into three main categories: 1) large cities, 2) rural habitats (grouping villages and farmland, i.e., a mosaic of small villages and houses embedded in agricultural lands), and 3) natural habitats (grouping coniferous, tropical rainforest and tropical dry forests). We thus relied on an index of relative abundance of each species in each habitat as the number of individuals recorded / number of km surveyed (Tella et al. 2013, 2016b, Blanco et al. 2015). Nonetheless, results obtained through this index were highly correlated with those obtained through distance sampling modelling in other parrot communities (Dénes et al., 2018). Differences in relative abundances of each parrot species among large cities, rural and natural habitats were tested using generalized linear models (GLM, Poisson error distribution and log link function), with the number of individuals recorded in each sub-transect as the response variable, the length (in km) of each sub-transect as a covariate, and habitat as a fixed factor (Tella et al. 2013). The obtained results could be biased due to potential biases in distances of detection, which ranged between 0 and 1,200 m (n = 76). Parrots seemed to do not avoid the proximity of the roads surveyed. In fact, 15% of the observations were recorded just in the border of the roads (distances close to 0 m), and 35% of the observations were recorded at distances < 10 m from the roads. On the other hand, a GLM (with log-transformed detection distances as response variable, normal distribution and identity function) showed no differences between species (Wald ϰ2 = 0.91, df = 1, p = 0.327) nor an effect of flock size (Wald ϰ2 = 1.48, df = 1, p = 0.233), with a marginally significant effect of habitat (Wald ϰ2 = 5.11, df = 2, p = 0.078). This effect resulted from a slightly higher detectability of parrots in rural (median detection distance = 68.5 m, range = 5-132 m) and natural habitats (median = 80.0 m, range = 15 – 1200 m) than in large cities (median = 66.0, range = 0-350m). From our experience, the highly intense and noisy car traffic and presence of tall buildings made difficult both the oral and visual detection of parrots in cities at larger distances. If anything, this slight bias in detectability would underestimate the relative abundance of parrots in cities compared to natural habitats, thus making our results conservative.

In addition to the above systematic survey, we also looked for flocks of parrots flying at sunset to potential communal roosts. When we located a communal roost, 3-5 people were situated at vantage points to count the number of individuals gathering at the roost site until night time. This information on roost sizes could help future long-term monitoring programs of these species (Dénes et al. 2018).

2.7.3 Recording conservation threats

We wanted to know whether the main conservation threats highlighted in the literature, namely poaching for the pet trade and hunting (Latta et al. 2006; BirdLife International 2016a, 2016b), still affect parrot populations in the Dominican Republic. We discarded the possibility of conducting a systematic survey using questionnaires (see methodological recommendations by Young et al. 2018), given that most people could be reluctant to respond as hunting, trapping and trading parrots are illegal activities in Dominican Republic since 2000. Therefore, to answer our simple question (i.e., whether these threats are still alive in the country despite of prohibitions), we simply stopped in different villages while travelling across the country to informally converse with local people we found in the streets. We presented ourselves as foreign ornithologists interested in the observation and conservation of birds and especially of parrots, and thus people viewed us as birdwatching tourists that could not constitute a threat for their potential illegal activities. During these informal talks, we asked people about the current or past presence of parrots in the surroundings and their conservation problems. The fact that we speak the same language (Spanish) surely facilitated the long and friendly conversations we had, thus gaining confidence on the information obtained (Young et al. 2018). Most people freely responded, providing their perception of past and current status of parrot populations and their threats, and often guided us to the homes of neighbors, family or friends who kept parrots as pets. In such cases, we were allowed by owners to take pictures of their pets and often received voluntary much more information than we expected, including the age of pets, where and how they were obtained, and how much they paid for them. In some cases people also provided details on other threats such as hunting as a food source or to avoid crop damage. We did not record the names of informants, so their identities remain anonymous.

2.7.4 Recording seed dispersal

During and outside of the roadside surveys, we looked for foraging parrots to record seed dispersal through stomatochory, i.e. when parrots fly from a fruiting plant carrying fruits with the beak to handle and consume them in a distant perching tree, then measuring dispersal distances with a laser rangefinder (Tella et al. 2015, 2016a, 2016b; Blanco et al. 2015; Baños-Villalba et al. 2017). We also looked below the identified perching trees for dispersed fruits and seeds that parrots dropped after consumption, and thus estimated a minimum dispersal distance for each seed as the distance to the nearest fruiting plant of the same species (see Tella et al. 2016b). All perching trees were species different to the plant species that produced the dispersed fruits, so there is not the possibility of making mistakes by recording seeds naturally falling to the ground or handled by parrots in the mother tree. We examined every dispersed fruit or seed to determine the proportion of mature, intact seeds (parrots often consumed the fruit pulp and discarded entire seeds) that had the potential to germinate after dispersal by parrots.

2.8 Methods: The widespread poaching of wild pets as an overlooked risk of zoonosis in the Neotropics

We use information from a large-scale study on parrots across the Neotropics, where we performed road census from 2011 to 2019 crossing 12 countries, from Argentina to Panamá and Dominic Republic (Figure 3.7.1.1). We surveyed villages crossed during road surveys to record the presence of pets from any native species, often visible from the streets or exposed in public establishments, and randomly ask people whether they had or knew others who had pets. This methodology proved to be useful to estimate poaching pressure in most Neotropical areas, where this activity is not actively prosecuted and thus animals are not hidden (Luna et al., 2018; Romero-Vidal et al., 2020). After informal talks with pet owners, we collected information on species kept as pets, how and where they were obtained, and if they were bought, where they were obtained (markets or other people).

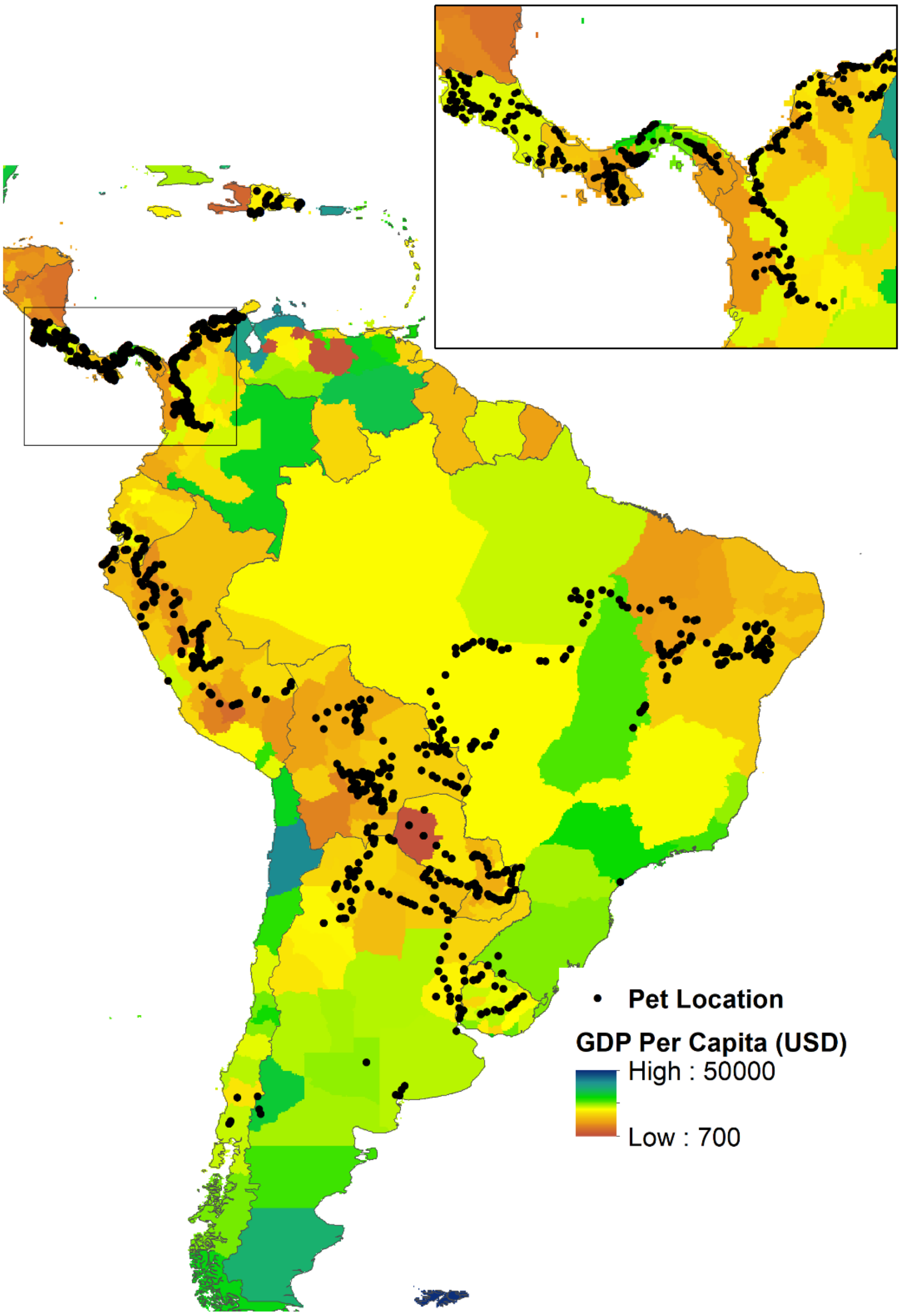


Figure 3.7.1.1. Pet locations of all surveyed areas, showing differences on GDP Per Capita (USD) for the different areas.

3.Results

3.1 Results: Captive breeding counteracts illegal trade as a major threat for parrots worldwide

Although most parrots were listed by the IUCN as of Least Concern (57.7%) or Near Threatened (13.9%), near 30% of species were threatened with extinction (14.9% Vulnerable, 9% Endangered, 4.2% Critically Endangered, and 0.2% Extinct in the Wild). Most of these threatened species were spatially aggregated, with large hotspots in the Neotropics (Figure S1). Illegal trade was considered as a threat for 31.3% of the species, with similar percentages of species threatened by international (23.9%) and domestic illegal trade (20.6%), and 13.2% sharing both threats. The proportion of species threatened by illegal trade and, specifically, by domestic illegal trade significantly differ among regions (Table S1), and these species also clustered in hotspots mainly in the Neotropics (Figure 3.1.2.1). Most parrot species (93.5%) were used as pets and/or for display, and reproduction in captivity has been achieved for 80.3% of all parrot species.

Parrots illegally traded were more threatened, especially those subject to the illegal domestic trade. However, species used as pets were less threatened (Figure 3.1.2.2, Table S2), possibly because they were most commonly bred in captivity (χ^2=54.81, p<0.0001). Moreover, when captive breeding was included in models to explain the conservation status of species, we found that species more commonly bred in captivity were also the least threatened (Table S3).

About 18.4 million parrots (9.3 wild-caught and 9.1 captive-bred) from 317 species were legally traded worldwide since 1975. The numbers of wild-caught traded parrots have decreased over years while captive-bred individuals have increased (Figure 3.1.2.3a; S2), especially after international bans on wild-caught birds (Figure 3.1.2.4). Similar temporal patterns were found for the number of legally traded wild and captive-bred species (Figure 3.1.2.3b, S3) and the heavily traded African grey parrots (Figure

S4). Seizures of illegally traded parrots, however, did not change during the study period (Figure 3.1.2.3, Fig. S5). Parrots more frequently bred in captivity were those that were legally traded in higher numbers (estimate: 2.32E-03, SE: 7.69E-04, $\chi^2=75.84$, $p<0.0001$).

3.1.2 Tables and Figures

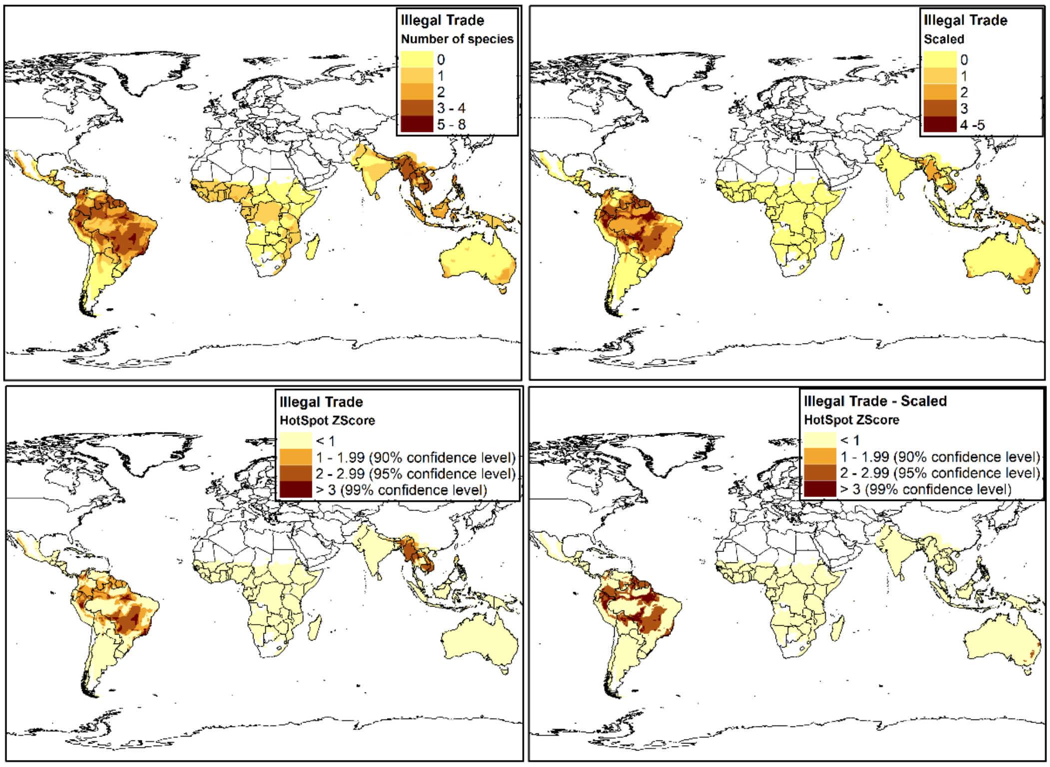


Figure 3.1.2.1. Global distribution of the number (A) and the scaled number (B) of parrot species threatened by illegal trade. The hotspots of illegal trade are shown in panels C (calculated from data in panel A) and D (from data in panel B).

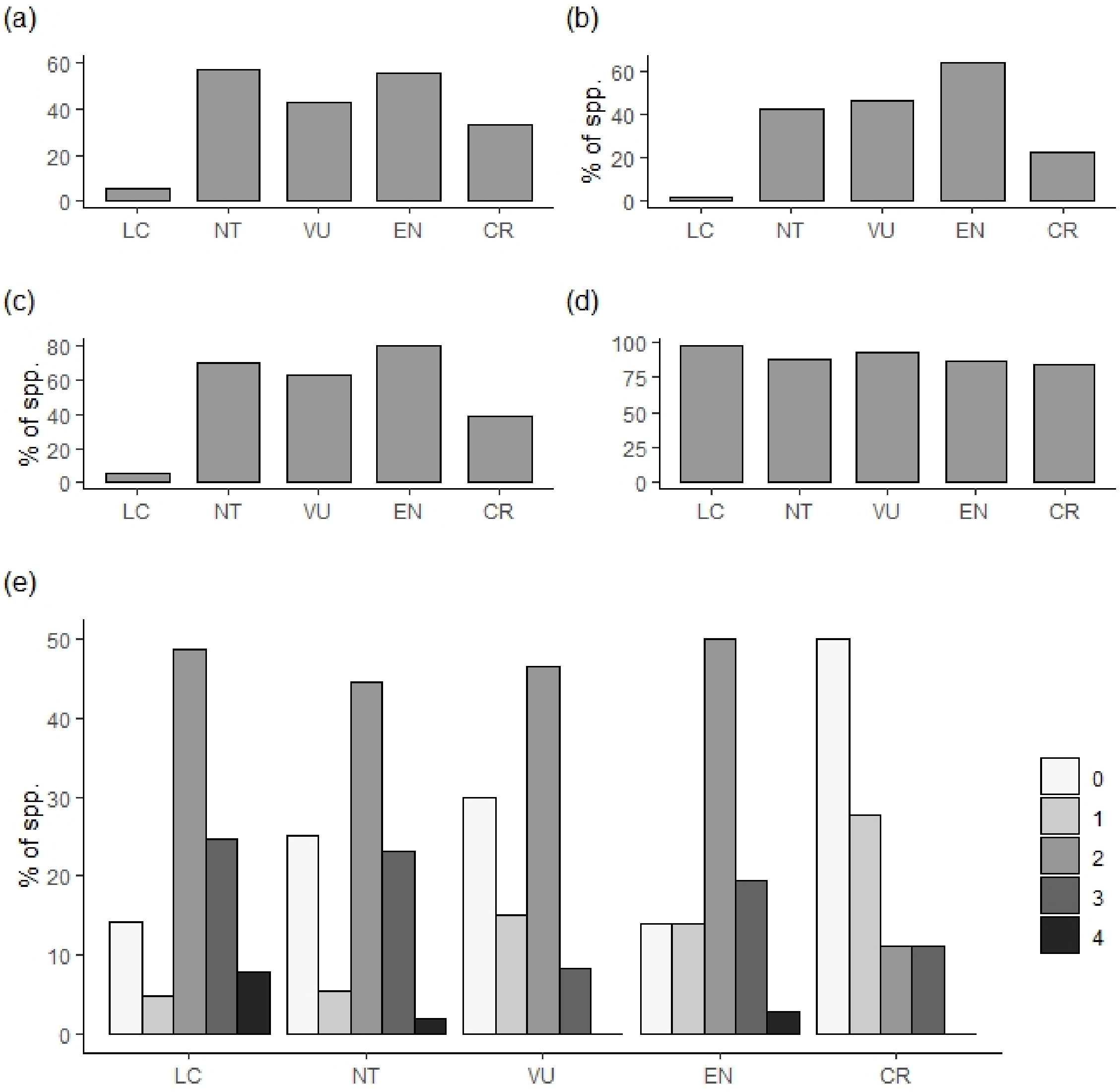


Figure 3.1.2.2. Percentage of parrot species categorized as of Least Concern (LC), Neat Threatened (NT), Vulnerable (VU), Endangered (EN), and Critically Endangered (CR) by the IUCN (2020) threatened by illegal international trade (a), illegal domestic trade (b), and illegal trade (i.e., both international and domestic illegal trade) (c), used as pets and/or for display (d), and bred in captivity (e), in a scale from =0 (never bred in captivity) to 4 (very easily bred in captivity). See Methods for further details.

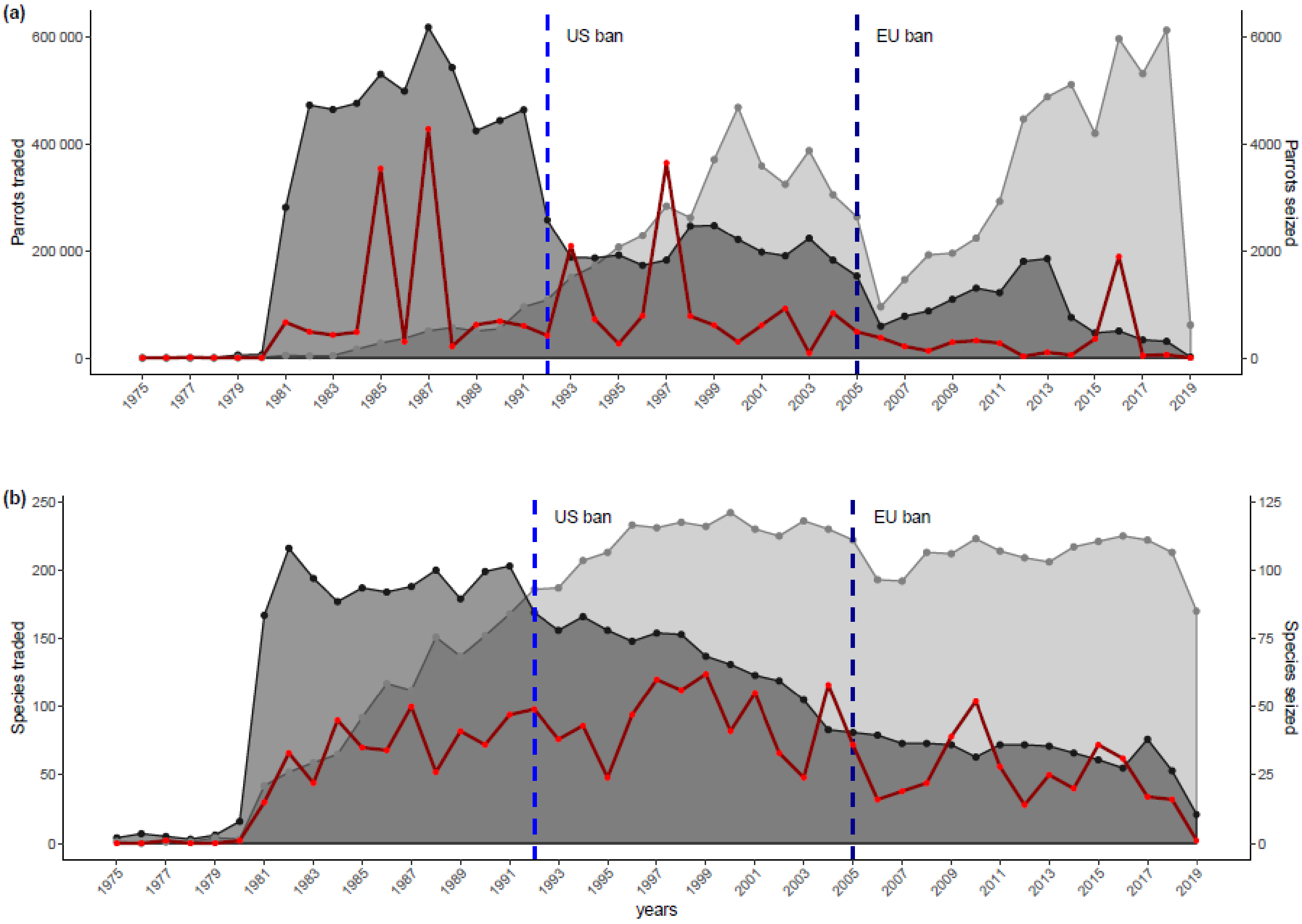


Figure 3.1.2.3. Exports per year of wild-caught (dark grey) and captive-bred (pale grey) parrots, in number of individuals (a) and number of species (b) (indicated on the left y axis). The red line shows the number of parrots (a) and parrot species (b) exported illegally and seizure by authorities (right y axis). The U.S. and EU bans are indicated by the blue dashed lines.

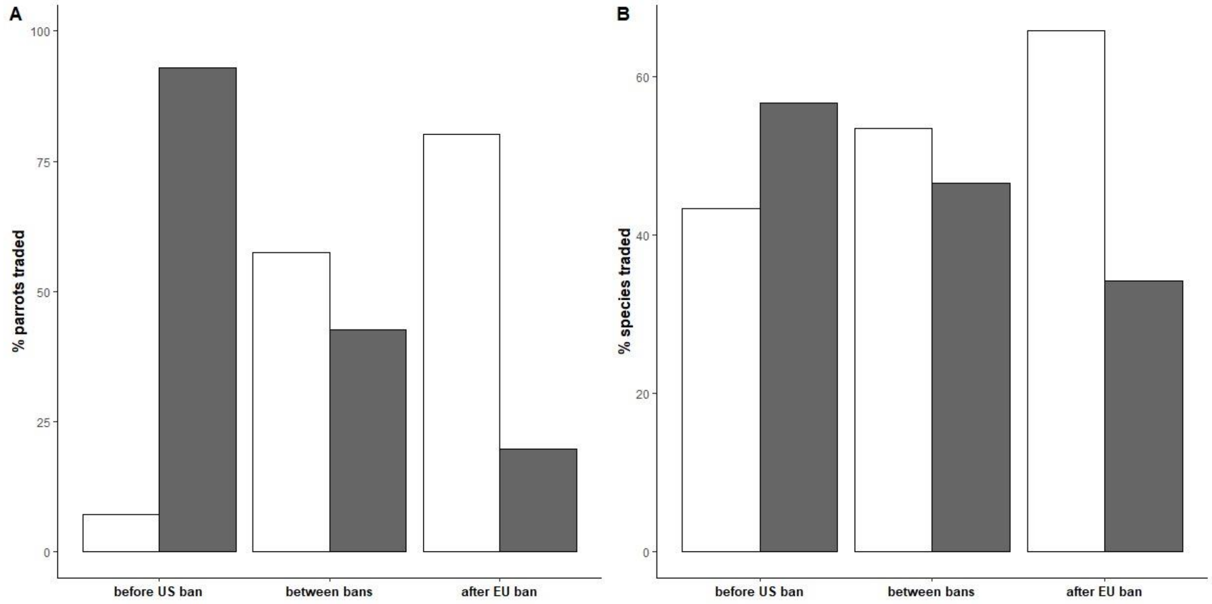


Figure 3.1.2.4. Percentage of wild-caught (black bars) and captive-bred (white bars) internationally traded individuals (A) and species (B) before bans, after the US ban, and after the EU ban on wild birds.

3.1.3 SUPPLEMENTARY INFORMATION

3.1.3.1. Identification of hotspots of threatened species and species threatened by illegal trade

We evaluated the existence of hotspots of threatened parrots and of parrots threatened by illegal trade using the ArcGis Hot Spot Analysis Tool (*Getis-Ord Gi** spatial statistic) (Getis & Ord, 1992; Ord & Getis, 1995) implemented in ArcGis 10.3. This hotspot index identifies tendencies for spatial clustering and can distinguish between the locations of high and low spatial associations. *Getis-Ord Gi** values were calculated for the aggregated number of threatened parrots or parrots threatened by illegal trade recorded within each square of a Universal Transverse Mercator (UTM) grid of ca. 90km^2 (0.1º x 0.1º), defining neighbors as grids sharing a common edge or a common vertex (i.e., queen contiguity criterion). As *Getis-Ord* Gi* values are normally distributed, they can be standardized using its sample mean and variance to obtain a Z score and a statistical significance, such that high, positive, and significant *Gi** values indicate hotspots. We used this same methodological approach to identify hotspots for the number of threatened parrots or parrots threatened by illegal trade scaled by the maximum number of parrot species usualy found in each grid square (e.g., number of species found in each class divided by total number of parrot species).

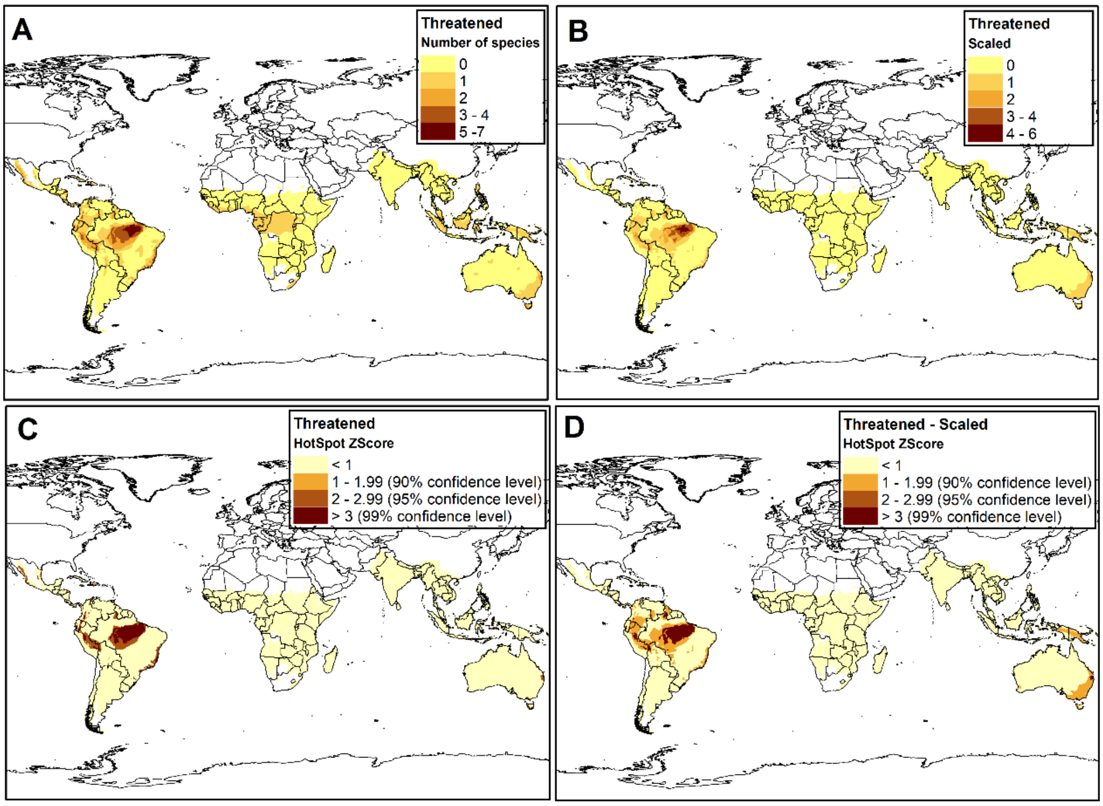


Fig S1. Global distribution of the number (A) and the scaled number (B) of threatened parrot species. The hotspots of threatened species are shown in panels C (calculated from data in panel A) and D (from data in panel B).

3.1.3.2. Factors affecting the conservation status of parrots

We used ordinal logistic regressions implemented in the package MASS (Venables & Ripley, 2002) to assess whether the conservation status of parrots (ranked from 0 to 4) was related to their illegal trade and use as pets/display. Due to differences in illegal trade pressure among regions (mainly due to domestic illegal trade; Table S1), we included the region as a fixed factor in models. This variable can help to control for other potential common regional threats affecting the unequal distribution of threatened species across regions (Fig. S1).

Table S1. Ordinal logistic regressions to test differences in the conservation status of parrots (dependent variable; ranked from 0 to 4) among regions (Neotropical, Afrotropical, Indomalaysia, and Australasia).

Illegal trade	χ^2	**df**	**P**
Region	14.81	3	0.0020
International illegal trade	χ^2	**df**	**P**
Region	5.49	3	0.1394
Domestic illegal trade	χ^2	**df**	**P**
Region	44.36	3	<0.0001

Table S2. Ordinal logistic regressions to test whether differences in the conservation status of parrots (dependent variable; ranked from 0 to 4) was related to illegal trade variables and the use of species as pets/display, while controlling for potential differences among regions (Neotropical, Afrotropical, Indomalaysia, and Australasia).

Variables	**Estimate**	**SE**	χ^2	**df**	**p**	**dev.expl%**
Use as pets/display	-1.85	0.38	23.43	1	<0.0001	11.63
Region			14.26	3	0.0026	
International illegal trade	2.11	0.23	89.61	1	<0.0001	

Variables	**Estimate**	**SE**	χ^2	**df**	**p**	**dev.expl%**
Use as pets/display	-2.03	0.38	27.51	1	<0.0001	13.10
Region			0.94	3	0.8154	
Domestic illegal trade	2.53	0.26	104.14	1	<0.0001	

Variables	**Estimate**	**SE**	χ^2	**df**	**p**	**dev.expl%**
Use as pets/display	-2.19	0.39	30.41	1	<0.0001	18.41
Region			5.92	3	0.1155	
Illegal trade	2.82	0.25	156.75	1	<0.0001	

We then tested the effect of captive breeding (ranked from 0 to 4) on the conservation status of parrots by including this variable in models shown in Table S2. Although the use of a species as a pet/display is more likely among species more intensively bred in captivity, the addition of this last variable slightly improved the percentage of deviance explained by models.

Table S3. Ordinal logistic regressions to test differences in the conservation status of parrots (dependent variable; ranked from 0 to 4) was related to illegal trade variables, the use of species as pets/display, and their commonness in captive breeding, while controlling for potential differences among regions (Neotropical, Afrotropical, Indomalaysia, and Australasia).

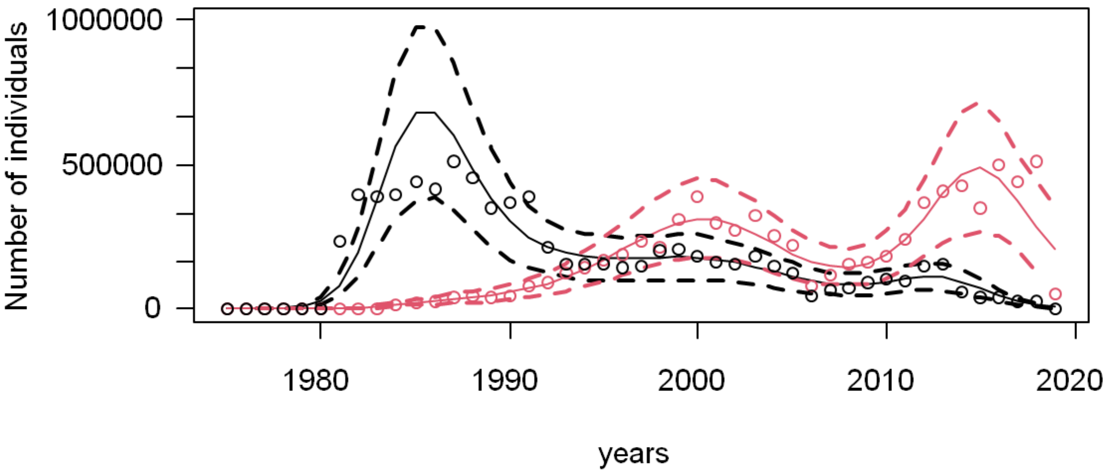
Variables	**Estimate**	**SE**	χ^2	**df**	**p**	**dev.expl%**
Use as pets/display	-1.10	0.41	7.24	1	0.0071	14.44
Region			15.02	3	0.0018	
International illegal trade	2.26	0.24	98.49	1	<0.0001	
Captive breeding	-0.55	0.11	27.81	1	<0.0001	
Variables	**Estimate**	**SE**	χ^2	**df**	**p**	**dev.expl%**
Use as pets/display	-1.35	0.41	10.81	1	0.0010	15.46
Region			0.86	3	0.8353	
Domestic illegal trade	2.63	0.27	108.55	1	<0.0001	
Captive breeding	-0.51	0.11	23.34	1	<0.0001	
Variables	**Estimate**	**SE**	χ^2	**df**	**p**	**dev.expl%**
Use as pets/display	-1.45	0.42	12.23	1	0.0005	20.91
Region			5.11	3	0.1637	
Illegal trade	2.92	0.25	162.48	1	<0.0001	
Captive breeding	-0.55	0.11	24.65	1	<0.0001	

3.1.3.3. Trade

We used Generalized Additive Models (GAM) to analyze the temporal trend in the number of individuals and number of species of wild-caught and captive-bred parrots legally traded from 1975 to 2019, as reported by CITES Database. In all cases, we first assessed whether the response variable fitted better to a Gaussian, Poisson, or Negative Binomial distribution, selecting for posterior modeling the distribution with the lower AIC value. The number of individuals was modeled using the negative binomial error distribution while for the number of species we used the Poisson error distribution.

The number of wild-caught and captive-bred parrots legally traded show opposite trends along time, with an increase in captive-bred individuals as wild-caught ones decrease (smooth line for years for wild-caught individuals: 8.17, SE: 8.81, χ^2=811, $p < 0.0001$; smooth line for years for captive-bred individuals: 7.97, SE: 8.70, χ^2=1055, $p < 0.0001$; Fig. S2).

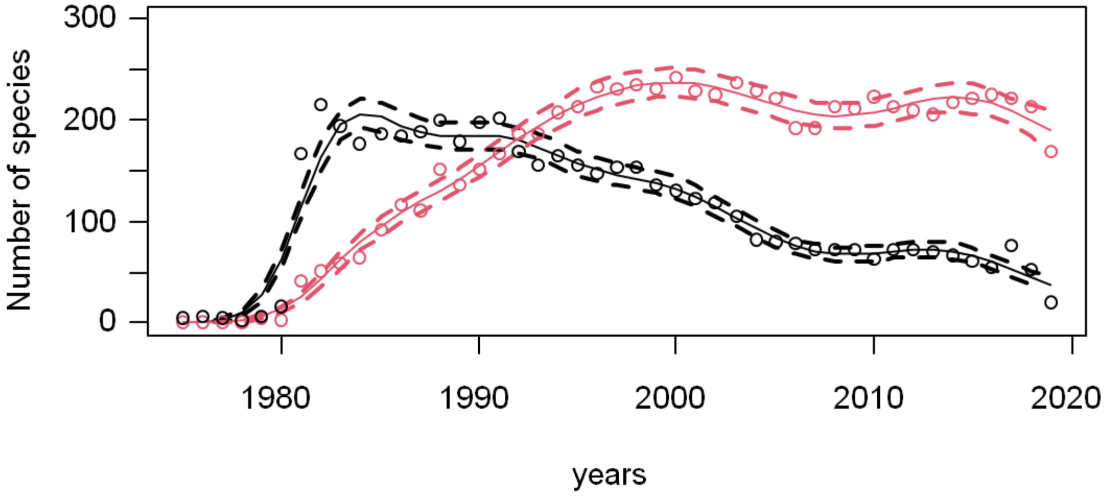
Figure S2. Temporal trend (solid lines: GAM adjustments; dashed lines: 95% confidence intervals) in the number of wild-caught (black symbols) and captive-bred (red symbols) parrots from 1975 to 2019. Raw data (points) are shown.



The number of wild-caught and captive-bred parrot species legally traded also shows opposite trends along time, with an increase in captive-bred species as wild-caught ones decreased (smooth line for years for wild-caught individuals: 8.96, SE: 8.99,

χ^2=1055.6, p < 0.0001; smooth line for years for captive-bred individuals: 8.90, SE: 8.99, χ^2=864.7, p < 0.0001; Fig. S2).

Figure S3. Temporal trend (solid lines: GAM adjustments; dashed lines: 95% confidence intervals) in the number of wild-caught (black symbols) and captive-bred (red symbols) parrot species from 1975 to 2019. Raw data (points) are shown.



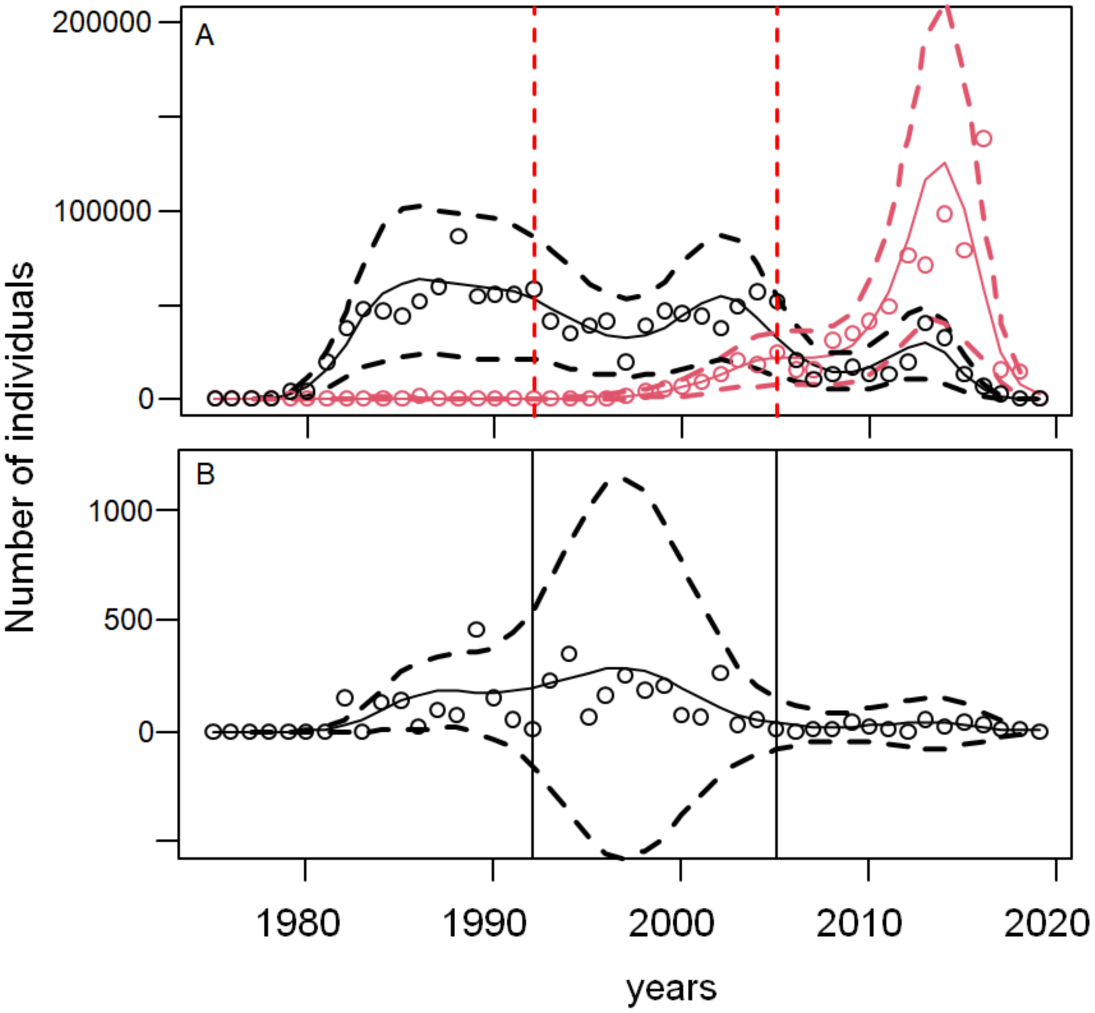
3.1.3.4. African grey parrot

We used Generalized Additive Models (GAM) to analyze the temporal trend in the number of wild-caught and captive-bred African grey parrots legally traded (negative binomial error distribution, log link function) and seized (Poisson error distribution, log link function) from 1975 to 2019. Data from Grey (Psittacus erithacus) and Timneh (P. timneh) parrots were pooled since most records from CITES considered them as a single species.

The number of wild-caught individuals decreases over time while captive-bred ones increases (smooth line for years for wild-caught individuals: 8.17, SE: 8.81, χ^2=367.5, p < 0.0001; smooth line for years for captive-bred individuals: 8.11, SE: 8.73,

χ^2=470.3, p < 0.0001; Fig. S4). US and EU bans did not increase the number of seized individuals (z=-0.24, p=0.8085).

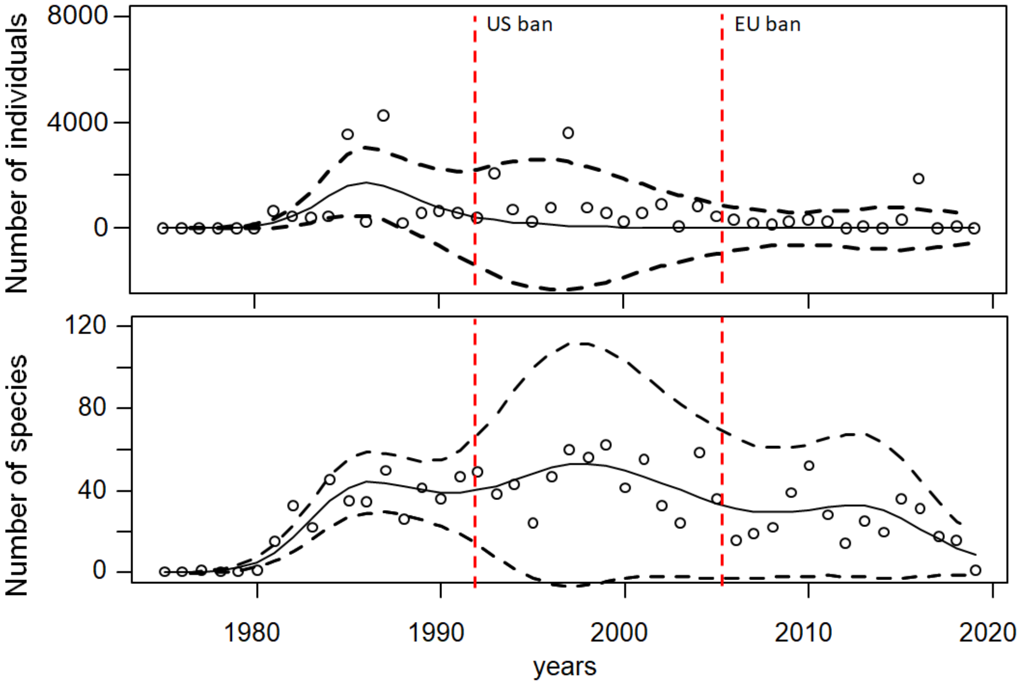
Figure S4. Temporal trend (solid lines: GAM adjustments; dashed lines: 95% confidence intervals) in A) of the number of wild-caught (black symbols) and captive-bred (red symbols) African grey parrots legally traded and B) seized from 1975 to 2019. Raw data (points) are shown.



3.1.3.5. Seizures

We also used GAM to test the hypothesis that bans can be promoting illegal trade, measured through seizure data provided by CITES. Our models show that US and EU bans did not increase the number of seized individuals (z=0.12, p=0.9050), nor the number of species (z=-0.08, p=0.9350; Fig. S5).

Figure S5. Temporal trend (solid lines: GAM adjustments; dashed lines: 95% confidence intervals) in the number of parrot species from 1975 to 2019. Raw data (points) are shown. Red lines indicate the years of the US and EU bans.



3.2 Results: The hidden face of parrot poaching: local demand of pets largely outnumbers domestic and international trade on parrots

As a result of the daily surveys carried out on Los Pozos market in Santa Cruz between 2004 and 2009, we registered a total of 150,000 native parrots illegally traded from 37 species (40,000- 50,000 annually).

A total of 150 municipalities were surveyed, obtained information on poached parrots (Figure 3.2.1.1). We collected data in 2000 poached individuals from 41 parrot species. On average, only 3% of the parrots poached were transported to Santa Cruz to sell them there, based on the informal interviews conducted. The rest of poached parrots remained as household pets or were sold locally in the same or close municipalities, without entering domestic trade. From the total amount of parrots transported to Santa Cruz, only 9.6% were sold in the main city market (Los Pozos), the rest were sold in smaller markets, streets, of directly sold to demanding people. Taking into account the number of parrots sold in Los Pozos market, and that this figure represents only 3% of total the total parrots caught in Bolivia, we estimate an annual number of 1-1,5 millions of individuals to satisfy the in situ demand.

Regarding past legal international trade, a total of 166,702 native parrots were exported between 1975 and 2019 (CITES), and 53 were confiscated between 1980-2005.

A total of 636 ages (1 year median, n=636) were obtained for alive individuals, as well as 484 ages of parrots already dead, escaped or sold at the moment when informal interviews were conducted (0.25 year median, n=484). This data allowed us to estimate survival probabilities for the 6 species with enough information to estimate the survival curves. The median survival time for all parrots was estimated in two years, being the same time for *A.aestiva*, *A. rubrogenys*, *P.mitratus* and *T.acuticaudatus*. *B. chiriri* showed a median survival time of 0.8 years, while *E.aurea* was 1 year.

The majority of individuals detected during the pet surveys conducted were alive (65,30%), being 27,60% no longer with their owners and 7,10% unknown (n=2337). From the 27,60% not present 39,07% were sold, 34,88% were dead, 19,07% escaped, 4,65% given and 2,33% stolen. An important percentage of the dead parrots were confirmed by the owners to be dead by predation (22, 22%) due mainly to companion animals (cats 70%, dogs 14%, 8% unknown and only 8% by wild animals).

Although most families hold a single parrot pet, 46 % kept two or more (up to 16, N = 840, Fig. 3c). In addition, from the informal interviews we observed that 50% of people have or had native parrots as pets, and 60% knows somebody in the area who has or had one.

3.2.1 Tables and Figures

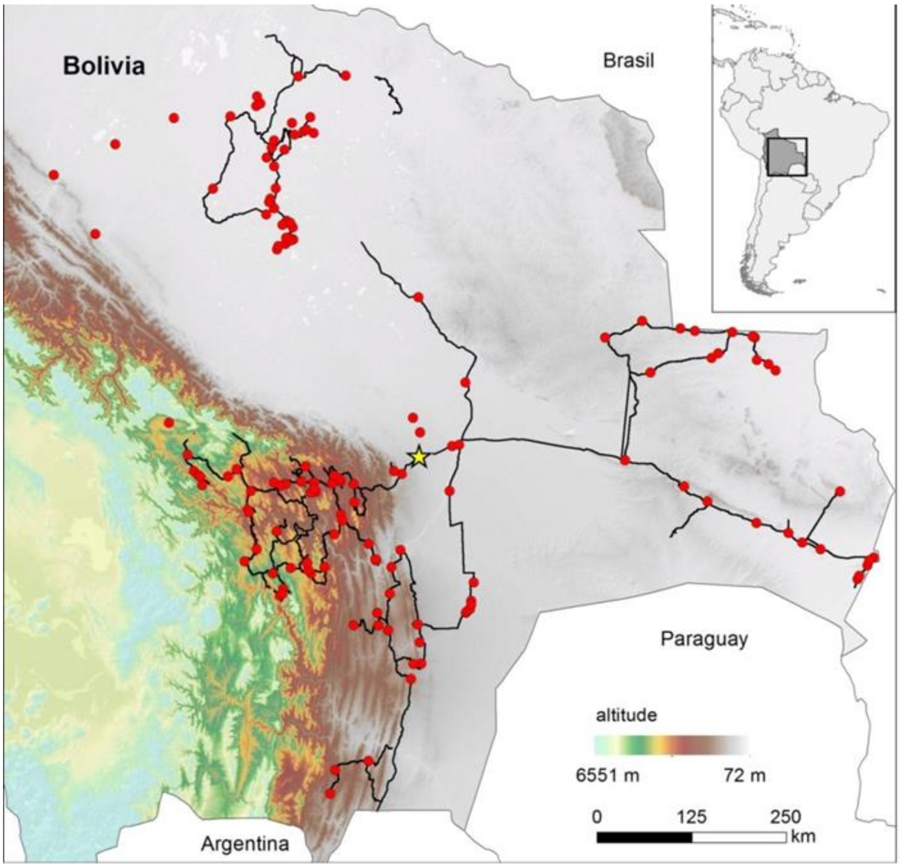


Figure 3.2.1.1. Map of Bolivia, showing road-side transects conducted to estimate parrot abundance (black lines), communities where people were interviewed to estimate parrot poaching intensity and destination (red points), and the location of Los Pozos market in Santa Cruz de la Sierra (yellow star).

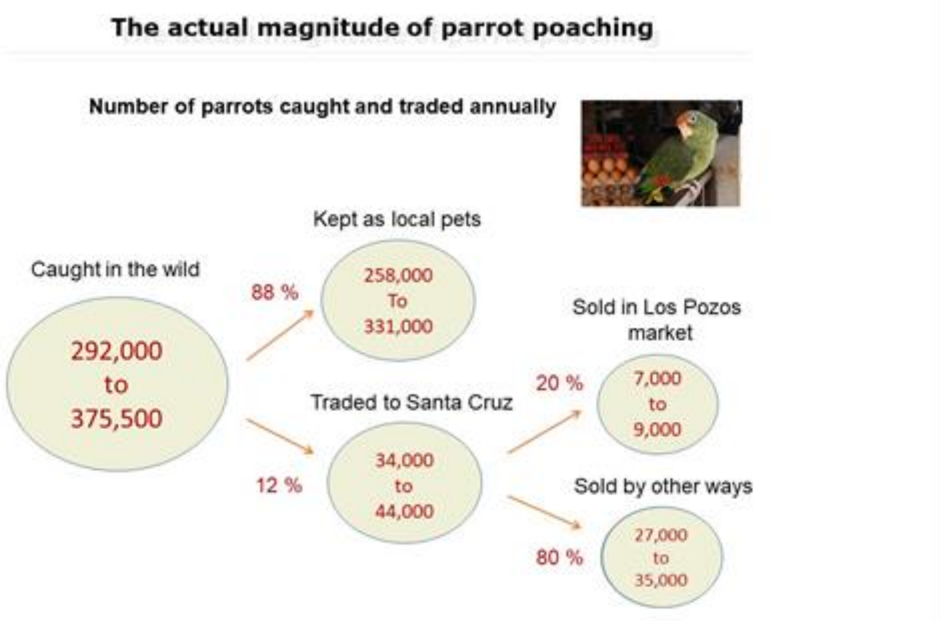


Figure 3.2.1.2. Percentage of parrots caught that remains locally or are send to Santa Cruz city and main market.

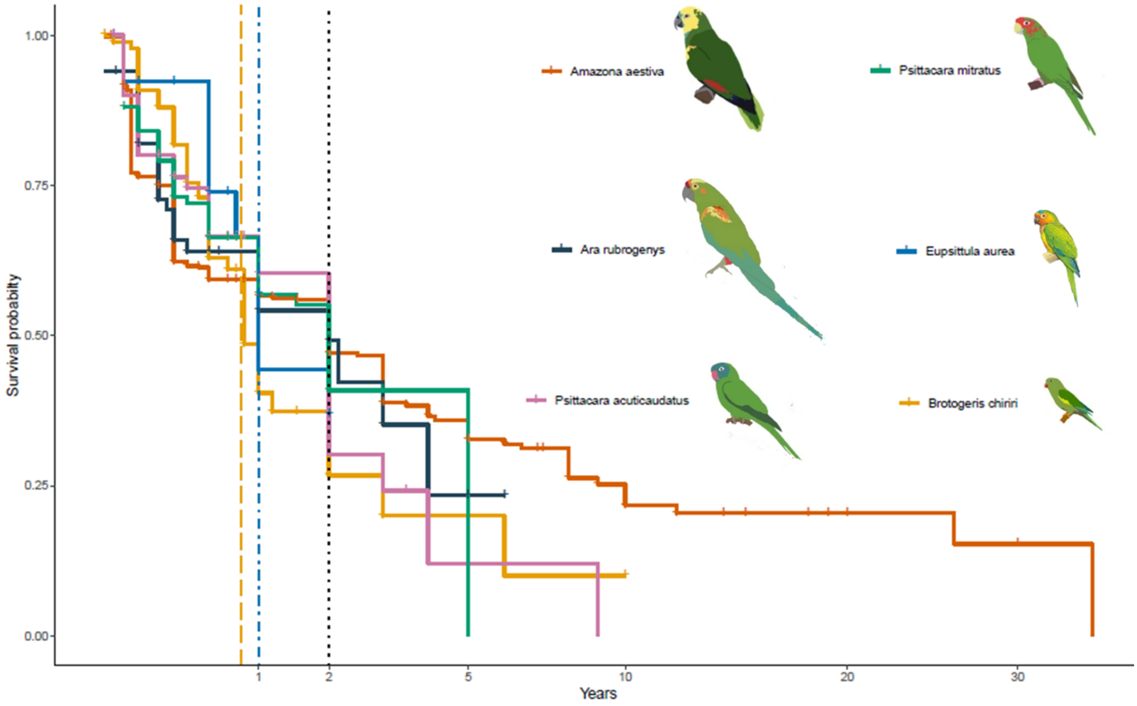


Figure 3.2.1.3. Survival estimates for six species of parrots commonly kept as pets.

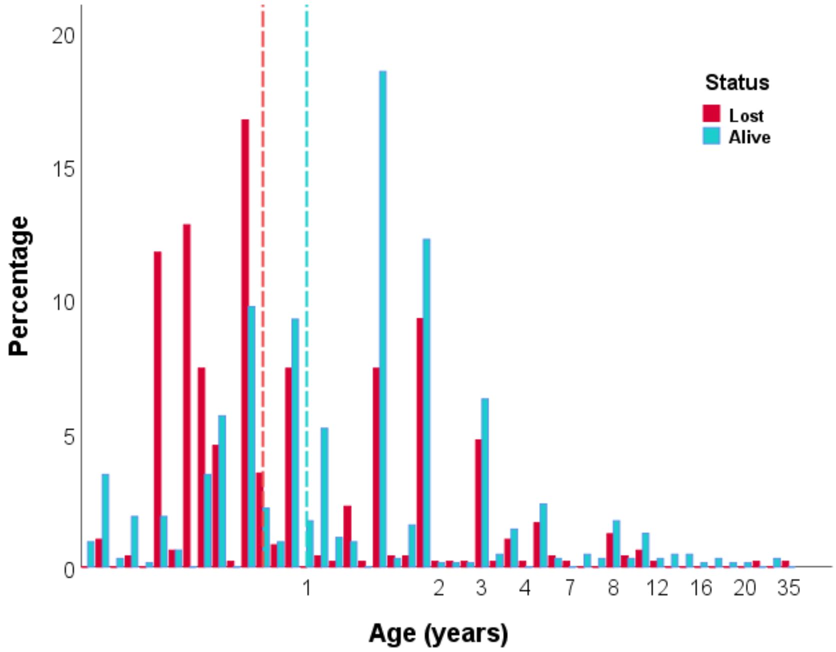


Figure 3.2.1.4. Age of parrot pets lost and still alive at the survey time. Dashed lines show median ages for each group.

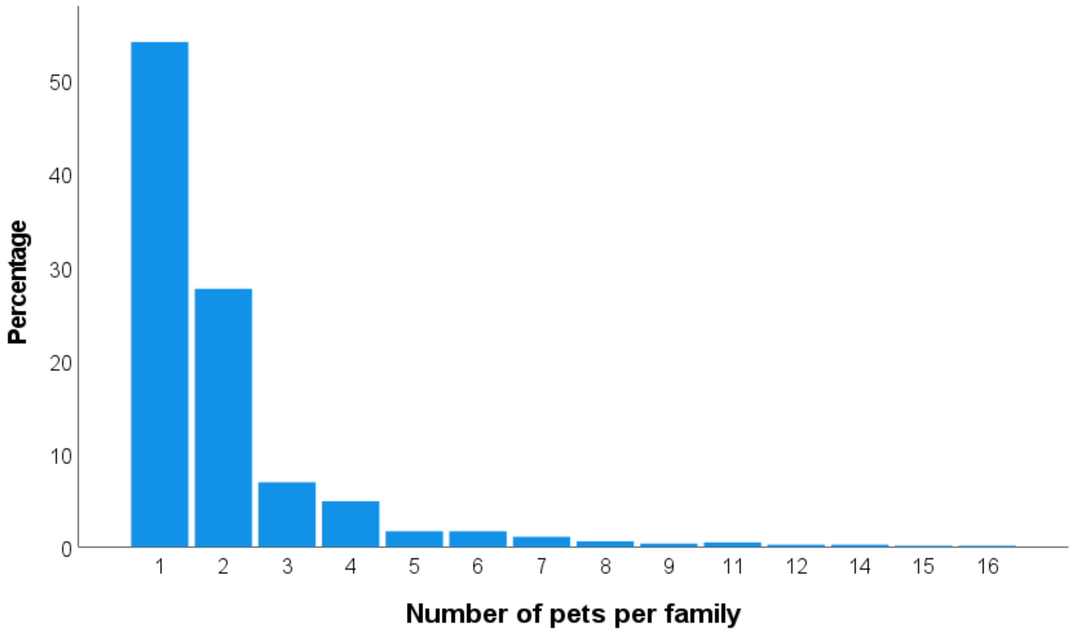


Figure 3.2.1.5. Number of parrot pets kept by each family.

3.3 Results: Opportunistic or Non-Random Wildlife Crime? Attractiveness rather than Abundance in the Wild Leads to Selective Parrot Poaching

We recorded 10,811 wild individuals from 25 parrot species (Table 2.4.1.1) across the 2,221 km of roadside surveys conducted, covering a wide variety of biomes with different degrees of human alteration. Overall abundance reached 4.87 ind./km, although most records (80.31%) corresponded to just two parakeets (orange-chinned parakeet *Brotogeris jugularis* and brown-throated parakeet *Eupsittula pertinax*). The other species were present in low numbers, were extremely rare or even unrecorded in the wild (Table 3.3.2). Simultaneously, we recorded a total of 2,465 pets from 124 species, kept by 818 owners in 92.9% of the 282 villages surveyed (Figure 1), from which 1,179 (47.8%) were pets from 21 native parrot species (Table 2). The rest of the pets were mostly songbirds (Passeriformes, 32.7%), non-native parrots (12.7%), other birds (3.0%), mammals (1.3%), and reptiles (0.4%). Among the 358 local people we met, 58.4% of them kept poached native parrot pets at the time of our survey or recently, and 38.0% knew other people also keeping them.

Table 3.3.2. Parrot species included in the study, their body size (in cm), the scores (0-2) for the brightness of body and head coloration, the total number of colors (Color), their ability to imitate human speech (speech, 0-2, with ranges), their price in US$ (with SD), the number of individuals recorded in the wild (N wild) and as poached pets (N pet), and the Savage selectivity index (W). * Statistically significant W values after Bonferroni correction ($p < 0.002$).

Species	**Size**	**Body**	**Head**	**Color**	**Speech**	**Price**	**N Wild**	**N Pet**	**W**	
Amazona amazonica (Aam)	31	0.2	1	3	1.5 (1-2)	34.85 (-)	93	12	1.17	
Amazona autumnalis (Aau)	34	0.2	1	3	1.5 (1-2)		61	25	3.73	*
Amazona farinosa (Afa)	38	0.2	0.2	1	1.9 (1-2)	38.72 (13.4)	20	18	8.18	*
Amazona mercenarius (Ame)	34	0.2	0	1	1.0 (1-1)		93	0	0.00	*
Amazona ochrocephala (Aoc)	31	0.2	0.8	2	2.0 (1-2)	34.41 (16.0)	136	359	24.00	*
Ara ambiguus (Aab)	85	1.5	0.5	3	1.5 (1-2)		0	3	27.28	*
Ara ararauna (Aar)	85	2	1.8	3	0.9 (0-2)	43.57 (20.5)	80	76	8.64	*
Ara chloropterus (Ach)	90	2	2	3	1.5 (1-2)		0	14	127.28	*
Ara macao (Ama)	85	2	2	3	2.0 (2-2)	145.22 (0.00)	4	74	168.20	*
Ara militaris (Ami)	75	1.5	0.5	3	1.5 (0-2)		10	7	6.36	*
Ara severus (Ase)	46	1	0	2	1.0 (1-1)		54	5	0.84	
Bolborhynchus lineola (Blin)	16	0	0	1	0.0 (0-0)		1	0	0.00	
Brotogeris jugularis (Bju)	18	0	0	1	0.4 (0-2)	6.53 (1.45)	6230	344	0.50	*
Eupsittula pertinax (Epe)	25	0.1	0	1	0.5 (0-2)	5.68 (3.67)	2445	189	0.70	*
Forpus conspicillatus (Fco)	12	0.1	0	1	0.0 (0-0)		83	0	0.00	
Forpus passerinus (Fpa)	12	0.1	0	1	0.0 (0-0)	5.81 (0.00)	35	6	1.56	
Forpus spengeli (Fsp)	12	0.1	0	1	0.0 (0-0)		80	9	1.02	
Hapalopsittaca fuertesi (Hfu)	23	0.5	0.9	3	0.0 (0-0)		1	0	-	
Ognorhynchus icterotis (Oic)	42	0.8	0.8	2	0.5 (0-1)		85	2	0.21	
Pionus chalcopterus (Pch)	29	0.2	0	2	0.0 (0-0)		134	3	0.21	
Pionus menstruus (Pme)	28	0.3	1.5	2	0.2 (0-2)	16.46 (9.22)	497	19	0.35	*
Pionus seniloides (Pse)	30	0.2	0	2	0.0 (0-0)		2	0	0.00	
Pionus sordidus (Pso)	28	0.2	0	1	0.0 (0-0)		17	1	0.52	
Psittacara wagleri (Pwa)	36	0	0.5	2	0.5 (0-1)		628	10	0.14	*
Pyrilia haematotis (Pha)	21	0.1	0	2	0.0 (0-0)		0	1	-	
Pyrilia pyrilia (Ppy)	24	0.1	2	3	0.0 (0-0)		1	0	-	
Thectocercus acuticaudatus (Tac)	37	0	0.1	1	0.5 (0-1)		20	13	5.91	*

Touit batavicus (Tba)	14	0.1	0	3	0.0 (0-0)	1	0	-

In absolute numbers, *B. jugularis* and *E. pertinax* made up almost half (45.20%) of all pet parrots. However, these species were actually negatively selected when considering their abundances in the wild (Table 3.3.2, Figure 3.3.5). On the contrary, most amazons (*Amazona* spp.), large macaws (*Ara* spp.) and *Thectocercus acuticaudatus*, mostly uncommon or extremely rare in the wild, were strongly positively selected as pets (significant W > 1). The other species showed non-significant selection (i.e., were kept as pets in proportion to their availability in the wild; Table 3.3.2, Figure 3.3.5).

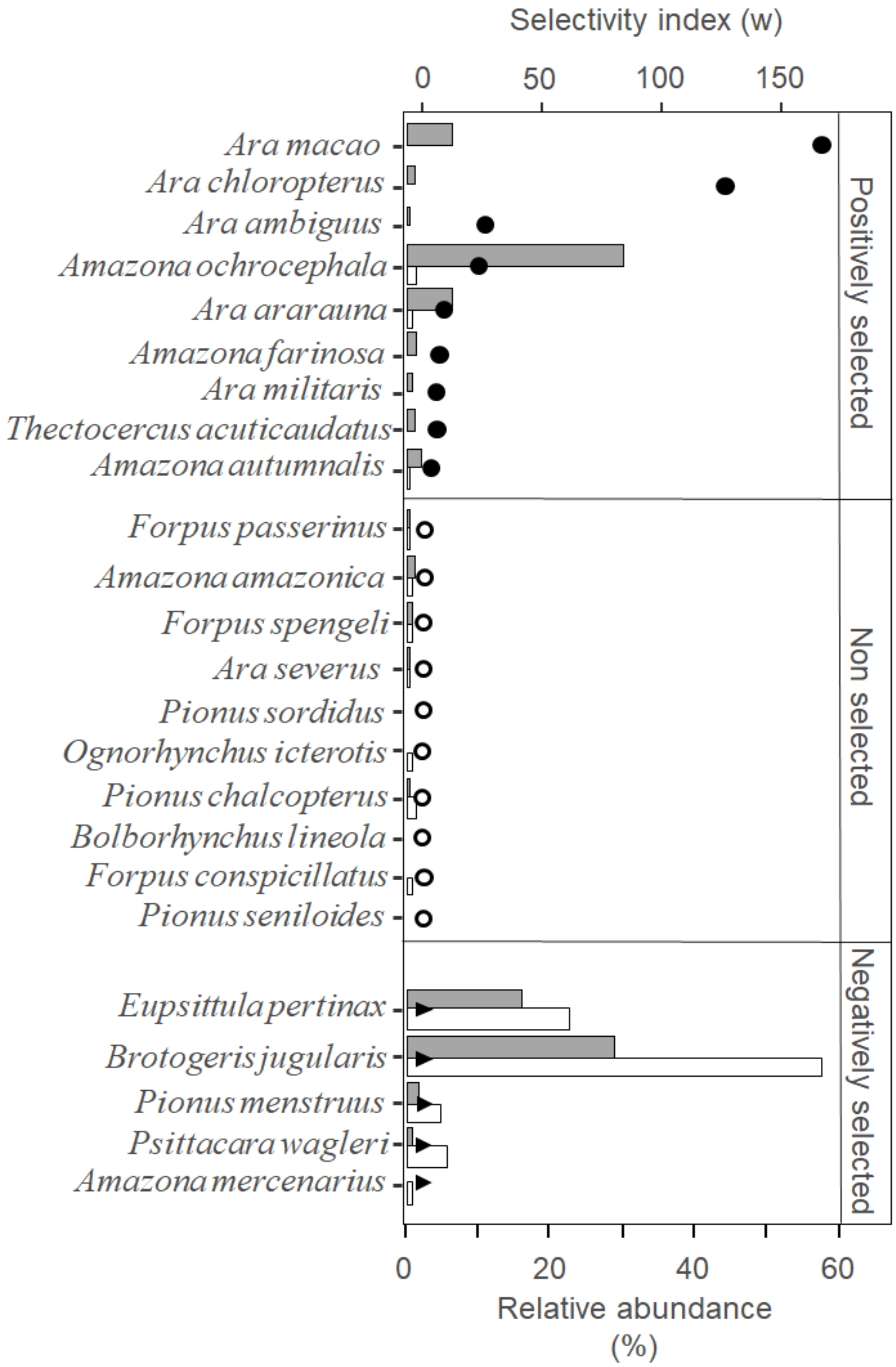


Figure 5. Relative abundance of parrots in Colombia as pets (dark gray bars) and in the wild (white bars), and Savage selectivity index (W; black dots: significant positive selection; black triangles: significant negative selection; white dots: not selected).

The PCA analyses (Bartlett's Test of Sphericity: $\chi^2 = 99.24$, $p<0.0001$, df=10) rendered a single dimension with an eigenvalue > 1 (3.40), which positively correlated with body size (0.92), coloration (bright body: 0.91, bright head: 0.79, number of colors: 0.77) and ability to imitate human speech (0.71), explaining 68.08% of the total variance. Thus, PC1 can be interpreted as a descriptor of parrot attractiveness, large, colorful and talkative species being more attractive (positive values) than their counterparts (negative values; Figure 3.3.6).

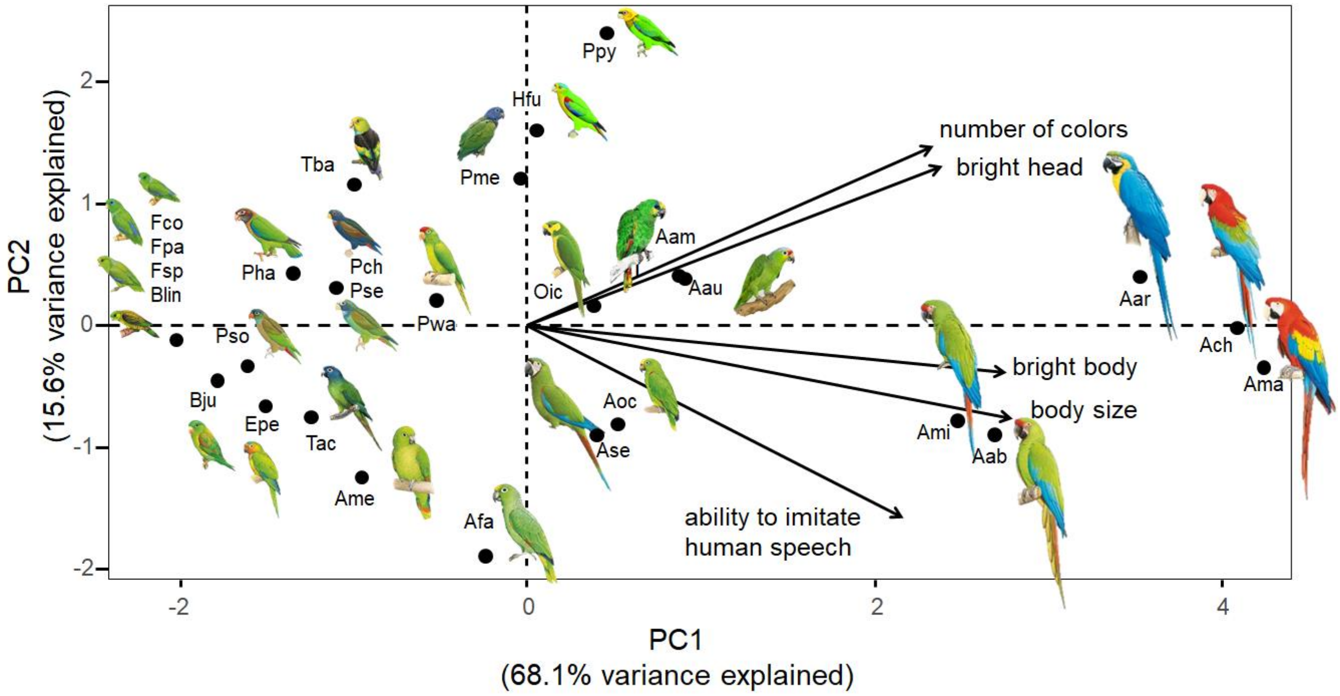


Figure 3.3.6. Principal component analysis (PCA) of Colombian parrot traits, namely: body size, coloration (bright body, bright head and number of colors) and ability to imitate human speech. See Table 3.3.2 for species abbreviations. Drawings of parrots are not scaled. PC2 is plotted to allow better visualization of species across the PC1 axis, which reflects parrot attractiveness, but was not used for further analysis (eigenvalue < 1).

PC1 was positively related to the Savage index (estimate: 0.27, SE: 0.04, t = 6.40, $p < 0.0001$, adjusted-R^2 = 0.63), showing that the most attractive species were poached in larger numbers than expected based on their availability in the wild (Figure 3.3.7a). The price of the species increased with their attractiveness (estimate: 16.24, SE: 4.06, t = 4.00, $p < 0.0052$, adjusted-R^2 = 0.65, Figure 3.3.7b) but was unrelated to their abundances in the wild (estimate: 0.85, SE: 0.78, t = -1.09, p = 0.3139, Figure 3.3.7c), indicating that the most attractive but not the rarest species were more valuable.

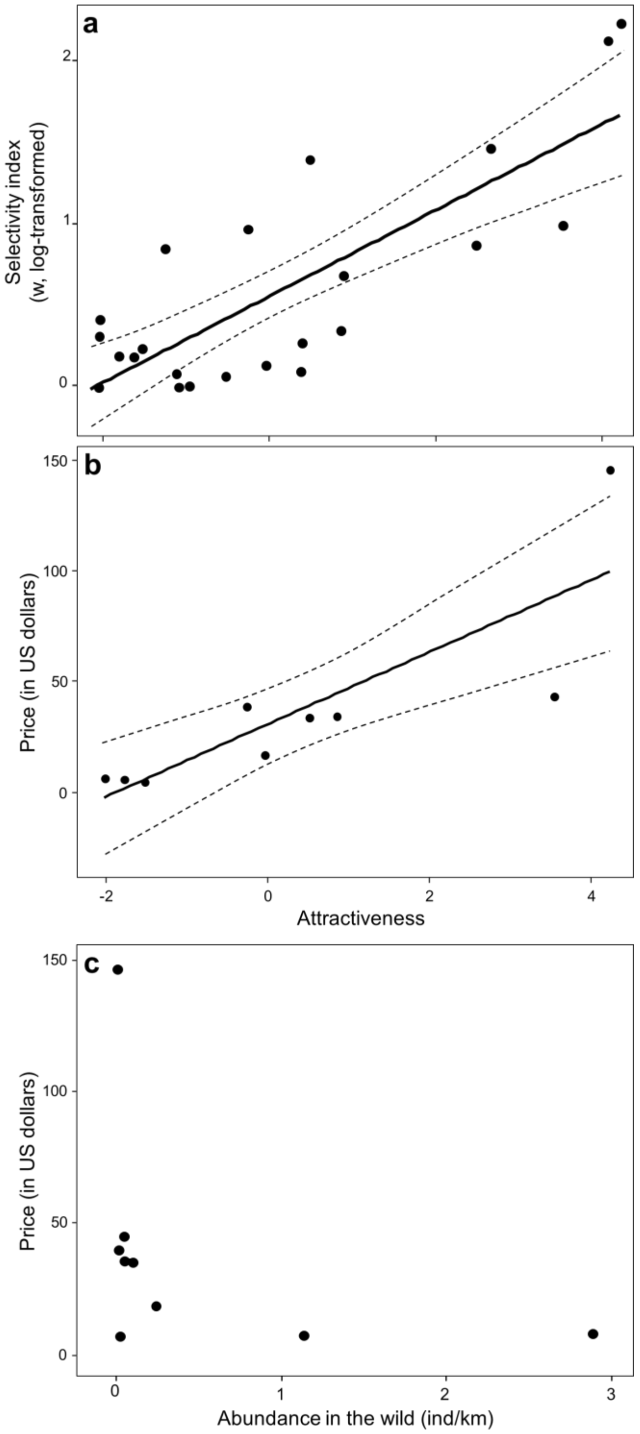


Figure 3.3.7. Preferred parrots in Colombia (measured through their Savage selective index) were the most attractive (i.e., large, colorful, and able to imitate human speech) species (**a**), which were also the most expensive (**b**), independently of their abundance in the wild (**c**).

3.4 Results: Selective poaching as the main pet source in Peru and Ecuador: warns on the unsustainable domestic demand for preferred parrot species

We recorded 1,340 pets in 97% of the villages surveyed (n = 198), which were distributed across the whole study area (Figure 2.5.1.1). 73% of these pets were parrots (793 in Peru and 186 in Ecuador) from 33 native species (Table 3.4.1.1). The others belonged to 11 bird, mammal, and reptile orders. All parrots had been poached and most of them (86.1%) were obtained by local people and kept as own pets (71.6%) or bought from private poachers (28.4%), without entering markets. Only 13.9% of the parrots were bought in markets, with just 0.3% corresponding to coastal markets (one parrot in Lima and two in Chiclayo) and the rest to Amazonian markets (Figure 2.5.1.1).Poachers mainly extracted chicks from their nests (62.4% of cases) and captured adults in crops with traps and nets (37.6%). 57.2% of interviewed people (n = 247) had or recently had poached parrot pets and 59.8% knew other people keeping them.

Through the roadside surveys, we recorded 7,475 wild parrots from 40 species. Relative abundances in the wild greatly varied among species, with just eight species summing 82% of all recorded parrots (Table 3.4.1.1). The SI showed a non-random poaching pressure. While the most abundant species were negatively selected, several of the uncommon species were poached more than expected (i.e., positively selected) attending to their relative abundances in the wild (Figure 3.4.1.2, Table 3.4.1.1). SI did not differ between species with quotas for its legal exportation and the rest of the species (Mann-Whitney, $U = 99.00$, $p = 0.58$), with two of the former species being positively selected (Brotogeris sanctithomae and Psittacara frontatus, Table 3.4.1.1). As expected, amazons (genus Amazona) and large macaws (genus Ara) were the most preferred pets (Kruskal-Wallis, $H = 19.12$, $df = 2$, $p < 0.0001$; Figure 3.4.1.3).

Most parrots not obtained in markets included local individuals (i.e., those kept as pets within their native distribution range; n=612) but also birds from distant areas (n=145; distance range: 19.38 – 1009.79 km). Local parrot pets had lower SI (mean=7.65; SD=19.62) than those moved from farther areas (mean=35.20; SD=40.48; Figure 3.4.1.4a). However, for pets moved outside their native ranges, distances covered did not relate to SI (Figure 3.4.1.4b). Parrots bought in markets were obtained at local or distant ones (distances to markets: 0 - 1048 km; Table 3.4.1.1). The largest distances corresponded to two individuals (*Ara ararauna* and *Ara macao*) moved from Peru to Ecuador. Most of these parrots came from the Amazonian markets (99.7% of bought parrots; Figure 3.4.1.1), and mainly belong to species with high SI (Figure 3.4.1.4d). The relationship between SI and distances to markets was not estimated due to the small percentage of parrots obtained from markets (14%). Median and ranges are shown in Table 3.4.1.1.

As predicted, species' prices were positively related to their SI (Figure 3.4.1.5a). Although it was unrelated to the global conservation status of a species (Figure 3.4.1.5b), SI strongly correlated with population trends, species with more marked population declines having higher SI than those with stable or increasing populations (Figure 3.4.1.5c).

3.4.1 Tables and Figures

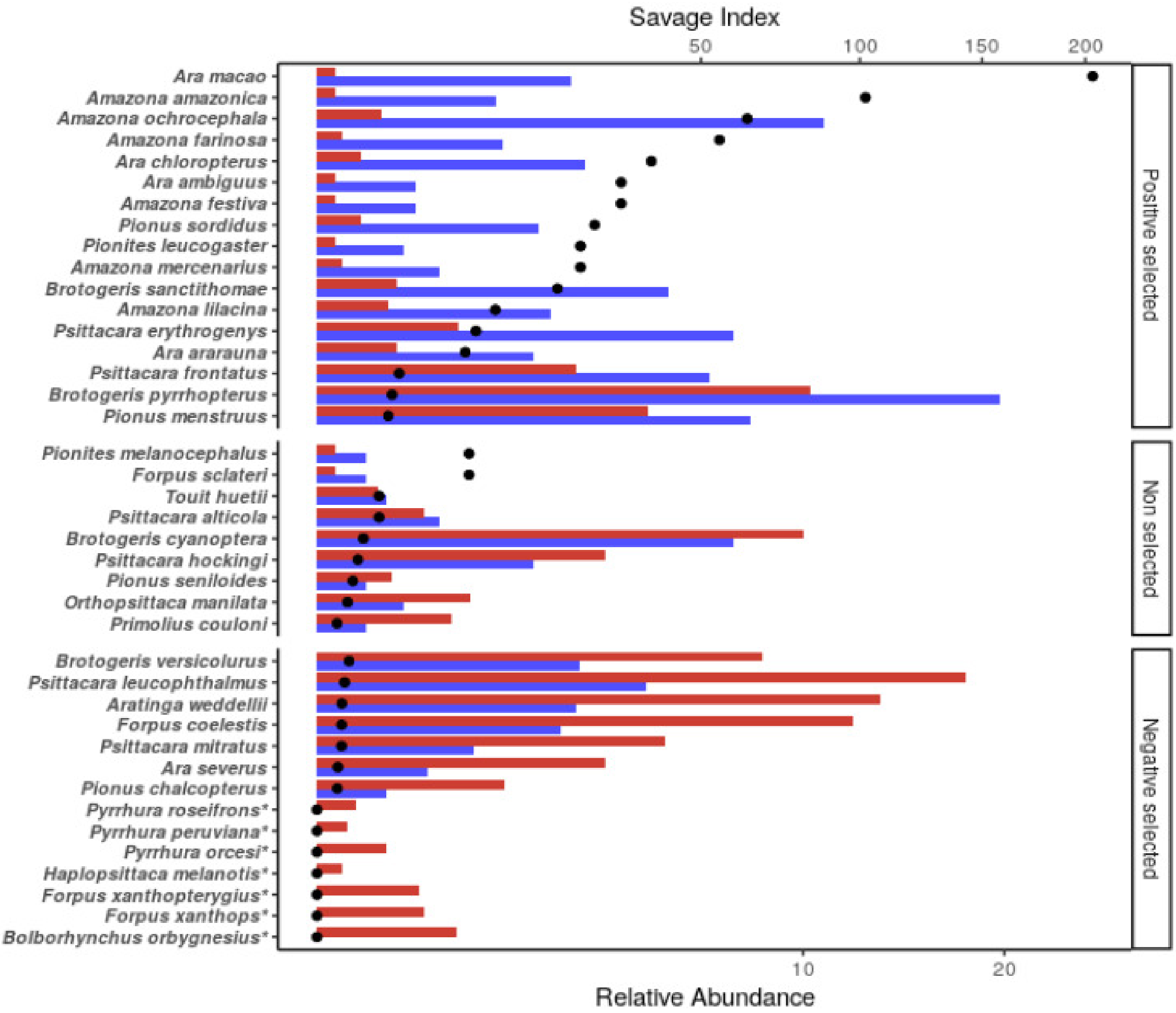
Figure 3.4.1.2. Poaching selection (selectivity index; black dots) and relative abundances in the wild (red bars) and as pets (blue bars) for each parrot species. Species are grouped as positively, negatively and non-selected. *: Species only recorded in the wild but not as pets.

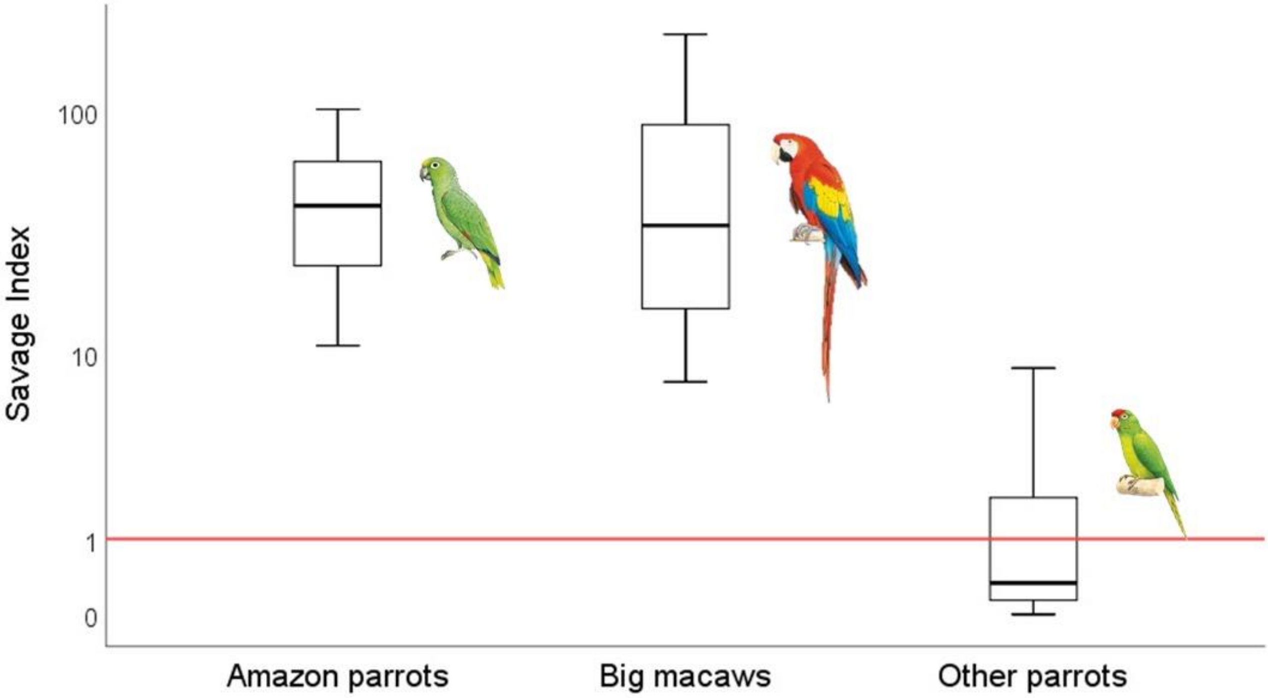
Figure 3.4.1.3. Mean (± 95% confidence intervals) poaching pressure (i.e., selectivity index) calculated for amazons (SPP), large macaws (SPP), and the other parrot species recorded in road surveys. The red line indicates non-selection, with values above or below 1 indicating positive or negative selection. Different letters indicate significant differences among groups in the *post hoc* pairwise Wilcoxon rank-sum exact tests after

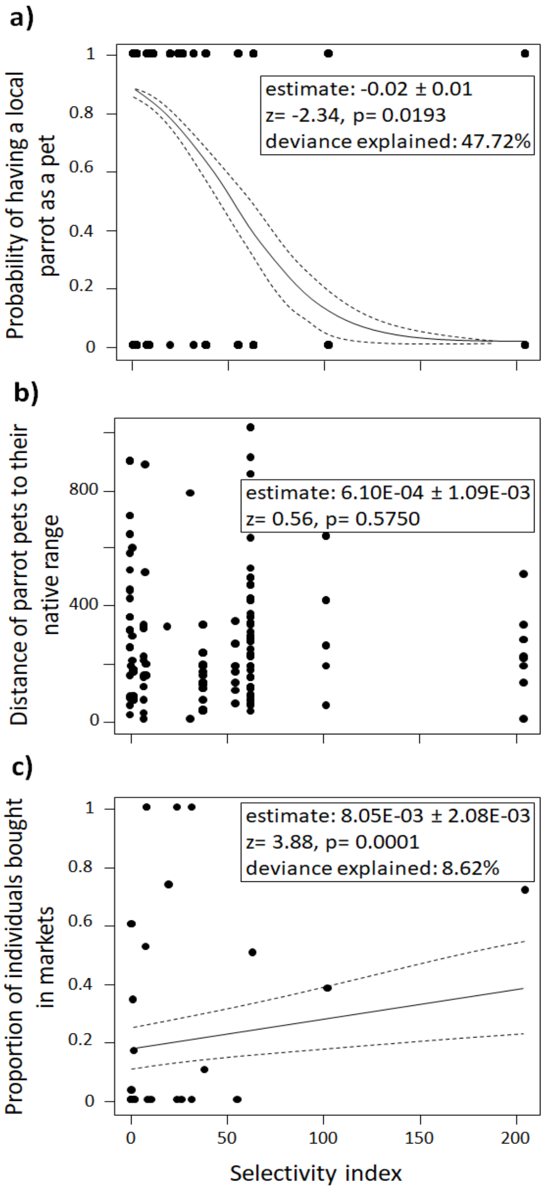
applying Bonferroni correction: a) Amazons and large macaws (p=1), b) other species (Amazons and other species: p=0.0009; large macaws and other species: p= 0.0122).

Figure 3.4.1.4. **a)** Local parrots kept as a pet show a lower selectivity index (SI) than those moved from their native ranges. However **b)** distances from the native range to their locations as pets were not related to SI. **c)** Most individuals of species with high SI were bought at markets. Model fit (solid lines) and 95% confidence intervals (dashed lines) are shown. See Fig. S1 and S2 for model fits.

Figure 3.4.1.5. **a)** Parrots with high SI were the more expensive (price in US$) than non-preferred ones. **b)** Mean (± 95% confidence intervals) poaching pressure (selectivity index) observed for species classified as Least Concern (LC), Near Threatened (NT), Vulnerable (VU), and Endangered (EN). **c)** Relationship between poaching pressure and probability of a parrot species experiencing a decreasing population trend. See Fig. S3 and S4 for model fit.


Savage Index
50
100
150
200
Ara macao
Amazona amazonica
Amazona ochrocephala
Amazona farinosa
Ara chloropterus
Ara ambiguus
Amazona festiva
Pionus sordidus
Pionites leucogaster
Amazona mercenarius
Brotogeris sanctithomae
Amazona lilacina
Psittacara erythrogenys
Ara ararauna
Psittacara frontatus
Brotogeris pyrrhopterus
Pionus menstruus
Pionites melanocephalus
Forpus sclateri
Touit huetii
Psittacara alticola
Brotogeris cyanoptera
Psittacara hockingi
Pionus seniloides
Orthopsittaca manilata
Primolius couloni
Brotogeris versicolurus
Psittacara leucophthalmus
Aratinga weddellii
Forpus coelestis
Psittacara mitratus
Ara severus
Pionus chalcopterus
Pyrrhura roseifrons*
Pyrrhura peruviana*
Pyrrhura orcesi*
Haplopsittaca melanotis*
Forpus xanthopterygius*
Forpus xanthops*
Bolborhynchus orbygnesius*
Positive selected
Non selected
Negative selected
10
20
Relative Abundance


Savage Index
100
10
1
0
Amazon parrots
Big macaws
Other parrots


a)
Probability of having a local parrot as a pet
1
0.8
0.6
0.4
0.2
0
estimate: -0.02 ± 0.01
z= -2.34, p= 0.0193
deviance explained: 47.72%
b)
Distance of parrot pets to their native range
800
400
0
estimate: 6.10E-04 ± 1.09E-03
z= 0.56, p= 0.5750
c)
Proportion of individuals bought in markets
1
0.8
0.6
0.4
0.2
0
estimate: 8.05E-03 ± 2.08E-03
z= 3.88, p= 0.0001
deviance explained: 8.62%
0
50
100
150
200
Selectivity index

361

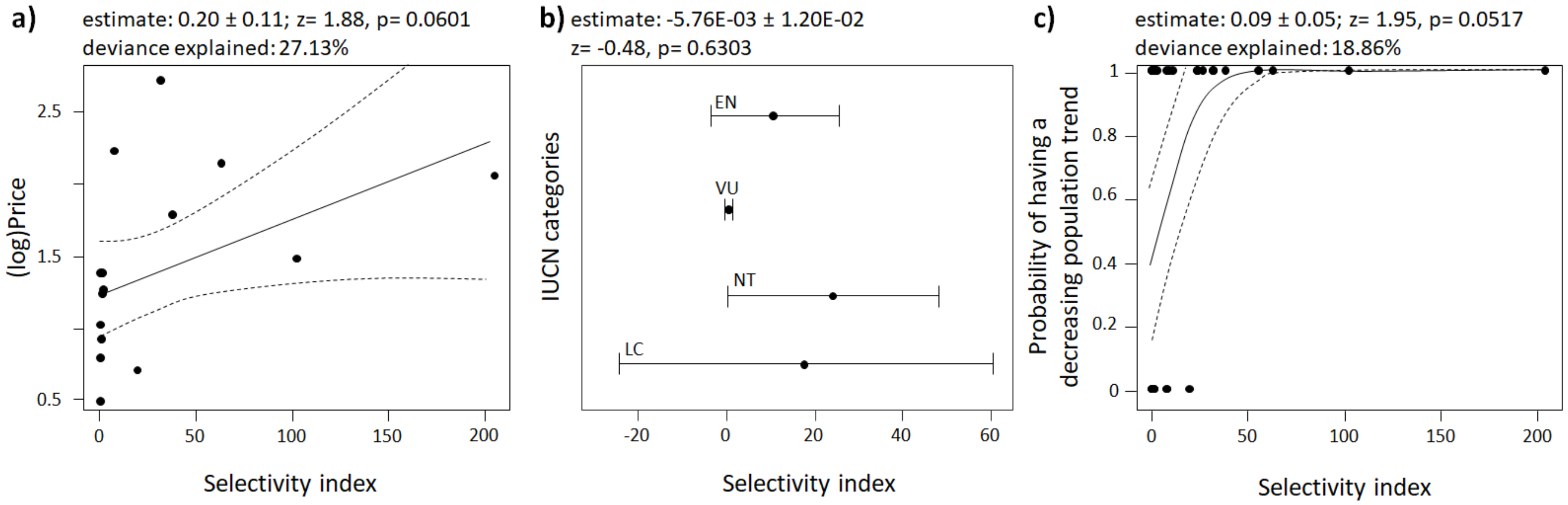

a)
estimate: 0.20 ± 0.11; z= 1.88, p= 0.0601
deviance explained: 27.13%
(log)Price
2.5
1.5
0.5
0
50
100
150
200
Selectivity index
b)
estimate: -5.76E-03 ± 1.20E-02
z= -0.48, p= 0.6303
IUCN categories
EN
VU
NT
LC
-20
0
20
40
60
Selectivity index
c)
estimate: 0.09 ± 0.05; z= 1.95, p= 0.0517
deviance explained: 18.86%
Probability of having a decreasing population trend
1
0.8
0.6
0.4
0.2
0
0
50
100
150
200
Selectivity index

Table 3.4.1.1. Parrot species recorded as pets, including their conservation status (CS; LC: Least Concern, NT: Near Threatened, VU: Vulnerable, EN: Endangered), population trends (PT; 0 = decreasing, 1 = stable, 2 = increasing), number of individuals recorded in the wild (Nwild) and as poached pets (Npet), poaching pressure (SI: Savage selectivity index), distances (median and range; in km) of household pets to the distribution range of the species and to markets (for individuals bought in markets), and prices (in US$). Species in bold have harvest quotas for legal international trade. *: significant SI values after Bonferroni's correction for multiple tests.

Species	CS	PT	Nwild	Npet	SI	Distances to distribution	Distances to markets	Price
Amazona amazonica	LC	0	1	13	101.93 *	186.1 (0 - 633.9), n=13	278.3 (0 - 851), n= 5	59.01
Amazona farinosa	NT	0	2	14	54.88 *	130.2 (0 - 343), n=14		
Amazona festiva	NT	0	0	4	31.36 *	3.5 (0-788), n=4	38.7 (0-737), n=4	
Amazona lilacina	EN	0	16	22	10.78 *	0 (0 - 0), n=22		50
Amazona mercenarius	LC	0	2	6	23.52 *	0 (0 - 0), n=6		
Amazona ochrocephala	LC	0	13	104	62.73 *	219.9 (0 - 1009.8), n=104	0 (0 – 404.5), n=52	299.95
Ara ambiguus	EN	0	0	4	31.36 *	0 (0 - 0), n=4		500
Ara ararauna	LC	0	20	19	7.45 *	115.7 (0 - 332.7), n=19	327.1 (0 - 1039), n=10	324.54
Ara chloropterus	LC	0	6	29	37.9 *	127.6 (0 - 329.9), n=29	343.5 (343.5 - 376.3), n=3	59.01
Ara macao	LC	0	0	26	203.86 *	0 (0 - 502.2), n=26	0 (0 - 1048), n=18	115.06
Ara severus	LC	0	263	5	0.15 *	0 (0 - 82.4), n=5	0 (0 - 0), n=3	
Aratinga weddellii	LC	2	1006	27	0.21 *	0 (0 - 0), n=27	0 (0 - 0), n=15	5.41
Bolborhynchus orbygnesius	LC	1	62	0	0.00			
Brotogeris cyanoptera	LC	1	750	70	0.73	0 (0 - 189.5), n=70	0 (0 - 0), n=24	7.56
Brotogeris pyrrhopterus	EN	0	769	188	1.92 *	0 (0 - 175), n=188		
Brotogeris sanctithomae	LC	1	20	50	19.60 *	0 (0 - 325.2), n=50	0 (0 - 0), n=37	6.56
Brotogeris versicolurus	LC	1	627	28	0.35 *	353 (0 - 897.1), n=28	0 (0 -0), n=1	10.82
Forpus coelestis	LC	1	912	24	0.21 *	0 (0 - 0), n=24		2.95
Forpus sclateri	LC	1	0	1	7.84	882.2 (882.2 - 882.2), n=1	299.2 (299.2 - 299.2), n=1	
Forpus xanthops	VU	1	36	0	0.00			
Forpus xanthopterygius	LC	1	33	0	0.00			
Hapalopsittaca melanotis	LC	1	2	0	0.00			
Pionites leucogaster	LC	0	1	3	23.52 *	0 (0 - 0), n=3	0 (0 - 0), n=3	
Pionites melanocephalus	LC	1	0	1	7.84	512.5 (512.5 - 512.5), n=1	171.3 (171.3 - 171.3), n=1	
Pionus chalcopterus	LC	0	111	2	0.14 *	0 (0-0), n=2		
Pionus menstruus	LC	0	346	76	1.72 *	0 (0 - 595), n=76	0 (0 - 0), n=13	15.82
Pionus seniloides	LC	0	18	1	0.44	0 (0 - 0), n=1		
Pionus sordidus	LC	0	6	20	26.14 *	0 (0 - 0), n=20		

Primolius couloni	VU	0	57	1	0.14	0 (0 - 0), n=1	
Psittacara alticola	LC	1	36	6	1.31	0 (0 - 0), n=6	
Psittacara erythrogenys	NT	0	64	70	8.58 *	0 (0 - 191.5), n=70	
Psittacara frontatus	NT	0	212	62	2.29 *	0 (0 - 69.5), n=62	14.96
Psittacara hockingi	LC	1	262	19	0.57	0 (0 - 0), n=19	
Psittacara leucophthalmus	LC	0	1331	44	0.26 *	0 (0 - 446.1), n=44	
Psittacara mitratus	LC	1	382	10	0.21 *	0 (0 - 0), n=10	23.6
Orthopsittaca manilata	LC	1	74	3	0.32	0 (0 - 0), n=3	
Pyrrhura orcesi	EN	0	15	0	0.00		
Pyrrhura peruviana	LC	0	3	0	0.00		
Pyrrhura roseifrons	LC	0	5	0	0.00		
Touit huetii	VU	1	12	1	1.31	0 (0-0), n=1	

3.5 Results: Deforestation or overharvesting? Pet-keeping cultural burden rather than habitat transformation causes selective parrot defaunation in Costa Rica

We performed 1,921 km of road surveys crossing all Costa Rican biomes, which were subjected to a variable degree of human transformation (Figure 3.5.3.1; Table 3.5.4.S1). During this survey, we registered more than 3,500 free-living parrots (1,258 different contacts) belonging to 17 species (Table 3.5.4.S1, Appendix S1).

3.5.1. Habitat characteristics and parrot communities

Analysis at the patch-level showed that the presence, abundance, and richness of parrots greatly varied among biomes, even after controlling for differences associated with the hour of the day (Table 3.5.3.1; Figure 3.5.3.1B). Abundance and richness showed a bimodal distribution, with peaks at natural and more perturbed, rural areas (mainly villages, Table 3.5.3.1), depending on the biome (Figure 3.5.3.1B). The presence of parrots followed a similar pattern (maximum in natural habitats and villages), although the 95% confidence interval of the quadratic estimate of habitat transformation barely overlapped zero (Table 3.5.3.1).

Models obtained using point-level data highlighted the importance of the spatial autocorrelation term in explaining the presence, abundance, and richness of parrots (Table 3.5.3.2). At a small spatial scale (1km buffer), all these community indexes increased at closer distances to villages (Table 3.5.3.2; Table 3.5.4.S1, 3.5.4.S2 and 3.5.4.S3). At the medium and large scales (5 and 10km buffers), no other variable is related to parrot community indicators (Table 3.5.3.2).

Except for the abundance of individuals, models obtained at the patch-level explained less variability than models performed at the point-level (Table 3.5.3.3). Of this explained variability (always lower than 32%), the hierarchical partitioning showed that variables describing habitat features had a low, mostly non-significant, independent effect on community indexes (Table 3.5.3.3). Conversely, the spatial autocorrelation variable was, by far, the most important variable.

3.5.2. Poaching pressure on Costa Rican parrot species

We found a total of 361 captive birds in different localities distributed all across Costa Rica (Figure 3.5.3.1B). Most of them (n=280) were native parrots, all illegally captured and maintained in cages in private houses or local businesses, such as small shops or hotels. *Brotogeris jugularis* was the commonest pet in all the localities sampled , although its abundance in captivity was lower than expected based on its abundance in the wild (negative Savage selectivity index; Figure 3.5.3.3A; Table 3.5.3.5). Conversely, other species kept as pets showed a significant positive Savage selectivity index (Figure 3.5.3.3A). Compared to their low abundance in the wild, yellow-naped amazon (*Amazona auropalliata*) was the species most positively selected as a pet (Figure 3.5.3.3A; Table 3.5.3.5). The preference for this species is so strong that many individuals have been found as pets even far from their distribution area (Figure 3.5.3.1B).

Seizure data were highly skewed toward species of the genus *Ara* and *Amazona* ($\chi^2 = 73.53$; df = 2; $p < 0.0001$; Table 3.5.3.5; Figure 3.5.4.S13), which due to their long lifespan would have been counted as pets if not seized, justifying the need of calculating the Savage selectivity index combining both source of data. Using this combined data, the red-lored amazon (*Amazona autumnalis*), the Northern mealy parrot (*A. guatemalae*), the two native macaw species (the Scarlet *Ara macao* and the great green macaw *A. ambiguus*), the white-crowned parrot (*Pionus senilis*) and the Crimson-fronted parakeet (*Psittacara finschi*) also show significant positive Savage selectivity indexes (Figure 3.5.3.3B; Table 3.5.3.5).

The proportion of exposed pets and their abundance and richness were not related to the distance to protected areas or the number of visitors they received (foreign, local, and total number of tourists; Table 3.5.3.4; Figure 3.5.3.4A). However, the mean Savage selectivity index of species kept as pets obtained using our field data combined with seizures was lower closer to these areas, while the same selectivity index obtained using only our field data was negatively related to the number of visitors at the closest protected area (Table 3.5.3.4; Figure 3.5.3.4B).

3.5.3 Tables and Figures

Table 3.5.3.1. Generalized Linear Mixed Models obtained to assess the effects of habitat alteration on the presence, abundance (number of individuals/km) and richness (number of species/km) of parrots at the patch-level along transects performed across Costa Rica. Estimates and 95% confidence intervals were assessed after model averaging. We considered that a given variable has no, weak or strong support (bolded) when the 95% confidence interval strongly overlapped with zero, barely overlapped with zero, or did not overlap with zero, respectively. All models were corrected for zero-inflation and run including transect as a random term. k: number of parameters, ΔAICc: difference between the AICc, i.e. Akaike Information Criterion corrected for small sample sizes of model *i* and that of the best model i.e. the model with the lowest AICc, w: Akaike weights. The fit of the final models can be checked in Figure 3.5.4.S1, 3.5.4.S2 and 3.5.4.S3.

Model selection

Models for the presence of parrots per patch	**k**	**ΔAICc**	**w**
habitat transformation + biome + hour	10	0.00	0.57
habitat transformation + habitat transformation^2 + biome + hour	11	0.62	0.41
habitat transformation + biome	8	8.58	0.01
habitat transformation + habitat transformation^2 + biome	9	9.08	0.01
biome + hour	9	9.13	0.01

Model averaging

Variable	**Estimate**	**2.5% CI**	**97.5%CI**
habitat transformation	0.05	-0.41	0.52
habitat transformation^2	0.05	-0.03	0.13
biome(TH)	**-1.30**	**-2.32**	**-0.29**
biome(TM)	**-0.24**	**-1.03**	**0.56**
biome(TP)	**1.05**	**0.37**	**1.73**

biome	7	17.78	0.00	**biome(TS)**	**0.88**	**0.25**	**1.50**
habitat transformation + hour	6	17.99	0.00	**hour(midday)**	**-0.81**	**-1.28**	**-0.35**
habitat transformation + habitat transformation^2 + hour	7	18.80	0.00	hour(evening)	-0.48	-1.03	0.07
habitat transformation	4	23.64	0.00				
habitat transformation + habitat transformation^2	5	24.36	0.00				
hour	5	27.23	0.00				
null	3	33.04	0.00				

Models for the abundance of parrots per patch	**k**	**ΔAICc**	**w**	**Variable**	**Estimate**	**2.5% CI**	**97.5%CI**
habitat transformation + habitat transformation^2 + hour + biome	11	0.00	1.00	habitat transformation	-0.29	-0.46	-0.11
habitat transformation + hour + biome	10	20.79	0.00	**habitat transformation^2**	**0.07**	**0.04**	**0.09**
hour + biome	9	74.61	0.00	**hour(midday)**	**-0.92**	**-1.05**	**-0.78**
Hour	5	94.75	0.00	**hour(evening)**	**-0.97**	**-1.15**	**-0.80**
biome + habitat transformation + habitat transformation^2	9	217.35	0.00	**biome(TH)**	**-1.77**	**-2.64**	**-0.90**
habitat transformation + habitat transformation^2	5	233.80	0.00	biome(TM)	-0.19	-0.79	0.40
biome + habitat transformation	8	236.95	0.00	biome(TP)	0.49	-0.03	1.01
habitat transformation	4	253.22	0.00	biome(TS)	0.40	-0.10	0.91
Biome	7	288.66	0.00				
Null	3	304.55	0.00				

Models for the richness of parrots	**k**	**ΔAICc**	**w**	**Variable**	**Estimate**	**2.5% CI**	**97.5%CI**
habitat transformation + habitat transformation^2 + hour + biome	11	0.00	0.80	habitat transformation	-0.26	-0.57	0.04
habitat transformation + hour + biome	10	3.00	0.18	**habitat transformation^2**	**0.05**	**0.01**	**0.10**
hour + biome	9	7.31	0.02	**hour(midday)**	**-0.67**	**-0.92**	**-0.43**
habitat transformation + habitat transformation^2 + hour	7	21.57	0.00	**hour(evening)**	**-0.46**	**-0.77**	**-0.15**
biome + habitat transformation + habitat transformation^2	9	23.38	0.00	**biome(TH)**	**-1.24**	**-2.00**	**-0.49**

habitat transformation + hour	6	24.30	0.00	biome(TM)	-0.18	-0.69	0.34
biome + habitat transformation	8	26.53	0.00	**biome(TP)**	**0.65**	**0.24**	**1.07**
Hour	5	29.21	0.00	**biome(TS)**	**0.51**	**0.12**	**0.89**
Biome	7	31.17	0.00				
habitat transformation + habitat transformation^2	5	41.70	0.00				
habitat transformation	4	44.44	0.00				
Null	3	49.74	0.00				

Table 3.5.3.2. Estimates and 95% confidence intervals (2.5% and 97.5%) obtained after averaging models obtained to assess the effects of habitat characteristics on the presence (Table 3.5.4.S1), abundance (Table 3.5.4.S2) and richness (Table 3.5.4.S3) of parrots in 1, 5 and 10km radii around points distributed along transects performed across Costa Rica. We considered that a given variable has no, weak or strong (bolded) support when the 95% confidence interval strongly overlapped with zero, barely overlapped with zero, or did not overlap with zero, respectively. The fit of the final models can be checked in Figure 3.5.4.S4--3.5.4.S12.

Models for the presence of parrots									
1km				5km			10km		
variables	**Estimate**	**2.50%**	**97.50%**	**Estimate**	**2.50%**	**97.50%**	**Estimate**	**2.50%**	**97.50%**
AC	**1.66**	**1.49**	**1.83**	**1.50**	**1.34**	**1.67**	**1.57**	**1.40**	**1.75**
crops	-0.02	-0.13	0.09	0.06	-0.08	-0.01	-0.02	-0.14	0.10
distance population	**-0.22**	**-0.34**	**-0.09**	-0.14	-0.27	0.20	-0.05	-0.17	0.08
distance protected areas	-0.04	-0.15	0.07	-0.05	-0.17	0.08	-0.03	-0.15	0.09
forest	-0.01	-0.13	0.11	0.10	-0.03	0.24	0.05	-0.07	0.18
HF	-0.06	-0.20	0.08	-0.06	-0.22	0.09	-	-	-
Models for the abundance of parrots									
1km				5km			10km		
variables	**Estimate**	**2.50%**	**97.50%**	**Estimate**	**2.50%**	**97.50%**	**Estimate**	**2.50%**	**97.50%**
AC	**0.41**	**0.34**	**0.48**	**0.40**	**0.32**	**0.48**	**0.42**	**0.33**	**0.50**

crops	-0.01	-0.08	0.06	0.03	-0.04	0.10	0.04	-0.04	0.12
distance population	**-0.12**	**-0.19**	**-0.04**	-	-	-	-	-	-
distance protected areas	0.02	-0.04	0.08	0.03	-0.04	0.10	0.07	-0.01	0.15
forest	**-0.10**	**-0.17**	**-0.03**	-0.01	-0.08	0.06	-0.05	-0.13	0.04
HF	**-0.09**	**-0.16**	**-0.01**	-0.02	-0.09	0.06	-0.08	-0.18	0.01
hour(midday)	-	-	-	0.11	-0.08	0.30	0.12	-0.08	0.31
hour(evening)	-	-	-	0.12	-0.05	0.29	0.13	-0.03	0.30

Models for the richness of parrots

1km				5km			10km		
variables	**Estimate**	**2.50%**	**97.50%**	**Estimate**	**2.50%**	**97.50%**	**Estimate**	**2.50%**	**97.50%**
AC	**0.36**	**0.33**	**0.39**	**0.57**	**0.52**	**0.62**	**0.40**	**0.36**	**0.43**
crops	-0.03	-0.07	0.02	0.03	-0.01	0.07	-0.01	-0.05	0.03
distance population	**-0.03**	**-0.07**	**0.00**	-0.01	-0.04	0.03	-	-	-
distance protected areas	-0.02	-0.06	0.02	-0.01	-0.04	0.03	-0.01	-0.05	0.03
forest	**-0.05**	**-0.09**	**0.00**	0.00	-0.05	0.06	0.01	-0.03	0.04
HF	0.01	-0.03	0.06	-0.01	-0.05	0.03	0.00	-0.04	0.03
hour(midday)	-0.02	-0.12	0.08	-	-	-	-0.02	-0.13	0.09
hour(evening)	0.05	-0.04	0.14	-	-	-	0.06	-0.02	0.15
biome(dry)				0.02	-0.07	0.10			
biome(high)				-0.27	-0.67	0.13			

biome(mid)	-0.09	-0.30	0.12
biome(pacific)	**0.16**	**0.06**	**0.26**

Table 3.5.3.3. Independent effects (in percentage) of the different variables on the presence, abundance and richness of parrots in Costa Rica as determined by hierarchical partitioning. Asterisks represent significant effects ($p<0.05$) as determined by randomization tests. R^2dev is the total deviance explained by the generalized linear or generalized linear mixed models including variables retained after model averaging (Table 3.5.3.2).

Community index	**Patch**		**Point**	**1km**	**5km**	**10km**
Presence	**Variables**	**% ind. expl.**	**Variables**	**% ind. expl.**	**% ind. expl.**	**% ind. expl.**
	biome	84.45 *	AC	95.36 *	98.65 *	99.29 *
	hour	15.55 *	crops	0.21	0.13	0.07
			distance population	1.96 *	0.42	0.09
			distance protected areas	0.31	0.23	0.10
			forest	1.88 *	0.51	0.45
			HF	0.28	0.07	-
	R^2dev =	16.63	R^2dev =	31.66	30.19	30.93
Abundance	**variables**	**% ind. expl.**	**variables**	**% ind. expl.**	**% ind. expl.**	**% ind. expl.**
	habitat transformation	10.39 *	AC	52.09 *	41.99 *	32.78 *
	hour	89.61 *	forest	37.93 *	7.06	3.96
			hour	-	46.60 *	40.17 *
			distance population	3.42	-	-
			crops	2.73	2.02	5.52
			distance protected areas	2.56	0.36	3.83
			HF	1.27	1.97	13.73
	R^2dev =	17.40	R^2dev =	0.80	0.10	0.10
Richness	**variables**	**% ind. expl.**	**variables**	**% ind. expl.**	**% ind. expl.**	**% ind. expl.**
	habitat transformation	3.38	AC	86.66 *	97.66 *	96.84 *

hour	27.28	*	forest	5.93	*	0.28	0.62
biome	69.33	*	distance population	2.78	*	0.22	-
			crops	0.66		0.19	0.10
			distance protected areas	1.63	*	0.43	0.20
			HF	0.56		0.15	0.58
			hour	1.78		-	1.67
			biome	-		1.07	-
R^2dev =	18.6		R^2dev =	20.06		31.93	22.88

Table 3.5.3.4. Generalized Linear Models obtained to assess we assessed whether the existence of environmental vigilance close to protected areas may help to reduce the abundance and richness of parrots kept as pets as well as the proportion of these individuals that were exposed and their mean Savage selectivity index. k: number of parameters, ΔAICc: difference between the AICc, i.e. Akaike Information Criterion corrected for small sample sizes of model *i* and that of the best model i.e. the model with the lowest AICc, w: Akaike weights. The fit of the final models can be checked in Figure S.

Model selection				**Model averaging**			
Models for the abundance of parrots as pets	**k**	**ΔAICc**	**w**	**Variable**	**Estimate**	**2.5% CI**	**97.5%CI**
null	3	0.00	0.34	number of foreign tourists			
number of foreign tourists	4	1.70	0.15	total number of tourists			
total number of tourists	4	1.82	0.14				
number of local tourists	4	2.05	0.12				
distance to protected areas	4	2.22	0.11				
distance to protected areas + number of foreign tourists	5	3.88	0.05				
distance to protected areas + total number of tourists	5	4.01	0.05				
distance to protected areas + number of local tourists	5	4.27	0.04				
Models for the richness of parrots as pets	**k**	**ΔAICc**	**w**	**Variable**	**Estimate**	**2.5% CI**	**97.5%CI**
distance to protected areas	3	0.00	0.23	distance to protected areas	0.09	-0.01	0.20
null	2	0.53	0.18	number of foreign tourists	-0.06	-0.17	0.06
distance to protected areas + number of foreign tourists	4	1.15	0.13	total number of tourists	-0.05	-0.17	0.06
distance to protected areas + total number of tourists	4	1.31	0.12	number of local tourists	-0.04	-0.15	0.07
distance to protected areas + number of local tourists	4	1.67	0.10				
number of foreign tourists	3	2.02	0.09				
total number of tourists	3	2.17	0.08				
number of local tourists	3	2.45	0.07				

Models for the proportion of pets exposed	**k**	**ΔAICc**	**w**	**Variable**	**Estimate**	**2.5% CI**	**97.5%CI**
null	2	0.00	0.37	-	-	-	-
distance to protected areas	3	2.16	0.13				
number of local tourists	3	2.16	0.13				
total number of tourists	3	2.16	0.13				
number of foreign tourists	3	2.16	0.13				
distance to protected areas + number of local tourists	4	4.38	0.04				
distance to protected areas + total number of tourists	4	4.38	0.04				
distance to protected areas + number of foreign tourists	4	4.38	0.04				

Models for the Savage selectivity index of pets	**k**	**ΔAICc**	**w**	**Variable**	**Estimate**	**2.5% CI**	**97.5%CI**
number of foreign tourists[1]	3	0.00	0.19	**number of foreign tourists**	**-0.15**	**-0.29**	**-0.02**
total number of tourists[1]	3	0.16	0.17	**total number of tourists**	**-0.15**	**-0.28**	**-0.02**
distance to protected areas + number of foreign tourists[1]	4	0.28	0.16	distance to protected areas	-0.09	-0.22	0.04
distance to protected areas + total number of tourists[1]	4	0.48	0.15	**number of local tourists**	**-0.14**	**-0.28**	**-0.01**
number of local tourists[1]	3	0.66	0.14				
distance to protected areas + number of local tourists[1]	4	1.06	0.11				
distance to protected areas[1]	3	3.00	0.04				
null[1]	2	3.54	0.03				
distance to protected areas[2]	3	0.00	0.42	**distance to protected areas**	**0.07**	**0.68**	**0.37**
distance to protected areas + number of foreign tourists[2]	4	2.20	0.14				
distance to protected areas + total number of tourists[2]	4	2.20	0.14				
distance to protected areas + number of local tourists[2]	4	2.21	0.14				
null[2]	2	3.41	0.08				
number of local tourists[2]	3	5.37	0.03				
total number of tourists[2]	3	5.37	0.03				
number of foreign tourists[2]	3	5.38	0.03				

[1] dependent variable: Savage selectivity index obtained using our field data

[2] dependent variable: Savage selectivity index obtained using our field data combined with seizures data

Table 3.5.3.5. Number of parrots recorded as pets (Pet) and in the wild (Wild) in Costa Rica. W: Savage selectivity index. * Statistically significant W values after Bonferroni correction.

Species	Field data				Seizures				Field data + Seizures			
	Pet	Wild	W		Seizure	Pet	W		Pet	Wild	W	
Amazona albifrons	12	266	0.58		8	12	0.32	*	20	266	0.31	*
Amazona auropalliata	46	22	26.68	*	44	46	0.46	*	90	22	17.11	*
Amazona autumnalis	26	377	0.88		162	26	3.01	*	188	377	2.09	*
Amazona guatemalae	3	31	1.23		32	3	5.15	*	35	31	4.72	*
Ara ambiguus	1	15	0.85		4	1	1.93		5	15	1.39	
Ara macao	2	33	0.77		71	2	17.13	*	73	33	9.25	*
Brotogeris jugularis	62	1578	0.50	*	118	62	0.92	*	180	1578	0.48	*
Eupsittula canicularis	90	546	2.10	*	43	90	0.23	*	90	546	0.69	*
Eupsittula nana	2	161	0.16		12	2	2.90		14	161	0.36	*
Eupsittula pertinax	0	6	0.00		-	-	-		0	6	0.00	
Pionus menstruus	1	108	0.12		1	1	0.48	*	2	108	0.08	*
Pionus senilis	3	139	0.28		51	3	8.20	*	54	139	1.62	*
Psittacara finschi	30	233	1.64		30	30	0.48		96	233	1.72	*
Pyrrhura hoffmanni	0	29	0.00		-	-	-		0	29	0.00	
Touit costaricensis	0	2	0.00		-	-	-		0	2	0.00	
Bolborhynchus lineola	0	1	0.00		-	-	-		0	1	0.00	

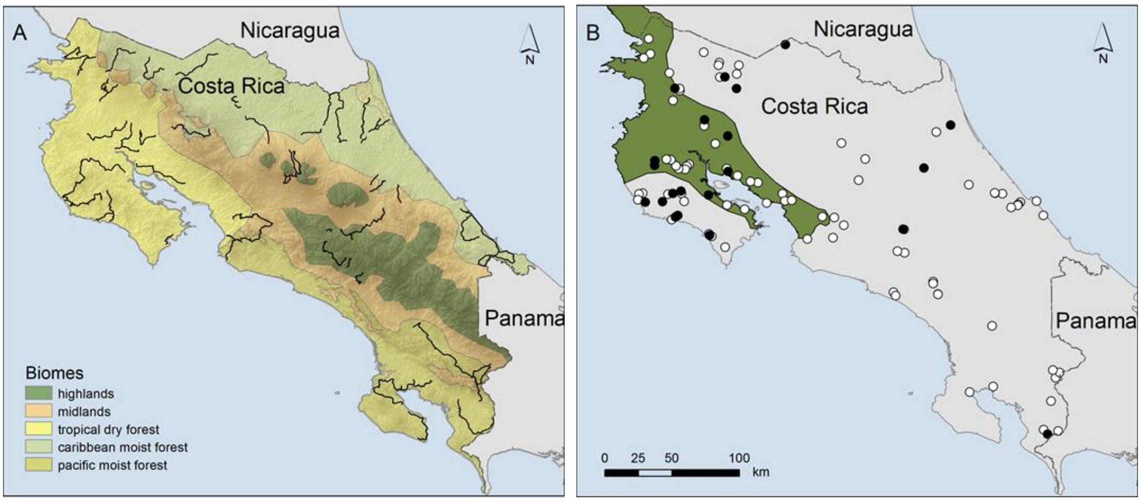


Figure 3.5.3.1. A) Road surveys (black lines) performed across the different biomes of Costa Rica between 10th April and 1st May of 2018. (B) Localities where we performed informal inquires to detect parrots kept as pets (white dots), and localities where *Amazona auropalliata* was found as a pet (black dots). The green area shows the distribution area of the species.

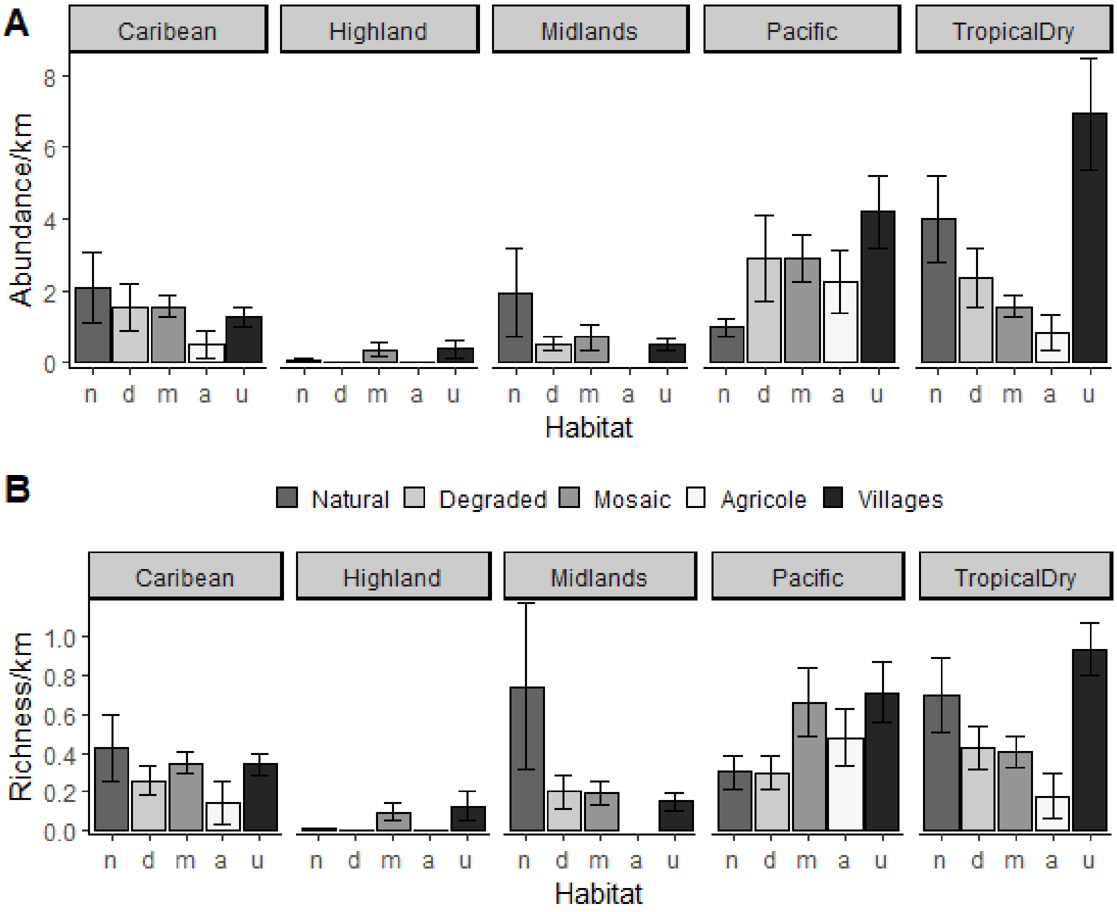
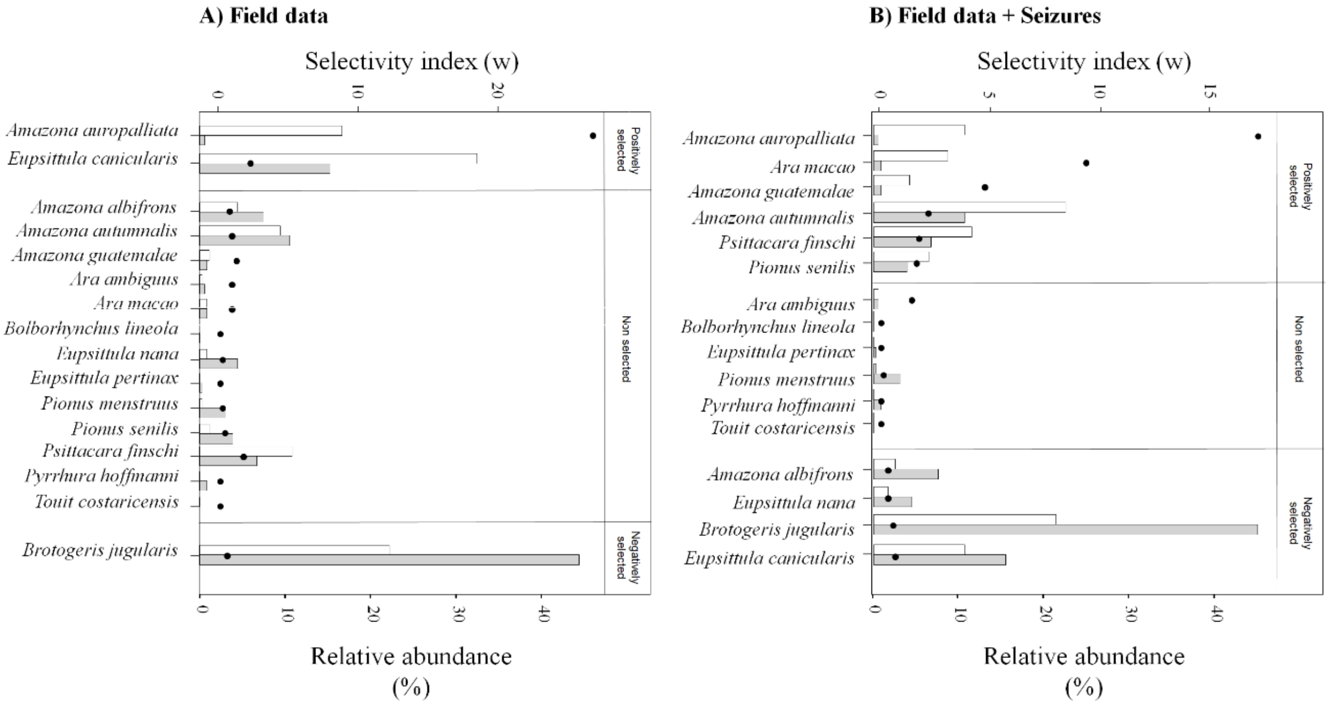


Figure 3.5.3.2. (A) Relative abundance (individuals/km) and (B) richness (number of species/km) of parrots in the different biomes of Costa Rica with variable degree of human transformation (n: natural; d: degraded; m: natural habitats mixed with agriculture; a: agriculture; and r: rural).



A) Field data

B) Field data + Seizures

Figure 3.5.3.3. Relative abundances of parrots observed in the wild (grey bars) and as pets (white bars). The Savage selectivity index, calculated for each species (black dots) based on **(A)** our informal inquiries and **(B)** combining these data with government seizures, allows us to categorize species as positively, negatively or non-selected as pets.

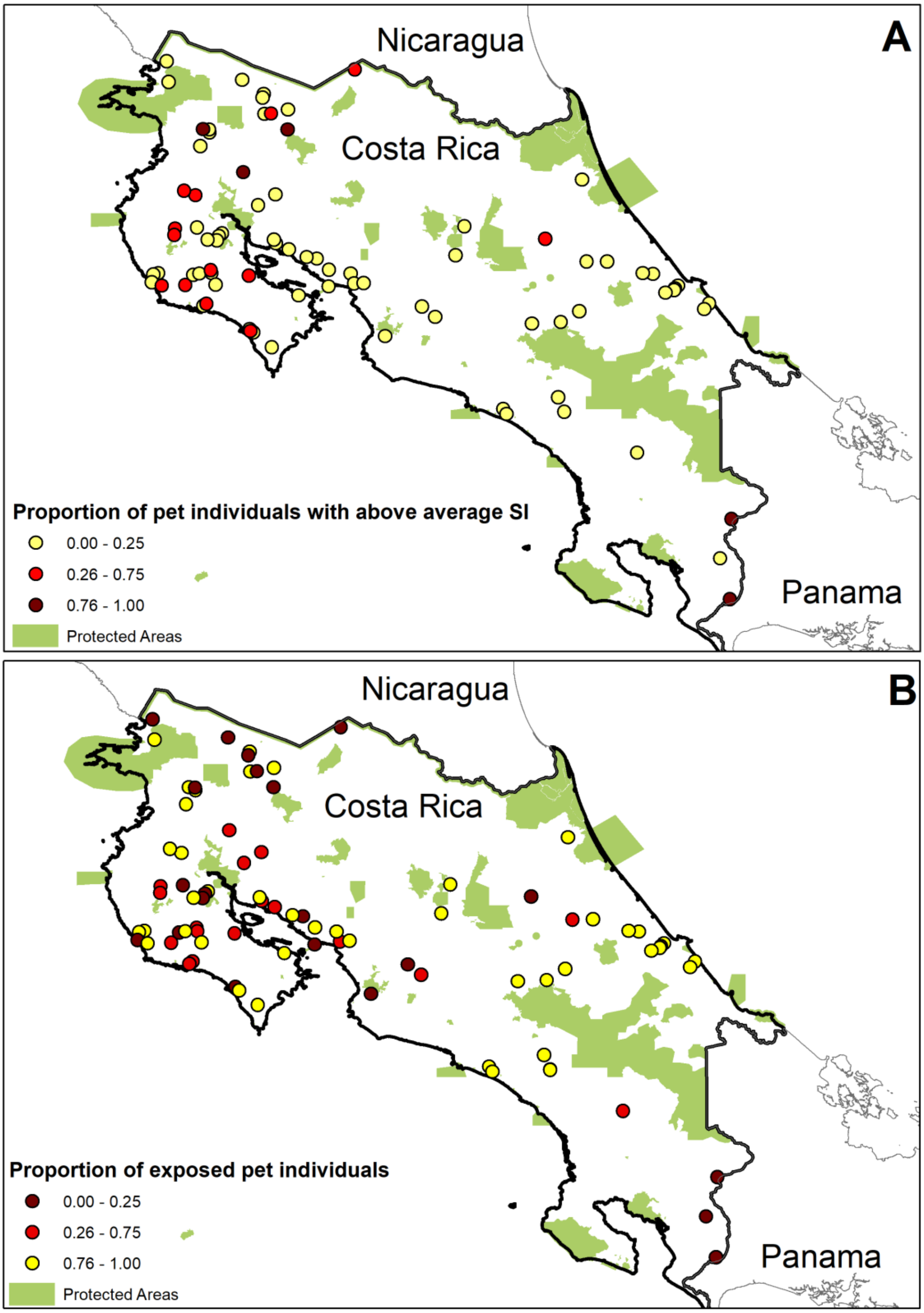


Figure 3.5.3.4. Proportion of parrots kept as pets with Savage selectivity index above the average **(A)** and exposed (i.e., easily visible from the street) **(B)**. Green areas shows protected areas across Costa Rica.

3.5.4 SUPPELEMENTARY INFORMATION

Table 3.5.4.S1. Models obtained to assess the effects of habitat alteration on the presence, abundance (number of individuals) and richness (number of species) of parrots in 1km radius around points distributed along transects performed across Costa Rica.

k: number of parameters, ΔAICc: difference between the AICc, i.e. Akaike Information Criterion corrected for small sample sizes of model *i* and that of the best model, i.e. the model with the lowest AICc, w: Akaike weights.

Only models with w > 0 are included.

Models for the presence of parrots	**k**	**ΔAICc**	**w**
AC + distance population	4	0.00	0.19
HF + AC + distance population	5	1.27	0.10
distance protected areas + AC + distance population	5	1.54	0.09
crops + AC + distance population	5	1.91	0.07
forest + AC + distance population	5	1.99	0.07
distance protected areas + HF + AC + distance population	6	3.03	0.04
hour + AC + distance population	6	3.13	0.04
forest + HF + AC + distance population	6	3.14	0.04
crops + HF + AC + distance population	6	3.27	0.04
crops + distance protected areas + AC + distance population	6	3.44	0.03
distance protected areas + forest + AC + distance population	6	3.47	0.03
crops + forest + AC + distance population	6	3.82	0.03
HF + hour + AC + distance population	7	4.60	0.02
distance protected areas + hour + AC + distance population	7	4.68	0.02
distance protected areas + forest + HF + AC + distance population	7	4.82	0.02
crops + distance protected areas + HF + AC + distance population	7	5.02	0.02
crops + forest + HF + AC + distance population	7	5.05	0.02
forest + hour + AC + distance population	7	5.11	0.01
crops + hour + AC + distance population	7	5.12	0.01
crops + distance protected areas + forest + AC + distance population	7	5.17	0.01
biome + AC + distance population	8	6.32	0.01
distance protected areas + HF + hour + AC + distance population	8	6.34	0.01
forest + HF + hour + AC + distance population	8	6.45	0.01
distance protected areas + forest + hour + AC + distance population	8	6.58	0.01
crops + HF + hour + AC + distance population	8	6.62	0.01
crops + distance protected areas + forest + HF + AC + distance population	8	6.64	0.01
crops + distance protected areas + hour + AC + distance population	8	6.67	0.01
crops + forest + hour + AC + distance population	8	7.04	0.01
Models for the abundance of parrots	**k**	**ΔAICc**	**w**

forest + HF + AC + distance population	7	0.00	0.25
distance protected areas + forest + HF + AC + distance population	8	1.59	0.11
crops + forest + HF + AC + distance population	8	1.93	0.09
forest + HF + hour + AC + distance population	9	2.55	0.07
forest + AC + distance population	6	2.72	0.06
crops + distance protected areas + forest + HF + AC + distance population	9	3.57	0.04
distance protected areas + forest + HF + hour + AC + distance population	10	4.08	0.03
crops + forest + HF + hour + AC + distance population	10	4.42	0.03
crops + forest + AC + distance population	7	4.54	0.03
distance protected areas + forest + AC + distance population	7	4.65	0.02
biome + forest + HF + AC + distance population	11	5.00	0.02
AC + distance population	5	5.77	0.01
forest + hour + AC + distance population	8	5.81	0.01
biome + forest + AC + distance population	10	5.83	0.01
HF + AC + distance population	6	5.91	0.01
crops + distance protected areas + forest + HF + hour + AC + distance population	11	6.03	0.01
forest + AC	5	6.25	0.01
crops + distance protected areas + forest + AC + distance population	8	6.51	0.01
biome + distance protected areas + forest + HF + AC + distance population	12	6.86	0.01
biome + crops + forest + HF + AC + distance population	12	6.90	0.01
distance protected areas + HF + AC + distance population	7	6.93	0.01
crops + HF + AC + distance population	7	7.05	0.01
biome + forest + HF + hour + AC + distance population	13	7.26	0.01
distance protected areas + AC + distance population	6	7.31	0.01
crops + AC + distance population	6	7.36	0.01
forest + HF + AC	6	7.58	0.01
crops + forest + hour + AC + distance population	9	7.58	0.01
biome + crops + forest + AC + distance population	11	7.62	0.01
distance protected areas + forest + hour + AC + distance population	9	7.74	0.01

Models for the richness of parrots	**k**	**ΔAICc**	**w**
forest + AC + distance population	6	0.00	0.08
crops + forest + AC + distance population	7	0.35	0.06
forest + AC	5	1.04	0.05
crops + distance protected areas + forest + AC + distance population	8	1.31	0.04
distance protected areas + forest + AC + distance population	7	1.35	0.04
forest + hour + AC + distance population	8	1.35	0.04
crops + forest + hour + AC + distance population	9	1.73	0.03
crops + forest + AC	6	1.75	0.03
forest + HF + AC	6	1.85	0.03
forest + HF + AC + distance population	7	1.93	0.03
AC + distance population	5	2.18	0.03
crops + forest + HF + AC + distance population	8	2.24	0.02
crops + forest + HF + AC	7	2.33	0.02
distance protected areas + forest + AC	6	2.64	0.02
distance protected areas + forest + hour + AC + distance population	9	2.68	0.02
crops + distance protected areas + forest + hour + AC + distance population	10	2.70	0.02
forest + hour + AC	7	2.82	0.02
crops + distance protected areas + forest + HF + AC + distance population	9	3.00	0.02

distance protected areas + forest + HF + AC	7	3.06	0.02
HF + AC	5	3.08	0.02
crops + distance protected areas + forest + HF + AC	8	3.11	0.02
crops + distance protected areas + forest + AC	7	3.12	0.02
distance protected areas + forest + HF + AC + distance population	8	3.15	0.02
forest + HF + hour + AC + distance population	9	3.24	0.02
forest + HF + hour + AC	8	3.35	0.01
HF + AC + distance population	6	3.41	0.01
crops + forest + HF + hour + AC + distance population	10	3.61	0.01
crops + forest + hour + AC	8	3.65	0.01
hour + AC + distance population	7	3.81	0.01
crops + forest + HF + hour + AC	9	3.97	0.01
distance protected areas + AC + distance population	6	4.00	0.01
AC	4	4.06	0.01
crops + AC + distance population	6	4.15	0.01
crops + distance protected areas + forest + HF + hour + AC + distance population	11	4.32	0.01
distance protected areas + forest + HF + hour + AC + distance population	10	4.41	0.01
distance protected areas + forest + hour + AC	8	4.47	0.01
distance protected areas + forest + HF + hour + AC	9	4.52	0.01
distance protected areas + HF + AC	6	4.64	0.01
crops + distance protected areas + forest + HF + hour + AC	10	4.74	0.01
HF + hour + AC	7	4.79	0.01
HF + hour + AC + distance population	8	4.96	0.01
crops + HF + AC	6	4.97	0.01
distance protected areas + HF + AC + distance population	7	4.99	0.01
crops + distance protected areas + forest + hour + AC	9	5.10	0.01
biome + forest + AC + distance population	10	5.27	0.01
crops + HF + AC + distance population	7	5.30	0.01
biome + crops + forest + AC + distance population	11	5.41	0.01

Table 3.5.4.S2. Models obtained to assess the effects of habitat alteration on the presence, abundance (number of individuals) and richness (number of species) of parrots in 5km radius around points distributed along transects performed across Costa Rica.

k: number of parameters, ΔAICc: difference between the AICc, i.e. Akaike Information Criterion corrected for small sample sizes of model *i* and that of the best model, i.e. the model with the lowest AICc, w: Akaike weights.

Only models with w > 0 are included.

Models for the presence of parrots	**k**	**ΔAICc**	**w**
forest + AC + distance population	5	0.00	0.11
AC + distance population	4	0.35	0.09
crops + forest + AC + distance population	6	1.30	0.06
distance protected areas + AC + distance population	5	1.57	0.05
distance protected areas + forest + AC + distance population	6	1.68	0.05
HF + AC + distance population	5	1.73	0.05
forest + HF + AC + distance population	6	2.00	0.04
AC	3	2.26	0.04
crops + AC + distance population	5	2.35	0.03
forest + AC	4	2.74	0.03
crops + distance protected areas + forest + AC + distance population	7	3.10	0.02
forest + HF + AC	5	3.13	0.02
crops + forest + HF + AC + distance population	7	3.29	0.02
distance protected areas + HF + AC + distance population	6	3.35	0.02
crops + distance protected areas + AC + distance population	6	3.57	0.02
forest + hour + AC + distance population	7	3.63	0.02
distance protected areas + forest + HF + AC + distance population	7	3.69	0.02
crops + HF + AC + distance population	6	3.74	0.02
hour + AC + distance population	6	3.80	0.02
HF + AC	4	3.90	0.02
crops + forest + AC	5	4.11	0.01
distance protected areas + AC	4	4.18	0.01
crops + AC	4	4.27	0.01
crops + forest + HF + AC	6	4.59	0.01
crops + forest + hour + AC + distance population	8	4.69	0.01
distance protected areas + forest + AC	5	4.75	0.01
distance protected areas + forest + HF + AC	6	4.80	0.01
crops + distance protected areas + forest + HF + AC + distance population	8	5.12	0.01
distance protected areas + hour + AC + distance population	7	5.14	0.01
distance protected areas + forest + hour + AC + distance population	8	5.35	0.01
crops + distance protected areas + HF + AC + distance population	7	5.37	0.01

HF + hour + AC + distance population	7	5.40	0.01
distance protected areas + HF + AC	5	5.46	0.01
hour + AC	5	5.62	0.01
forest + HF + hour + AC + distance population	8	5.65	0.01
crops + hour + AC + distance population	7	5.82	0.01
crops + HF + AC	5	5.88	0.01
crops + distance protected areas + forest + AC	6	6.12	0.01

Models for the abundance of parrots	**k**	**ΔAICc**	**w**
AC	4	0.00	0.10
distance protected areas + AC	5	1.17	0.06
crops + crops + AC	5	1.40	0.05
HF + AC	5	1.83	0.04
forest + AC	5	1.87	0.04
hour + AC	6	1.88	0.04
AC + distance population	5	2.01	0.04
distance protected areas + HF + AC	6	2.40	0.03
crops + crops + distance protected areas + AC	6	2.61	0.03
crops + crops + HF + AC	6	2.98	0.02
distance protected areas + hour + AC	7	3.01	0.02
distance protected areas + forest + AC	6	3.17	0.02
distance protected areas + AC + distance population	6	3.19	0.02
crops + crops + distance protected areas + HF + AC	7	3.32	0.02
crops + crops + hour + AC	7	3.39	0.02
forest + HF + AC	6	3.39	0.02
crops + crops + forest + AC	6	3.42	0.02
crops + crops + AC + distance population	6	3.42	0.02
HF + hour + AC	7	3.61	0.02
HF + AC + distance population	6	3.65	0.02
forest + hour + AC	7	3.73	0.02
hour + AC + distance population	7	3.86	0.02
forest + AC + distance population	6	3.89	0.01
distance protected areas + HF + hour + AC	8	4.03	0.01
distance protected areas + forest + HF + AC	7	4.09	0.01
distance protected areas + HF + AC + distance population	7	4.09	0.01
crops + crops + distance protected areas + forest + AC	7	4.51	0.01
crops + crops + distance protected areas + hour + AC	8	4.51	0.01
crops + crops + distance protected areas + AC + distance population	7	4.61	0.01
crops + crops + HF + AC + distance population	7	4.74	0.01
crops + crops + HF + hour + AC	8	4.88	0.01
crops + crops + distance protected areas + HF + AC + distance population	8	4.88	0.01
crops + crops + forest + HF + AC	7	4.95	0.01
crops + crops + distance protected areas + HF + hour + AC	9	5.00	0.01
distance protected areas + forest + hour + AC	8	5.00	0.01
distance protected areas + hour + AC + distance population	8	5.03	0.01
forest + HF + hour + AC	8	5.07	0.01
forest + HF + AC + distance population	7	5.12	0.01
distance protected areas + forest + AC + distance population	7	5.18	0.01
HF + hour + AC + distance population	8	5.20	0.01

crops + crops + distance protected areas + forest + HF + AC	8	5.34	0.01
crops + crops + hour + AC + distance population	8	5.39	0.01
crops + crops + forest + hour + AC	8	5.41	0.01
distance protected areas + HF + hour + AC + distance population	9	5.41	0.01
crops + crops + forest + AC + distance population	7	5.43	0.01
distance protected areas + forest + HF + hour + AC	9	5.61	0.01
distance protected areas + forest + HF + AC + distance population	8	5.66	0.01
forest + hour + AC + distance population	8	5.74	0.01

Models for the richness of parrots	**k**	**ΔAICc**	**w**
biome + AC	8	0.00	0.11
biome + crops + AC	9	0.08	0.10
biome + crops + HF + AC	10	1.72	0.04
biome + distance protected areas + AC	9	1.79	0.04
biome + crops + distance protected areas + AC	10	1.80	0.04
biome + AC + distance population	9	1.82	0.04
biome + crops + forest + AC	10	1.85	0.04
biome + forest + AC	9	1.94	0.04
biome + HF + AC	9	1.95	0.04
biome + crops + AC + distance population	10	2.04	0.04
biome + crops + HF + AC + distance population	11	2.91	0.02
biome + hour + AC	10	3.19	0.02
biome + HF + AC + distance population	10	3.25	0.02
biome + crops + hour + AC	11	3.29	0.02
biome + distance protected areas + AC + distance population	10	3.47	0.02
biome + distance protected areas + forest + AC	10	3.56	0.02
biome + crops + forest + HF + AC	11	3.65	0.02
biome + crops + distance protected areas + AC + distance population	11	3.66	0.02
biome + crops + distance protected areas + HF + AC	11	3.70	0.02
biome + crops + forest + AC + distance population	11	3.71	0.02
biome + crops + distance protected areas + forest + AC	11	3.73	0.02
biome + forest + HF + AC	10	3.78	0.02
biome + distance protected areas + HF + AC	10	3.81	0.02
biome + forest + AC + distance population	10	3.82	0.02
biome + crops + forest + HF + AC + distance population	12	4.81	0.01
biome + hour + AC + distance population	11	4.93	0.01
biome + crops + distance protected areas + HF + AC + distance population	12	4.94	0.01
biome + forest + hour + AC	11	5.00	0.01
biome + distance protected areas + hour + AC	11	5.02	0.01
biome + crops + HF + hour + AC	12	5.02	0.01
biome + crops + distance protected areas + hour + AC	12	5.10	0.01
biome + forest + HF + AC + distance population	11	5.10	0.01
biome + HF + hour + AC	11	5.17	0.01
biome + crops + hour + AC + distance population	12	5.19	0.01
biome + crops + forest + hour + AC	12	5.22	0.01
biome + distance protected areas + HF + AC + distance population	11	5.24	0.01
biome + distance protected areas + forest + AC + distance population	11	5.35	0.01
biome + crops + distance protected areas + forest + AC + distance population	12	5.53	0.01
biome + distance protected areas + forest + HF + AC	11	5.58	0.01

biome + crops + distance protected areas + forest + HF + AC	12	5.66	0.01
biome + crops + HF + hour + AC + distance population	13	6.06	0.01

Table 3.5.4.S3. Models obtained to assess the effects of habitat alteration on the presence, abundance (number of individuals) and richness (number of species) of parrots in 10km radius around points distributed along transects performed across Costa Rica.

k: number of parameters, ΔAICc: difference between the AICc, i.e. Akaike Information Criterion corrected for small sample sizes of model *i* and that of the best model, i.e. the model with the lowest AICc, w: Akaike weights.

Only models with w > 0 are included.

Models for the presence of parrots	**k**	**ΔAICc**	**w**
AC	3	0.00	0.12
forest + AC	4	1.32	0.06
AC + distance population	4	1.50	0.05
distance protected areas + AC	4	1.76	0.05
crops + AC	4	1.90	0.04
HF + AC	4	2.00	0.04
forest + AC + distance population	5	2.44	0.03
hour + AC	5	2.65	0.03
distance protected areas + AC + distance population	5	2.76	0.03
HF + AC + distance population	5	2.87	0.03
distance protected areas + forest + AC	5	3.20	0.02
forest + HF + AC	5	3.21	0.02
crops + forest + AC	5	3.30	0.02
crops + AC + distance population	5	3.33	0.02
crops + distance protected areas + AC	5	3.69	0.02
distance protected areas + HF + AC	5	3.73	0.02
distance protected areas + forest + AC + distance population	6	3.82	0.02
crops + HF + AC	5	3.92	0.02
hour + AC + distance population	6	3.93	0.02
forest + hour + AC	6	4.22	0.01
forest + HF + AC + distance population	6	4.32	0.01
crops + forest + AC + distance population	6	4.41	0.01
distance protected areas + HF + AC + distance population	6	4.52	0.01
distance protected areas + hour + AC	6	4.55	0.01
crops + distance protected areas + AC + distance population	6	4.62	0.01
HF + hour + AC	6	4.64	0.01
crops + hour + AC	6	4.65	0.01
distance protected areas + forest + HF + AC	6	4.80	0.01
crops + HF + AC + distance population	6	4.84	0.01
forest + hour + AC + distance population	7	5.16	0.01
crops + distance protected areas + forest + AC	6	5.18	0.01

crops + forest + HF + AC	6	5.19	0.01
distance protected areas + hour + AC + distance population	7	5.42	0.01
biome + AC	7	5.52	0.01
crops + distance protected areas + HF + AC	6	5.62	0.01
HF + hour + AC + distance population	7	5.62	0.01
crops + distance protected areas + forest + AC + distance population	7	5.80	0.01
distance protected areas + forest + HF + AC + distance population	7	5.84	0.01
crops + hour + AC + distance population	7	5.91	0.01
forest + HF + hour + AC	7	5.94	0.01
crops + forest + hour + AC	7	6.10	0.01
distance protected areas + forest + hour + AC	7	6.18	0.01

Models for the abundance of parrots	**k**	**ΔAICc**	**w**
distance protected areas + HF + AC	6	0.00	0.06
crops + distance protected areas + HF + AC	7	0.33	0.05
distance protected areas + forest + HF + AC	7	0.50	0.05
AC	4	0.55	0.05
distance protected areas + AC	5	1.12	0.04
distance protected areas + HF + hour + AC	8	1.48	0.03
HF + AC	5	1.62	0.03
distance protected areas + forest + HF + hour + AC	9	1.62	0.03
crops + AC	5	1.83	0.03
crops + distance protected areas + forest + HF + AC	8	1.95	0.02
distance protected areas + HF + AC + distance population	7	2.01	0.02
crops + distance protected areas + HF + hour + AC	9	2.04	0.02
distance protected areas + AC + distance population	6	2.05	0.02
AC + distance population	5	2.20	0.02
crops + HF + AC	6	2.21	0.02
crops + distance protected areas + HF + AC + distance population	8	2.33	0.02
forest + AC	5	2.42	0.02
distance protected areas + forest + HF + AC + distance population	8	2.43	0.02
forest + HF + AC	6	2.54	0.02
crops + distance protected areas + AC	6	2.59	0.02
hour + AC	6	2.68	0.02
distance protected areas + forest + AC	6	3.12	0.01
distance protected areas + hour + AC	7	3.27	0.01
crops + distance protected areas + AC + pop_dist	7	3.28	0.01
crops + AC + distance population	6	3.29	0.01
crops + distance protected areas + forest + HF + hour + AC	10	3.34	0.01
HF + hour + AC	7	3.35	0.01
distance protected areas + forest + HF + hour + AC + distance population	10	3.41	0.01
distance protected areas + HF + hour + AC + distance population	9	3.45	0.01
biome + distance protected areas + forest + HF + hour + AC	13	3.53	0.01
HF + AC + distance population	6	3.63	0.01
crops + forest + AC	6	3.82	0.01
crops + distance protected areas + forest + HF + AC + distance population	9	3.90	0.01
forest + AC + distance population	6	3.91	0.01
distance protected areas + forest + AC + distance population	7	3.92	0.01
crops + distance protected areas + HF + hour + AC + distance population	10	3.98	0.01

crops + forest + HF + AC	7	4.00	0.01
forest + HF + hour + AC	8	4.03	0.01
crops + hour + AC	7	4.17	0.01
distance protected areas + hour + AC + distance population	8	4.19	0.01
crops + HF + AC + distance population	7	4.21	0.01
crops + HF + hour + AC	8	4.22	0.01
hour + AC + distance population	7	4.31	0.01
crops + distance protected areas + forest + AC	7	4.49	0.01
forest + HF + AC + distance population	7	4.50	0.01
biome + crops + distance protected areas + HF + AC	11	4.55	0.01
forest + hour + AC	7	4.56	0.01
biome + distance protected areas + forest + HF + AC	11	4.59	0.01
biome + crops + distance protected areas + HF + hour + AC	13	4.75	0.01
biome + distance protected areas + HF + AC	10	4.83	0.01
crops + distance protected areas + hour + AC	8	4.86	0.01
biome + distance protected areas + HF + hour + AC	12	5.01	0.01

Models for the richness of parrots	**k**	**ΔAICc**	**w**
AC	4	0.00	0.10
hour + AC	6	0.71	0.07
crops + AC	5	1.66	0.04
distance protected areas + AC	5	1.83	0.04
forest + AC	5	1.92	0.04
HF + AC	5	1.96	0.04
AC + distance population	5	2.01	0.04
crops + hour + AC	7	2.46	0.03
hour + AC + distance population	7	2.68	0.03
forest + hour + AC	7	2.69	0.03
distance protected areas + hour + AC	7	2.69	0.03
HF + hour + AC	7	2.73	0.03
crops + distance protected areas + AC	6	3.53	0.02
crops + HF + AC	6	3.67	0.02
crops + AC + distance population	6	3.67	0.02
crops + forest + AC	6	3.67	0.02
distance protected areas + forest + AC	6	3.79	0.02
distance protected areas + AC + distance population	6	3.82	0.02
distance protected areas + HF + AC	6	3.84	0.02
forest + HF + AC	6	3.93	0.01
forest + AC + distance population	6	3.93	0.01
HF + AC + distance population	6	3.95	0.01
biome + AC	8	4.28	0.01
crops + hour + AC + distance population	8	4.40	0.01
crops + distance protected areas + hour + AC	8	4.46	0.01
crops + forest + hour + AC	8	4.46	0.01
crops + HF + hour + AC	8	4.47	0.01
distance protected areas + hour + AC + distance population	8	4.62	0.01
forest + hour + AC + distance population	8	4.63	0.01
HF + hour + AC + distance population	8	4.66	0.01
distance protected areas + forest + hour + AC	8	4.69	0.01

forest + HF + hour + AC	8	4.70	0.01
distance protected areas + HF + hour + AC	8	4.71	0.01
biome + hour + AC	10	4.83	0.01
crops + distance protected areas + AC + distance population	7	5.51	0.01
crops + distance protected areas + HF + AC	7	5.54	0.01
crops + distance protected areas + forest + AC	7	5.54	0.01
crops + HF + AC + distance population	7	5.67	0.01
crops + forest + HF + AC	7	5.68	0.01
crops + forest + AC + distance population	7	5.69	0.01
distance protected areas + forest + AC + distance population	7	5.77	0.01
distance protected areas + forest + HF + AC	7	5.80	0.01
distance protected areas + HF + AC + distance population	7	5.82	0.01
forest + HF + AC + distance population	7	5.93	0.01

Diagnostic tools provided by the DHARMa package in R (Hartig 2018) were used to evaluate the fit of the final models. DHARMa simulates quantile residuals from a fitted GLM or GLMM that are standardized to values between 0 and 1. For a correctly specified model, these residuals should have a uniform distribution regardless of the underlying model structure and can be interpreted similarly to residuals for linear models. The package includes statistical tests on the residuals to check for uniformity, overdispersion and zero inflation.

Figure 3.5.4.S1. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the presence of parrots at the patch-level along transects performed across Costa Rica. No significant problems were detected.

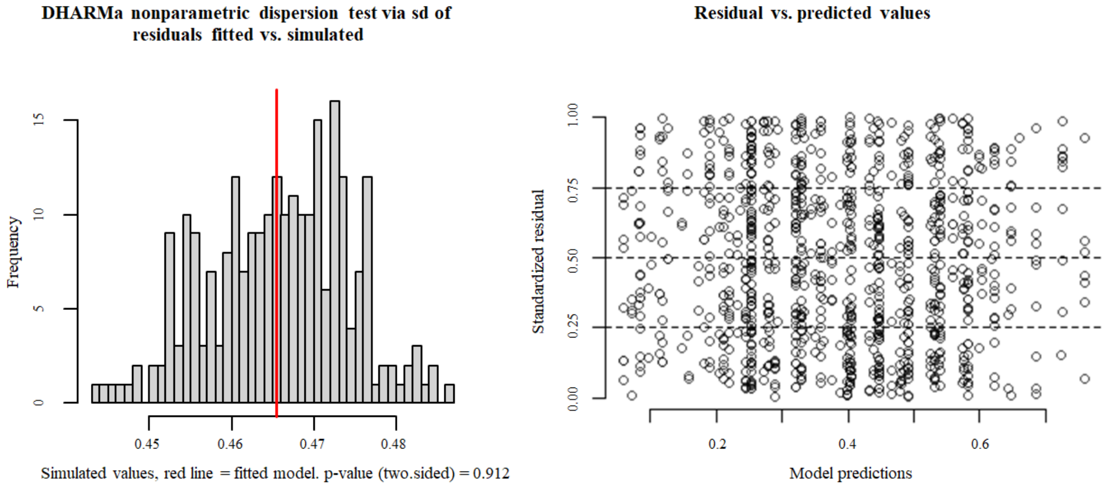


Figure 3.5.4.S2. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the abundance (number of individuals/km) of parrots at the patch-level along transects performed across Costa Rica. No significant problems were detected.

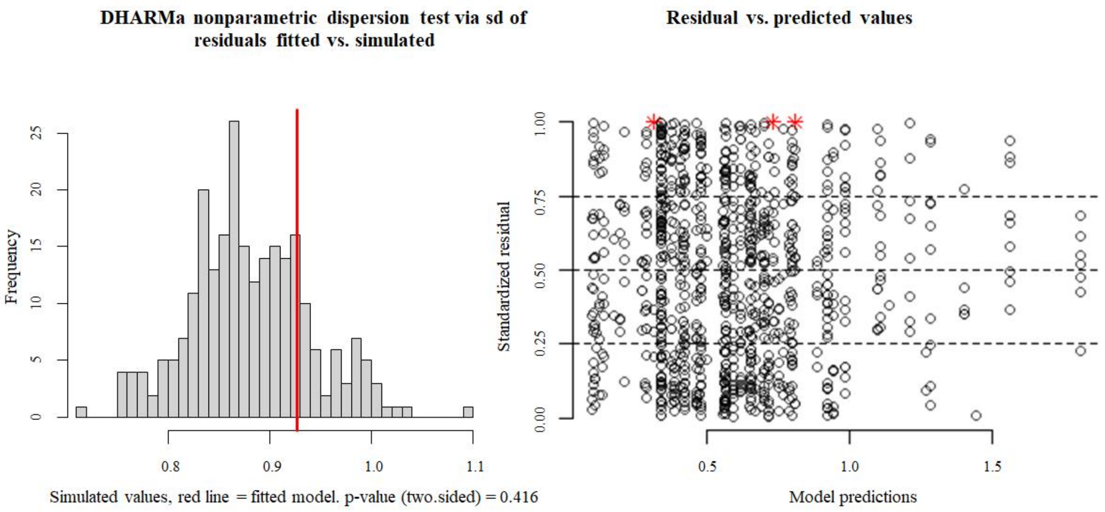


Figure 3.5.4.S3. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the richness (number of species/km) of parrots at the patch-level along transects performed across Costa Rica. No significant problems were detected.

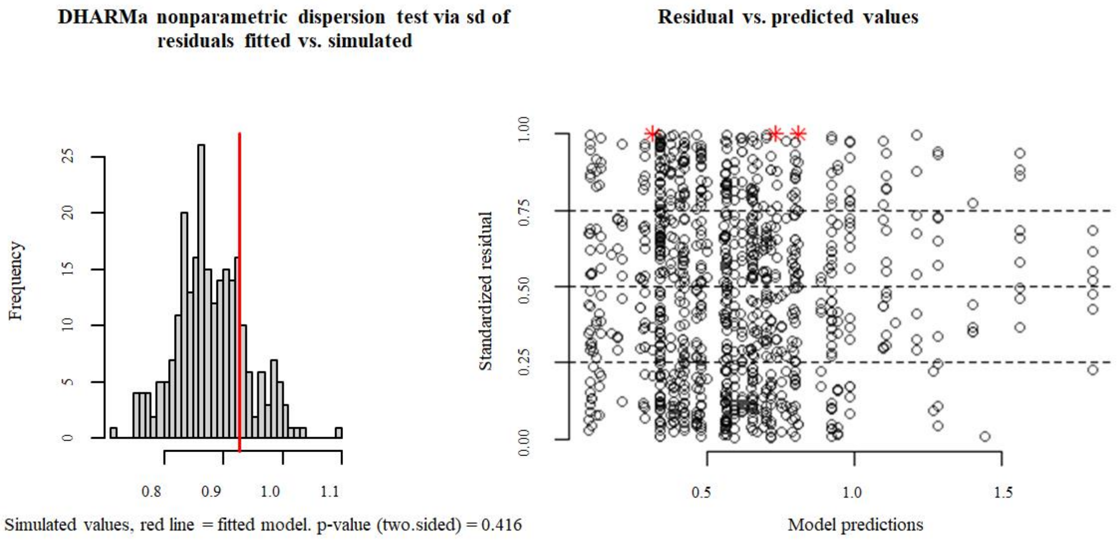


Figure 3.5.4.S4. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the presence of parrots in 1km radius around points distributed along transects performed across Costa Rica. No significant problems were detected.

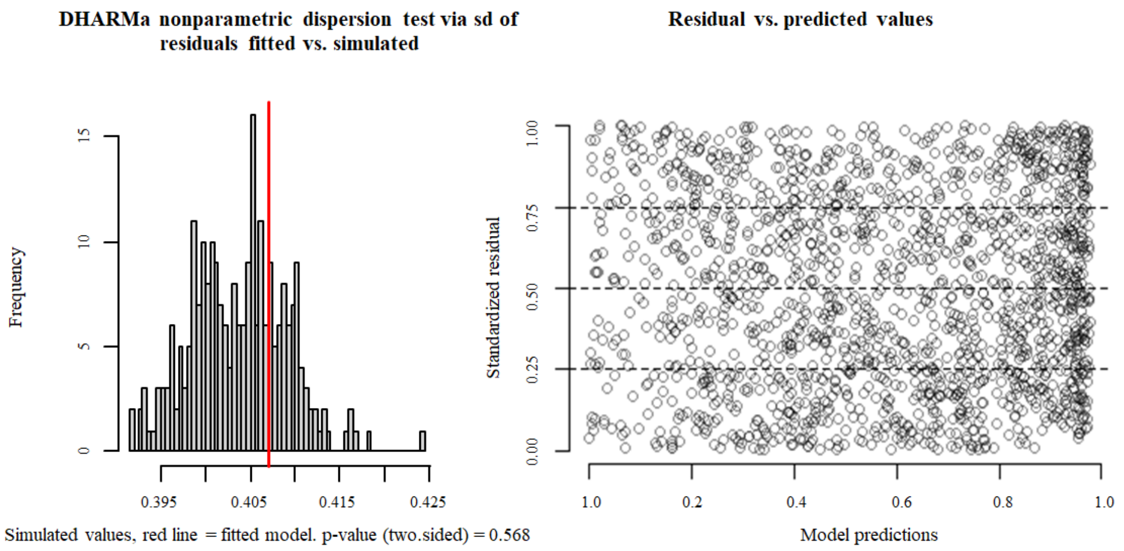


Figure 3.5.4.S5. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the abundance of parrots in 1km radius around points distributed along transects performed across Costa Rica. No significant problems were detected.

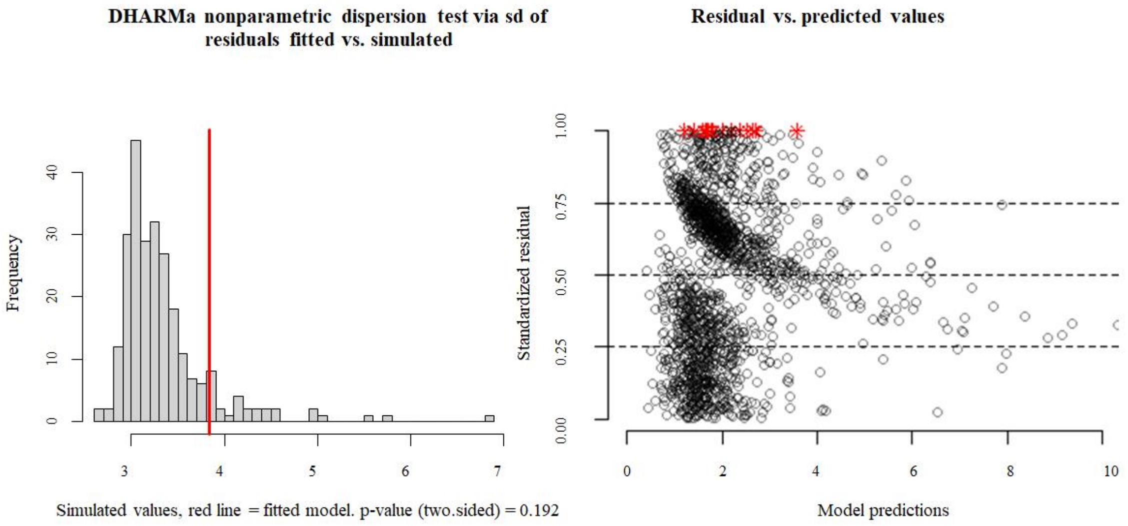


Figure3.5.4.S6. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the richness of parrots in 1km radius around points distributed along transects performed across Costa Rica. No significant problems were detected.

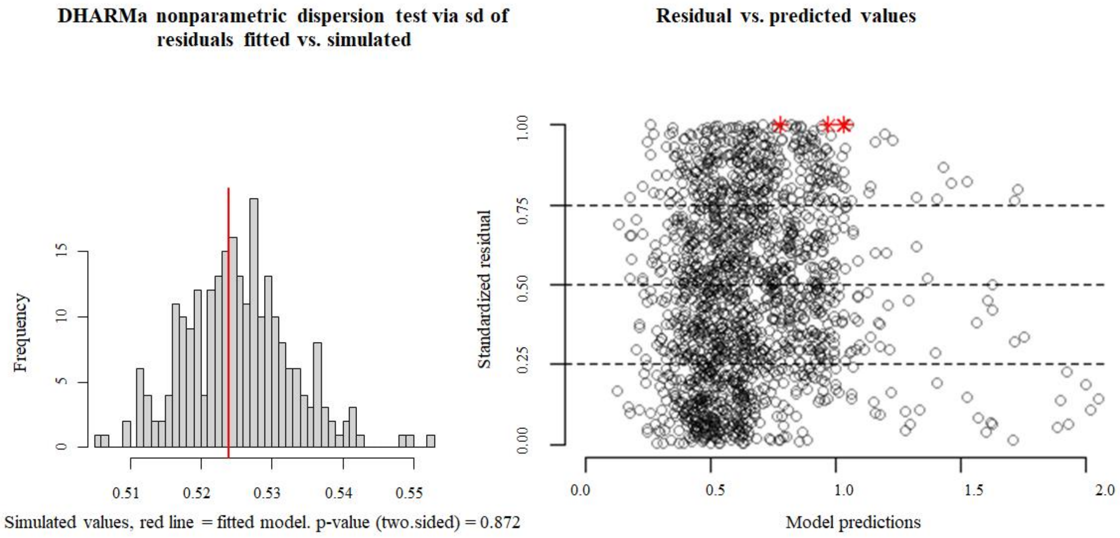


Figure 3.5.4.S7. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the presence of parrots in 5km radius around points distributed along transects performed across Costa Rica. No significant problems were detected.

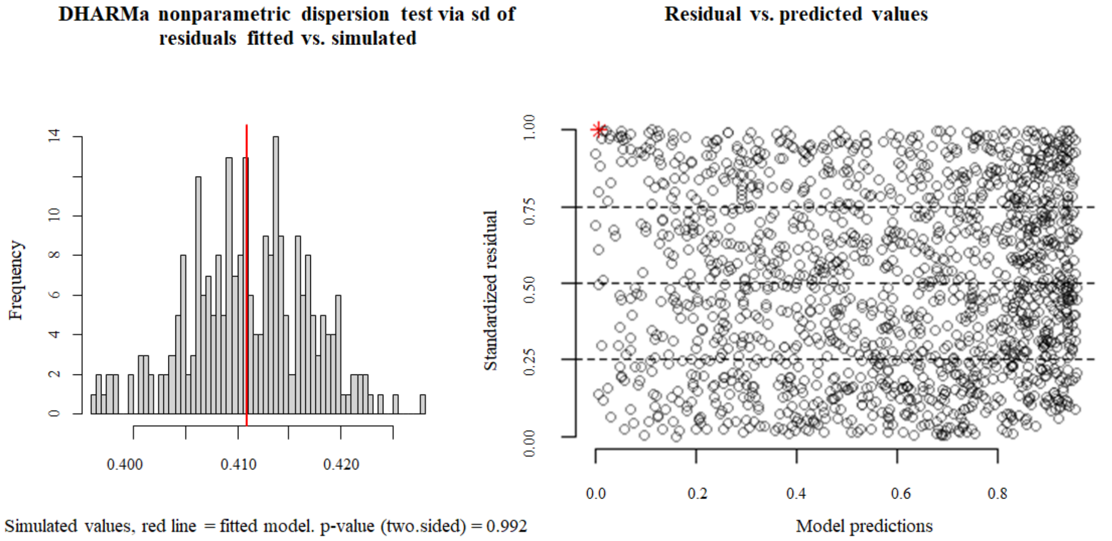


Figure 3.5.4.S8. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the abundance of parrots in 5km radius around points distributed along transects performed across Costa Rica. No significant problems were detected.

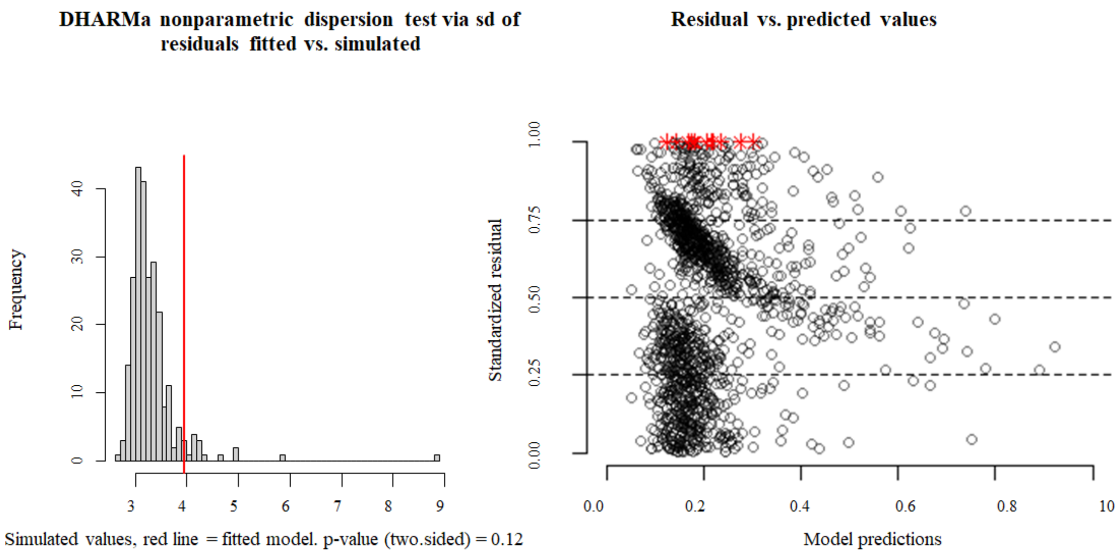


Figure 3.5.4.S9. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the richness of parrots in 5km radius around points distributed along transects performed across Costa Rica. No significant problems were detected.

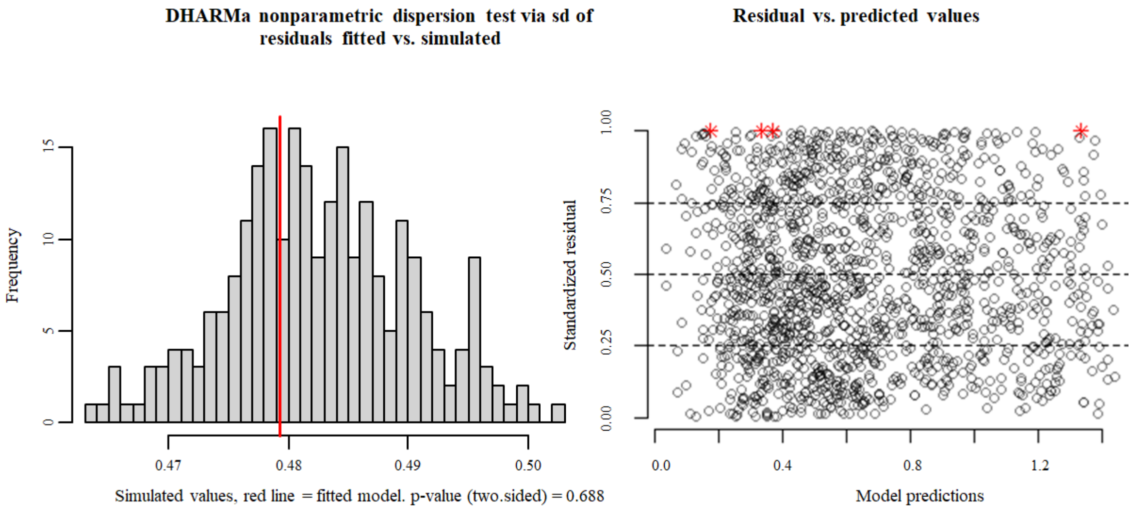


Figure 3.5.4.S10. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the presence of parrots in 10km radius around points distributed along transects performed across Costa Rica. No significant problems were detected.

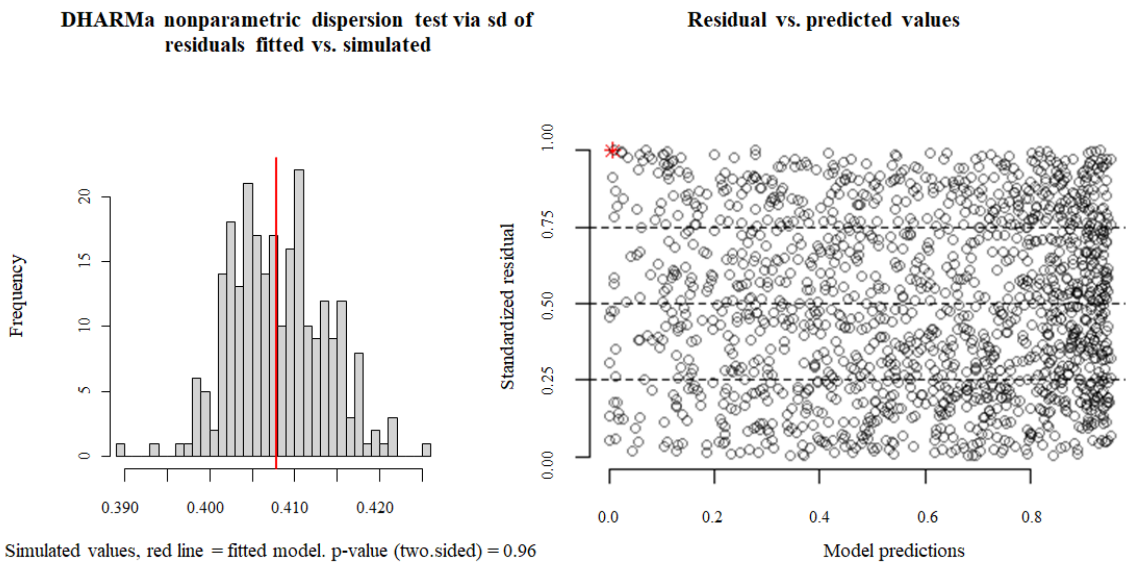


Figure 3.5.4.S11. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the abundance of parrots in 10km radius around points distributed along transects performed across Costa Rica. No significant problems were detected.

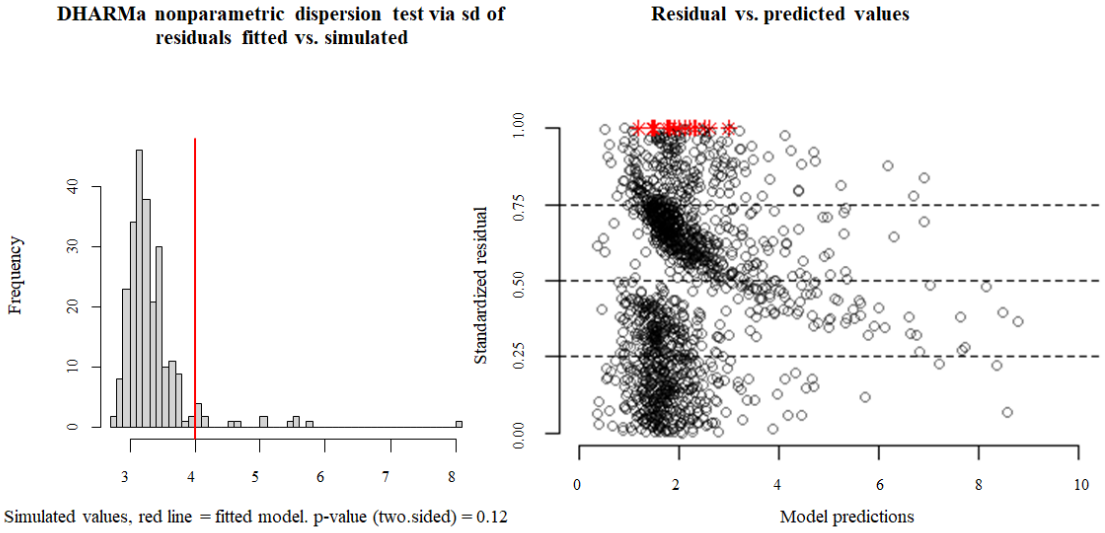


Figure 3.5.4.S12. Non-parametric dispersion test and standard residuals plots for the final models obtained to assess the effects of habitat alteration on the richness of parrots

in 10km radius around points distributed along transects performed across Costa Rica. No significant problems were detected.

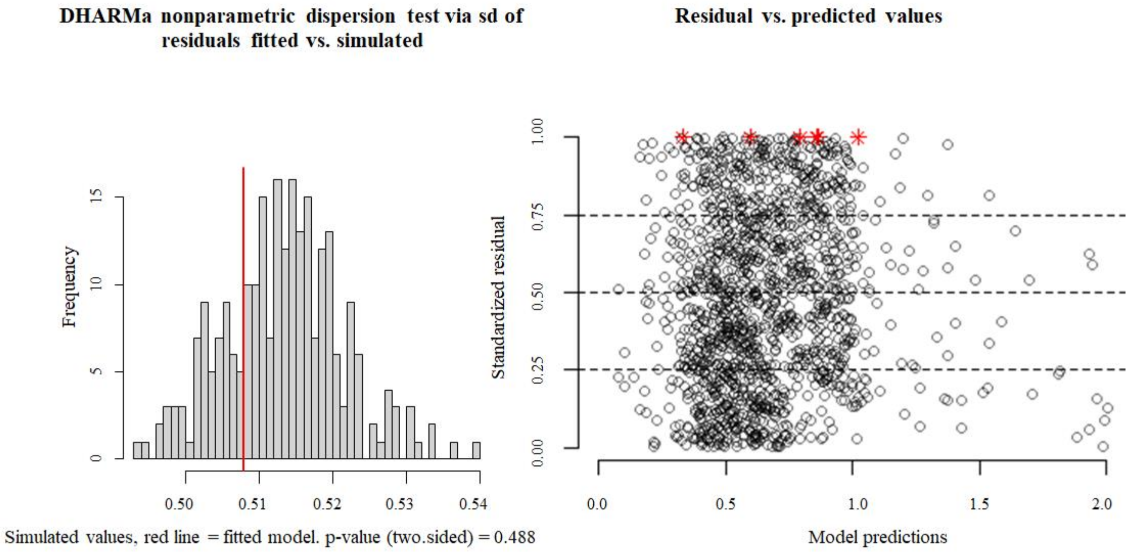
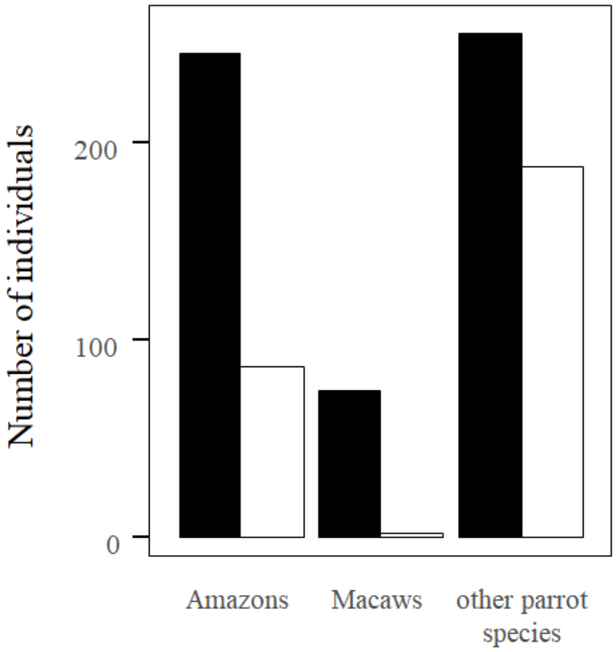


Figure 3.5.4.S13. Number of individuals detected as pets during our road surveys (white bars) and seizures carried out by the Costa Rican environmental police from 2011 to 2017 (black bars).



3.6 Results: Cities may save some threatened species but not their ecological functions

3.6.1 Habitat-related parrot abundances

Despite our large-scale roadside survey, covering 2,143.5 km, we only obtained 58 records of Hispaniolan parakeets and 18 records of Hispaniolan amazons throughout the country (Figure 2), totaling 438 and 71 individuals, respectively (Table 3.6.4.1). Most of the individuals were recorded in cities, where the largest relative abundances were obtained (Table 3.6.4.1). Only Hispaniolan amazons reached relative abundances close to that found in large cities in two natural habitats (tropical rain and dry forests, see table 3.6.4.1). Regarding the Jamaican parakeet, we only recorded this species through systematic roadside surveys in two localities of Sierra de Bahoruco (Figure 3.6.4.2), totaling 13 individuals. The scarcity of this species precluded an examination of its habitat-related abundances.

The low number of contacts obtained through the systematic roadside surveys in habitats other than cities (Table 3.6.4.1) led us to pool habitats into three categories for statistical analyses: 1) large cities, 2) rural habitats (grouping villages and farmland, i.e., a mosaic of small villages and houses embedded in agricultural lands), and 3) natural habitats (grouping coniferous, tropical rainforest and tropical dry forests) (see Methods). The models obtained showed a strong effect of habitat on the abundance of both wild Hispaniolan parakeets and amazons while controlling for the length of each sub-transect surveyed (Table 3.6.4.2). The resulting estimated marginal means indicate a very low abundance of both species in rural habitats, while their abundance was six times higher in cities than in natural habitats in the case of the Hispaniolan parakeet and three times higher in the case of the Hispaniolan amazon (Table 3.6.4.3).

We censused the urban communal roost of Hispaniolan parakeets in Santo Domingo found by one of the authors (AL) in 2016, and recorded 1,580 individuals at sunset. We could not find the urban communal roost for this species in Santiago, but we found a roost of Hispaniolan amazons with about 50 individuals. We were informed of only one communal roost in natural habitats, located in Sierra de Bahoruco, one of the best-preserved areas in the country, where we only counted 137 Hispaniolan parakeets, 15 Hispaniolan amazons and 7 Jamaican parakeets gathering together at sunset (Figure 2).

3.6.2 Conservation threats

Regarding the perception of local people of the threats and conservation status of parrots, people living in 12 distant villages located in natural areas said that parrots were abundant in the past but that they are currently extinct in their area due to overharvesting. They indicated that it is now necessary to travel to the most inaccessible sites within protected areas in order to view or poach parrots. Three people also living in distant natural areas indicated that hunting as a food source was the main cause of decline of parrots. They described how parakeets and amazons are considered game species (despite prohibition of this activity) and that large flocks were often hunted for food coinciding with the shooting of massive numbers of several species of pigeons. Moreover, one farmer explained how both parakeets and amazons are often killed to avoid crop damage, using guns and glue traps.

Regarding the illegal pet trade, we found 131 parrots in captivity (66 Hispaniolan parakeets, 63 Hispaniolan amazons, and 2 Jamaican parakeets; Figure 3.6.4.1) thanks to the help of 51 persons living in 20 different villages and cities. Owners knew that keeping wild parrots as pets is an illegal activity, so in all cases but one pets were hidden inside their homes. Our visual examination of the plumage and growth stage of these parrots allowed us to determine that most of them (74.8 %) were juvenile birds that were poached a few weeks or months prior to our visit. Attending to information provided by owners, the rest of the parrots were captured on average 4.4 years ago (range: 1 – 25 yr). They also informed us that most parrots were poached as chicks (96.7 %), often by cutting the nesting tree to gain access to the nest, while the rest were captured as adults using glue traps placed in crops. Parrot keepers also provided information on the areas where 110 parrots were poached. In most cases (95.45 %), parrots were poached within six protected areas (mostly in Bahoruco and Jaragua National Parks, 59% and 14% respectively) of the Dominican Republic, while four parrots were poached in the neighboring country (Haiti). Poached parrots were sold in the villages surrounding protected areas but also were transported to distant cities for sale in local markets. Pet owners said they prefer the Hispaniolan amazon over parakeets due to their ability to imitate human speech. This fact, together with the greater scarcity of amazons in the wild (see above), makes the average price of amazons indicated by pet owners (63.5 USD, range: 10.7 – 139 USD, n=45) twice as high as that of parakeets (31 USD, range: 10.7 – 64 USD, n=15), to the point that in two cases poachers sold very young parakeets as amazons.

3.6.3 Seed dispersal

We observed the three species of parrots feeding on a total of 19 plant species from 11 families of trees and palms, of which 14 species (74%) were dispersed by parrots by transporting fruits in their beaks to distant perching sites (Table 3.6.4.4). Five of the dispersed plant species were non-native to Hispaniola Island (Table 3.6.4.4). Given the scarcity of parrots in rural and natural habitats, all but one of the dispersal events was recorded in cities. We did not observe other species capable of dispersing these fruits through stomatochory in the urban areas surveyed. The structure of forested urban areas, urban parks and gardens mixed among buildings made it difficult to measure seed dispersal frequencies and exact dispersal distances (e.g., we could observe an amazon carrying a fruit in the beak but could not determine the exact tree from which the fruit was picked). We thus looked for trees in which both amazons and parakeets perched to handle and consume the fruits, and obtained minimum dispersal distances as the distance from each discarded seed to the nearest fruiting plant of the same species. In this way, we recorded 306 dispersed seeds under 66 perching sites, corresponding to 11 plant species (Figure 3.6.4.3). In 99.5% of the cases, undamaged mature seeds were discarded after pulp consumption by parrots, thus maintaining the potential for germination, with the rest being damaged or unripe seeds. The median minimum dispersal distance was 37 m (range: 8 – 155 m, Figure 3.6.4.3A). Most of the seeds (93.85%) were dispersed to minimum distances ranging between 20 and 60 m, while only a small fraction (4.85%) was dispersed > 60m (Figure 3.6.4.3A). Minimum dispersal distances varied among plant species (Figure 3.6.4.3B), but differences were not statistically significant (Kruskall-Wallis test, ϰ2 = 9.95 , df= 9, p = 0.35).

3.6.4 Tables and Figures

Table 3.6.4.1. Raw results of the roadside survey, showing the number of km surveyed in each habitat, the number of individuals (Nindiv), number of records (Nrec) and relative abundance (number of individuals / km surveyed) obtained for the Hispaniolan parakeet (*Psittacara chloropterus*) and Hispaniolan amazon (*Amazona ventralis*).

		P. chloropterus			***A. ventralis***		
Habitat	**km**	**Nindiv**	**Nrec**	**Indiv/km**	**Nindv**	**Nrec**	**Indiv/km**
City	370.34	262	38	0.70	25	10	0.06
Village	509.38	17	4	0.03	4	1	7.85x10-3
Farmland	375.39	12	1	0.03	1	1	$2.66x10^{-3}$
Coniferous forest	108.64	48	2	0.44	0	0	0.00
Tropical rain forest	314.46	70	10	0.22	19	3	0.06
Tropical dry forest	465.29	29	3	0.06	22	3	0.04
TOTAL	2143.5	438	58		71	18	

Table 3.6.4.2. Results of generalized linear models showing differences among habitats in the abundance of the two parrot species while controlling for the length (in km) of each subtransect.

	Estimate	**SE**	**95% CI**	**Wald χ^2**	**P**
P. chloropterus					
Intercept	-1.951	0.46	[-2.85, -1.05]	17.96	0.000
City	3.297	0.49	[2.33, 4.27]	44.50	0.000
Natural	1.542	0.50	[0.57, 2.52]	9.63	0.002
Rural	0	.	.	.	.
Subtransect length	.039	0.01	[0.03, 0.05]	40.28	0.000
A. ventralis					
Intercept	-3.625	0.53	[-4.67, -2.58]	45.93	0.000
City	3.008	0.59	[1.85 ,4.17]	25.79	0.000
Natural	2.023	0.56	[0.92, 3.12]	12.97	0.000
Rural	0	.	.	.	.
Subtransect length	0.031	0.01	[0.2, 0.05]	17.78	0.000

Table 3.6.4.3. Estimated marginal means obtained from generalized linear models (see Table 2) for the relative abundance (number of individuals / km) of each parrot species in different habitats.

	A.ventralis		***P.chloropterus***	
	mean	**95% CI**	**mean**	**95% CI**
city	0.096	0.056 - 0.164	0.718	0.471 - 1,096
natural	0.036	0.024 - 0.051	0.124	0.082 - 0.187
rural	0.004	0.001 - 0.012	0.027	0.011 - 0.064

Table 3.6.4.4. List of plant species and families of which we observed the three species of parrots consuming and dispersing fruits. Asterisks indicate non-native plant species.

		A.ventralis		**P.chloropterus**		**E.nana**	
Plant species	**Family**	**Consumed**	**Dispersed**	**Consumed**	**Dispersed**	**Consumed**	**Dispersed**
Simarouba glauca	Simaroubaceae					Yes	Yes
Adonidia merrillii*(Vitchia merrillii	Arecaceae			Yes	Yes		
Dypsis (Chrysalidocarpus) lutescens *	Arecaceae			Yes	Yes		
Prestoea acuminata	Arecaceae			Yes	Yes		
Roystonea (hispaniolana) borinquena	Arecaceae			Yes	Yes		
Sabal dominguensis	Arecaeae	Yes		Yes	Yes		
Coccoloba uvifera	Polygonaceae			Yes	Yes		
Inga ruiziana (Gina sp)	Leguminosae			Yes	Yes		
Pithecellobium dulce	Leguminosae	Yes					
Tamarindus indica*	Leguminosae			Yes	Yes		
Mangifera indica*	Anacardiaceae	Yes		Yes	Yes		
Sapindus saponaria	Sapindaceae			Yes	Yes		
Melicoccus bijugatus	Sapindaceae			Yes			
Terminalia catappa	Combretaceae			Yes	Yes		
Sideroxylon foetidissimum	Sapotaceae	Yes					
Azadirachta indica	Meliaceae	Yes	Yes	Yes			
Casuarina sp*	Casuarinaceae	Yes					
Araucaria heterophylla*	Araucariaceae			Yes			
Unknown	Unknown	Yes	Yes				

Figure 3.6.4.1. Three species of parrots occur in the Dominican Republic: A) the Hispaniolan amazon (*Amazona ventralis*), B) the Hispaniolan parakeet (*Psittacara chloropterus*), and C) the Jamaican parakeet (*Eupsittula nana*). The three species are illegally trapped for sale as pets (D, E and F, respectively). Photographs taken by A. Luna (A ,C ,F) and J.L. Tella (B, D, E).

Figure 3.6.4.2. A) Map of the Hispaniolan island including the roadside transects surveyed in Dominican Republic (black lines, totaling 2134.5 kms), the records of *Psittacara chloropterus* (white dots), *Amazona ventralis* (black triangles), both species together (black squares), and *Eupsittula nana* (asterisks). Numbers 1, 2 and 3 show the location of communal roosts. B) and C) show details for the main cities, Santiago and Santo Domingo, respectively. The main habitats depicted (agriculture, natural and urban areas) were obtained from the Caribbean Land Cover Project (https://lca.usgs.gov/carland/index.php).

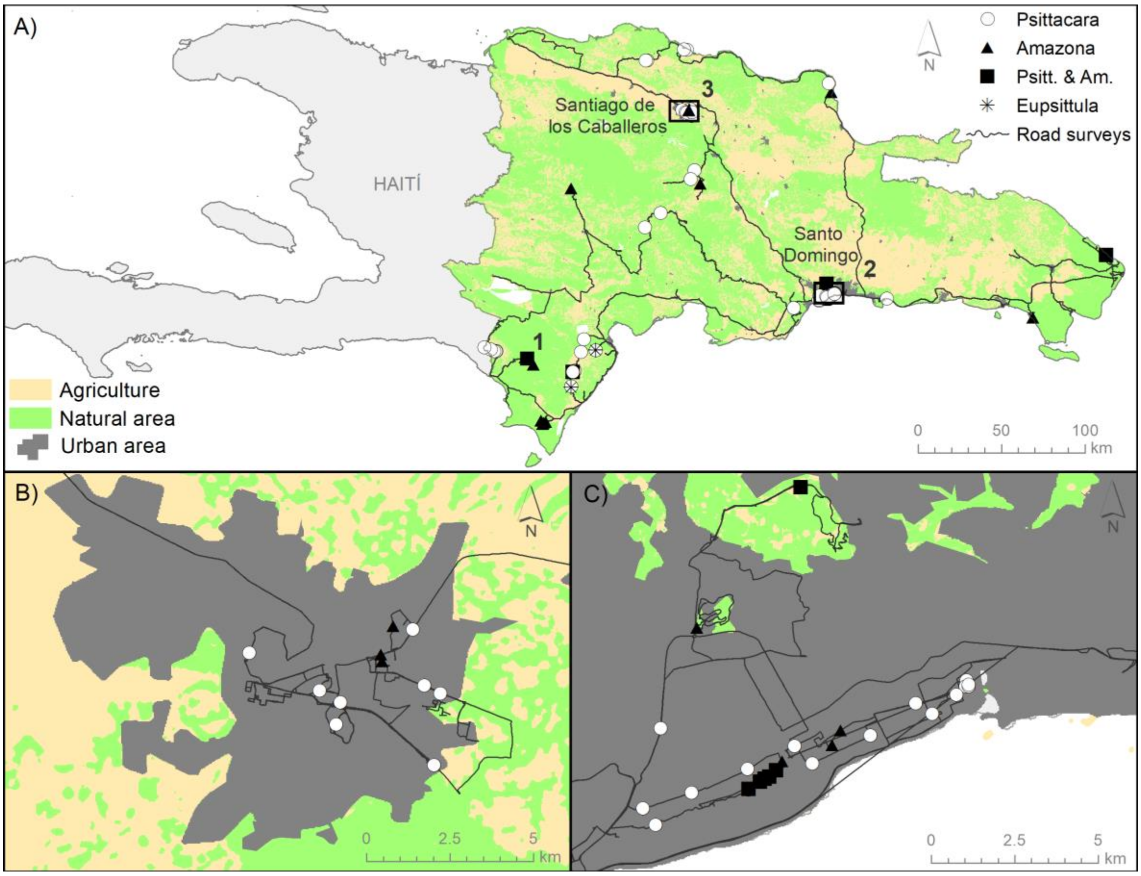
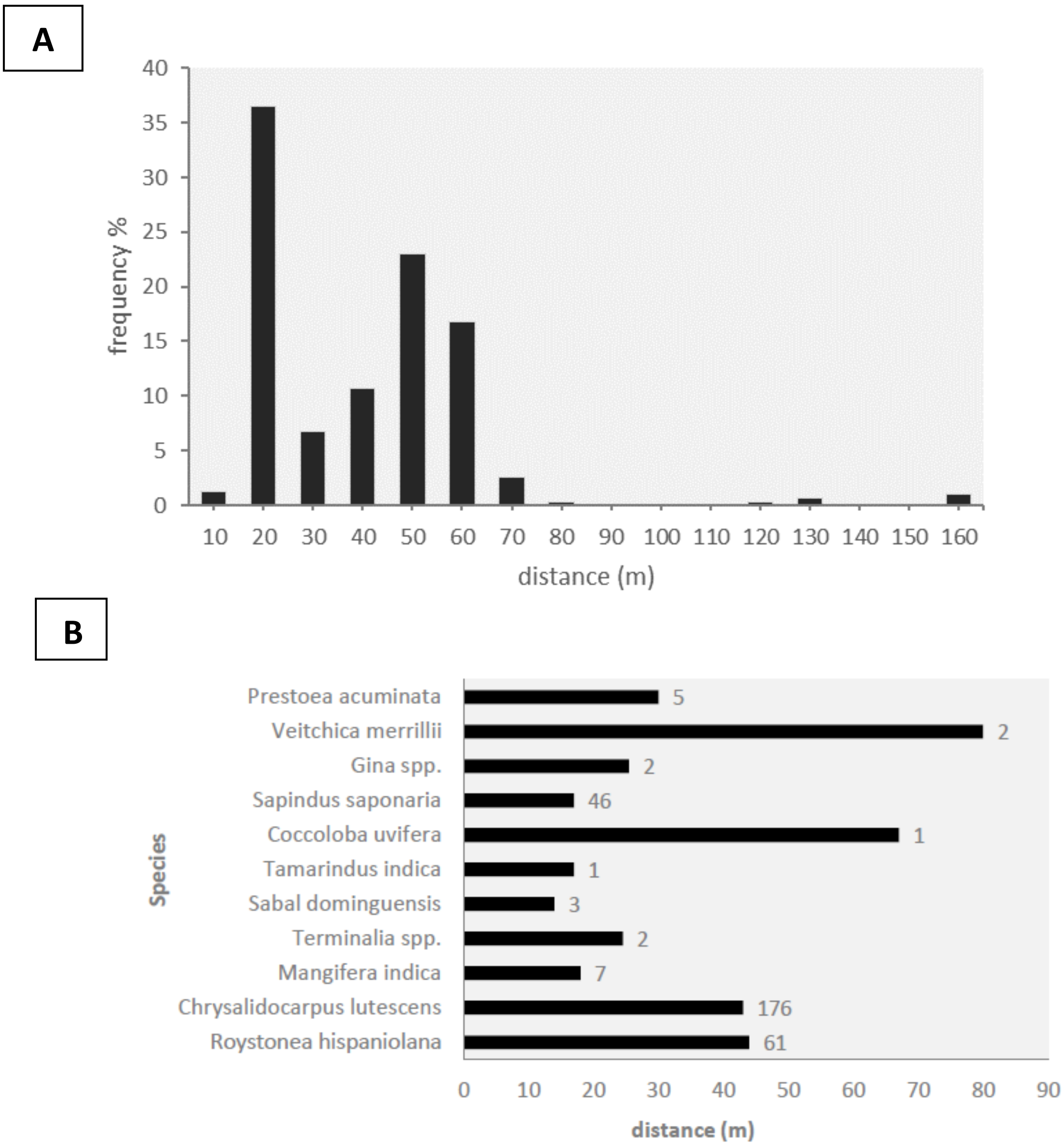


Figure 3.6.4.3. (A) Proportion of seeds dispersed by parrots (n = 306) grouped into ten-meter distance intervals. (B) Median dispersal distances for each plant species, with sample sizes indicated to the right of the bars.



3.7 Results: The widespread poaching of wild pets as an overlooked risk of zoonosis in the Neotropics

The maintenance of wild animals in captivity was so widespread and intense in the Neotropics that around 50% of asked people have or recently had or knew somebody that have a wild pet (Figure 3.7.1.1), and we documented up to 8,975 wild individuals from 252 species kept as household pets in the different countries. The vast majority of these pets were birds (8,861 individuals), mainly parrots (7,461 individuals), but also mammals (86 individuals), and reptiles (28 individuals). Most pets were captured and hold or bought locally (98.32%), although some individuals have been moved hundreds of kilometres after being bought at markets or to private buyers (1.68%). Wild pets are kept in houses under poor hygienic conditions, being in most cases in close contact with poultry and humans. Pets can be kept in cages placed in close contact with food or parts of the house as the dining room or bedrooms, or free inside and outside homes, even sharing food with eating people. Owners generally manipulate the pets with any hygienic measures, having food just after having the pets in their hands or even providing pieces of fruit from their own mouths (Figure 3.7.1.2b).

3.7.1 Tables and Figures

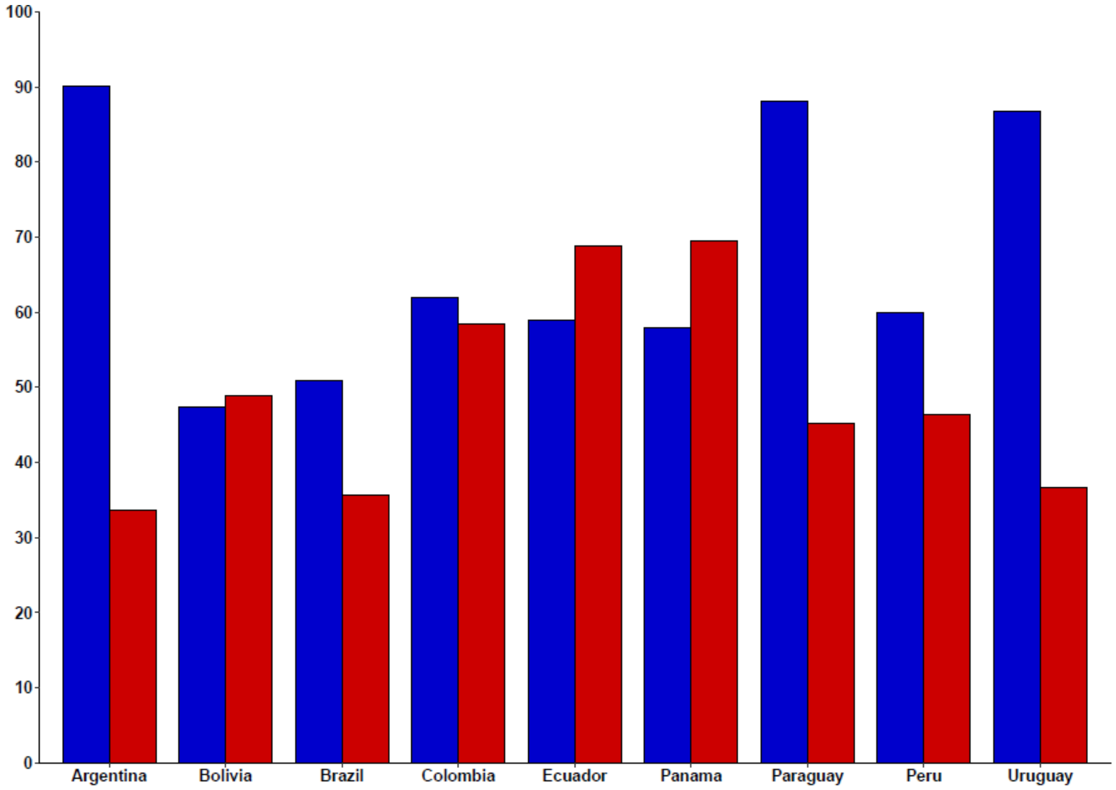


Figure 3.7.1.1. Proportion of interviewed people which acknowledge to have/had any wild pet (red bars) or to know somebody in the are who have/had any wild pet (blue bar).

Figure 3.7.1.2. Two Amazona auropalliata kept as pet together with poultry on a bar in Colombia (A). Several parrots kept as pet together with fruits on a market in Peru (B).

4. Discussion

Today, more than 90% of the parrot species are used as pets or for exhibitions (display) worldwide (IUCN 2020) mainly due to their ability to mimic the human voice (Silva, 2018) and colorful feathers (Tella and Hiraldo, 2014). However, our results show that parrots are not affected by their use as pets per se, coinciding with other authors (Olah et al., 2016), while illegal trade constitutes a main threatening factor for them worldwide, affecting more than 30% of species. The fact that most parrot species are successfully bred in captivity and the replacement of wild-caught by captive-bred individuals for international exports after CITES implementation (Cardador et al., 2019) may be the explanation for the lack of relation between the use of parrots as pets and their conservation status. In fact, the relationship between illegal trade and the conservation status of parrots is stronger when considering domestic illegal trade, showing the relevant threat that this activity represents for parrots worldwide.

The number of parrot species affected by illegal trade differs across regions. The Neotropical and Australasia regions show the highest number of species threatened by illegal trade, which is even higher for the Neotropics when scaled considering species richness. Keeping animals as pets is a rooted tradition in many areas (Ortiz-von Halle, 2018), especially the Neotropics, where only a few parrot species are bred in captivity (Daut et al., 2015) and their prices can exceed up to six times the price of wild ones (Cantú et al., 2007). The increment in human population size may even worsen the situation, explaining the existence of a “hotspot” of illegal trade in this area.

Domestic parrot poaching is still a poorly known activity. Estimating figures of poached parrots is challenging as this activity lacks organized networks, and an important part of individuals are kept as household pets or sold locally without entering the markets, making its control by authorities extremely difficult. This may be the reason why this activity was underestimated compared to international illegal trade, with far more records and registers of annual seizures. Moreover, the few estimates available were obtained from wildlife markets, and represent an insignificant percentage of the real figures (Gastañaga et al., 2011), as these data focus on big cities markets, excluding local markets and local trade which does not enter trade channels. An exhaustive survey conducted at the main wildlife market of Bolivia for 5 years, together with pet surveys conducted at 150 municipalities which are a common source for the parrots sold at this market, allowed us to estimate more accurate numbers for the annually poached parrots in this country. Our results are concerning and substantially larger than the estimated 80,000-90,000 individuals poached annually in Peru (Gastañaga et al., 2011). In fact, the number of parrots annually poached in Bolivia overpasses all the legal exports of wild-caught individuals and are remarkably higher than seizures of illegal exports recorded by CITES since the entry of the country in the convention.

The alarmingly large number of parrots poached annually in Bolivia seems to be related to the survival of these birds while in captivity. During our pet surveys, we constated that the median age of parrots kept in captivity was only 1 years, while dead parrots rounded 0.8. For species with enough data, we estimated the survival probabilities of individuals, obtaining a median survival age of 2 years. This high mortality rate forces the replacement of these pets once they are lost, making poaching an unsustainable activity in the long-term for most parrot populations in the country.

Another important gap regarding illegal domestic trade is whether this activity is opportunistic (i.e., focused on the most common and available species in the wild), as some studies on the wildlife criminology proposed (Pires and Clarke 2012, Pires), or directed towards certain species, which are preferred over others (Tella and Hiraldo, 2014). Studies conducted by criminologists, which suggest that poaching is an opportunistic activity, estimated parrot abundances in the wild using as proxies the number of years each species was allowed to be legally trapped (Pires and Clarke 2012) or their detectability based on field guides (Pires, 2015). Moreover, they also used univariate approaches, even after recognizing that a multivariate approach could lead to different results (Pires and Clarke 2012). Tella and Hiraldo (2014) analyzed the same data (Cantú et al., 2007) with a multivariate approach, finding that the most attractive species, according to their body size, coloration, and ability to mimic the human voice, were more poached than expected than their counterparts. These results, which depict completely different scenarios, could be also biased due to the use of poor proxies for the abundance of parrots in the wild and poaching pressure.

Our study conducted in Colombia helped to disentangle whether parrot poaching in the Neotropics is opportunistic or not, proving that this activity is directed towards certain species. Contrary to previous studies, we performed road-census surveys (Tella et al., 2013; Blanco et al., 2015; Tella et al., 2016; Baños-Villalba et al., 2017; Dénes et al., 2018; Blanco et al., 2020), which is the most direct way to actually estimate parrot abundances in the wild. Besides, our informal interviews conducted on 282 villages where we recorded 1,179 native parrots kept as pets allow us to assess poaching pressure. Finally, the use of an index such as the Savage Selectivity Index to quantitatively measure selection based on the availability of a resource (Manly et al.,

2007) allowed us to properly test whether a species is positive, negative or non-selected by people. Moreover, by exploring the relationship between poaching selection and parrot attractiveness, we were also able to show the drivers behind the positive selection toward species such as Amazons or Macaws.

Pires et al. (2016) and Pires (2015) found that most parrots sold at the main wildlife markets in Peru and Bolivia were poached within a radius of 250 km from these cities, with only a small percentage of individuals brought from larger distances. According to these results, they conclude that domestic trade is focused on the most available and common species and thus it has no impact on endangered and less abundant species (Pires, 2015). Performing market surveys in Peru, Daut et al. (2015) also observed that most of the parrots sold at wildlife markets belonged to species with quotas, so they considered that they are abundant and that this activity does not suppose a threat to parrot conservation. However, in this study, the authors observed that around 10% of the species sold at markets corresponded to endangered species. The fact that a proportion of parrots were moved across long distances and a significant percentage belonged to endangered species suggests that species attractiveness and people preferences could play a role in which species are traded in illegal markets.

To solve this question, we conducted a large-scale survey in Ecuador and Peru, covering more than XXX km. Applying the same methodology as in Colombia, we performed road-side census to estimate wild parrot abundances (Tella et al., 2013; Blanco et al., 2015; Tella et al., 2016; Baños-Villalba et al., 2017; Dénes et al., 2018; Blanco et al., 2020), and informal interviews in 198 localities distributed across all the study area. Besides, we calculate distances for each parrot found as a pet to their native range following the shortest path through the road-network. This approach allowed us to get a better image of the different scenarios of the pet trade in Peru and Ecuador. Our results confirmed that markets represented only a small proportion of the parrot trade in this area, with only 14% of parrots obtained by this mean and the rest poached by people for their own use as pets or to sell them in the same or close localities. This kind of trade was predominant in certain areas of Peru and Ecuador, as the area of Tumbes, whereas in Amazonia poached parrots remain locally or moved to different areas of the country. These parrots are usually sent to supply urban demand for parrots, following trade routes present in the area since pre-Columbian times (Guaman Poma de Ayala 1615) and observed as well in other taxa as primates (Shanee et al., 2017). As we observed in Colombia, there were important differences between species according to their selectivity index. Thus, Amazon and Macaw species were kept as pets more than expected according to their abundances, while other species more abundant were negatively selected. As we expected, preferred species were transported farther from their distribution range, being moved hundreds of km and even crossing to neighboring countries. However, once the individuals were moved from their distribution range, the distances were not explained by their selection index. Our conservative approach, measuring the closest and shortest path (while poachers could be using less transitable roads to minimize risks) and hypothetical native ranges (while we know by our census and informal conversations with locals that the species were absent from large areas in the wild, and therefore may have disappeared from those reflected in the IUCN maps) may be influencing this result.

The results obtained in Colombia and Peru represent an important difference from a conservation perspective regarding domestic parrot poaching. The fact that parrot poaching is non-opportunistic but an activity directed towards more attractive species (Pires and Clarke, 2012; Pires et al., 2016; Pires, 2015) poses a serious conservation problem. Positively selected species are caught disproportionally according to their abundance in the wild, and most of these species have already decreasing population trends or are threatened according to the IUCN (IUCN 2020). Preferred species can be moved far from their distribution ranges and even to neighboring countries, and therefore this selection may affect these species in different areas of their native ranges. The large distances at which these individuals are moved, combined with the fact that most of them are poached and sold locally and did not enter the markets indicate that local trade is more extended than previously thought and numbers obtained from markets, severely underestimated. The overharvesting of preferred species, which can be already rare or threatened by this or other factors, may drive them to a critical conservation status or even to the extinction in the wild, as has been already shown for some species in the Neotropics (Donald et al., 2010).

Habitat loss, especially land conversion for agriculture and logging, is often considered as one of the highest threats to parrot conservation (Olah et al., 2016). The fast conversion of forest into agricultural lands is considered as a driver of the negative population trends of parrots by reducing the availability of big trees for nesting (these species are obligate secondary cavity-nesters; Brightsmith, 2005). However, although poaching is a more unnoticeable activity compared with habitat loss, recent studies have proposed that illegal domestic trade may be as important as habitat loss in explaining the fast population declines experienced by certain parrot species (Dahlin et al., 2018; Dupin et al., 2020).

Our results from Costa Rica sheds light on the important role played by domestic trade compared to habitat loss. Costa Rica constitutes the forefront of tropical forest conservation and an important percentage of its territory is covered by protected areas (Robalino and Villalobos, 2015). However, habitat degradation was important in the past and continues to be important out and in the surroundings of protected areas (Sanchez-Azofeifa et al., 2001; Moran et al., 2019), whereas poachers still operate even inside protected areas (Molina-Murillo and Huson, 2014). Using large-scale surveys and remote sensing, we observed that parrot abundances were not affected by the degree of habitat transformation, even with higher abundances of individuals in villages than in more natural areas. However, pet-surveys and informal interviews with locals allowed us to identify 280 native parrots kept as pets in houses or local business. Savage Selectivity

Index demonstrates the strong selection towards *Amazona auropalliata* and Ara species (endangered in the country and even with specific recovery projects; Forbes, 2006; Brightsmith et al., 2005), which was even higher taking into account seizures data, showing the relevant threat that domestic poaching can possess to these species.

These results highlight the adaptability of parrots to habitat transformation, as proved by the high variety of species that can thrive well in highly transformed habitats, even cities (Lill, 2009; Davis et al., 2012; 2014; Tella et al., 2014). However, the results obtained for Costa Rica should be taken carefully, as this country does not show the same pattern of intensive agriculture shown by other Neotropical countries but a wide variety of croplands intercalated with forest patches (mosaic landscape; Soares-Filho et al., 2006). More intense habitat transformation may severely affect some species, which can not exploit these habitats, and therefore find their distribution ranges reduced to forestry patches. On the other hand, the intense poaching found during our survey reveals that despite the strong conservation measures present in the country (Quesada-Mateo and Solís-Rivera, 1990), this culturally rooted tradition represents a high threat for parrot conservation. Broader assessments on the impacts of habitat loss and poaching effects on Neotropical parrots are needed to better understand the relative importance of both factors at a higher scale.

Numerous species of parrots have populations living in highly human-modified areas, including cities (Lill, 2009; Davis et al., 2012; 2014; Tella et al., 2014). Thus, native and introduced populations can be found worldwide, becoming parrots a common sight in urban environments (Lever, 2005; Carrete et al., 2021). The fact that parrots can thrive in urban environments proofs the high adaptability of certain species to habitat alterations. Cities offer enough resources to allow parrots to develop their annual cycles, including predictable and abundant food (due to the high diversity of native and exotic plants), nesting and roosting sites (tree cavities and historic buildings), as well as a reduced predation pressure (Fitzsimons et al., 2003; Matuzak et al., 2008; Davis et al., 2012; Tella et al., 2014). The occupation of urban environments by several parrot species must be seen as an adaptative advantage for these species, which can expand their populations, and maybe induced by human pressure. Thus cities may act as a refuge for the negative effects of habitat loss or poaching present in more natural areas.

The case of the two endemic parrots of La Hispaniola Island (*Amazona ventralis* and *Psittacara chloropterus*) constitutes an example of cities acting as an urban refuge for parrots. These species, both endemic and listed as Vulnerable according to the IUCN Red List (IUCN 2020), have experienced a population decline as a direct consequence of habitat loss, and actual and historical hunting and trapping for the pet markets (Wiley & Kirwan, 2013; IUCN, 2020). Our large-scale survey on the country revealed the low densities of both species in their natural habitats, being significantly lower than congeneric species in other areas of the Neotropics (Blanco et al., 2015; Tella et al., 2016). Most observations have occurred in urban environments, where also the largest communal roosts were located. In rural areas, most people explained to us that both species have disappeared from most of the area and can only be seen nowadays in remote areas of nature reserves, a fact that we confirmed with our large-scale census. Illegal hunting and poaching seem to be the main drivers of this situation. In fact, habitat in several areas is still reasonably well preserved, and could no constitute an explanation for the low densities observed. In addition, we observed a high number of individuals of both species, mainly juveniles trapped a few weeks or months before our survey, kept as pets. These observations indicate the high trapping pressure suffered by the two endemic parrots, highlighting the key role played by cities in their conservation.

However, and although cities can act as a genetic stock for these endangered species, preserving urban populations but the ecological functions of a species can have loss lasting effect on the ecosystems. Parrots have several ecological functions that have been largely overlooked until recently (Blanco, Hiraldo & Tella, 2018), being considered just as seed predators. Nevertheless, parrots are effective long-distances dispersers of a wide variety of plant species with different seed sizes (Blanco et al., 2015; Blanco, Hiraldo & Tella, 2018; Tella et al., 2015, 2016a, 2016b; Baños-Villalba et al., 2017; Montesinos-Navarro et al., 2017). La Hispaniola island has a high variety of endemic plant species but a rather poor community of large fruit dispersers, formed by one trogon, two crows, and the two parrot species (Latta et al., 2006). Our results showed the capability of Amazona ventralis and Psittacara chloropterus as effective long-distance dispersers for a wide variety of plant species. However, all data were collected in urban parks and gardens, due to the low parrot densities in the natural habitats. The loss of these keystone species from the ecosystem can lead to declines in plant diversity (Cordeiro & Howe, 2003), seed recruitment (Terborgh et al., 2008), and gene flow between fragmented areas (González-Varo et al., 2017), with unknown ecological consequences (Blanco, Hiraldo & Tella, 2018). Finally, other ecological functions developed by parrots in other Neotropical areas, such as pollination or food facilitation, can have been also removed from La Hispaniola island with the confinement of these two parrot species to urban areas.

Domestic illegal trade constitutes a potential direct risk for Neotropical parrots, threatening their populations and leading several species to a critical situation. However, domestic illegal trade constitutes not only a serious issue for the conservation of this group itself but also a potential risk for human health (Chomel et al., 2007; Jones et al., 2008; Green et al., 2020). As an example, recent zoonotic outbreaks have been linked to bushmeat and wildlife trade practices (Woo et al., 2006; Edmunds et al., 2011; Olsen et al., 2006). Measures have been adopted at an international scale to control the introduction of wild-caught animals susceptible to carrying certain diseases (Morse et al., 2012; Daszak et al., 2020), as happened with the EU ban on 2005 to reduce the probability of Avian Flu transmission. Despite the existence of international regulations, individuals potentially carrying zoonoses are prone to enter through illegal international trade (REF). However, the high mortality rate associated (Thomsen et al., 1992) may change the original pool of individuals (Carrete et al., 2012; Baños-Villalba et al., 2020) minimizing the risk for introduced diseases (Colautti et al., 2004). On the other hand, wild-caught individuals which are kept as household pets closer to their native areas are expected to have lower mortality rates, increasing the probability of contact between infected individuals and poultry or humans.

The Neotropical area constitutes one of the expected hotspots for pathogens diversity prone to infect humans, as is strongly correlated with wildlife richness (Dunn et al., 2010). This region is experiencing a fast habitat loss and fragmentation process, which together with the increase of human population in these areas constitutes factors increasing the probability of spillover (Morse et al., 2012). Straight contact between wild-caught animals and poultry and humans is considered one of the main potential risks for cross-transmission, as proved by the several outbreaks arisen in the Asian wet markets (Woo et al., 2006; Edmunds et al., 2011). Neotropical markets are similar to Asian wet markets in the sense of the lack of hygienic conditions and straight contact between wild animals and poultry, so they represent a similar scenario for zoonoses spillover (Bodmer & Lozano, 2001; Pilco Lozano, 2012; Weston & Memon, 2009; Mendoza et al., 2014). On the other hand, most of the illegal trade at the domestic level in the Neotropics occurs at a more local scale, being widely distributed across the region. People has the tradition of keep wild animals in the houses in close contact with poultry or humans, acting as wet markets at a miniature scale across the all Neotropics, representing a perfect scenario for cross-transmission scenarios.

4.1 Captive breeding counteracts illegal trade as a major threat for parrots worldwide

When jointly analyzing the potential impacts of pet use and illegal trade, our results confirm that using parrots as pets is not a threatening factor, but highlights that illegal trade is a main factor affecting parrot conservation worldwide (Olah et al., 2016). The popularity achieved by these animals (Silva 2018), related to their colorful plumage and ability to mimic human voice (Tella & Hiraldo, 2014; Romero-Vidal et al., 2020), has motivated the use of 93.5% of parrot species as pets or display (exhibition) all across the world. However, while a significant proportion of parrots (31 %) are threatened worldwide by illegal trade, mainly Neotropical species, most pets belong to species successfully bred in captivity. The shifting from wild-sourced to predominantly captive-bred parrots on international exports, without increasing illegal trade, is the most suitable explanation for the lack of relation between the use of a parrot species as a pet and its conservation status. Thus, the use of a species as a pet or for display is not, per se, a factor of endangerment when done based on captive-bred individuals.

Trade on parrots greatly differs from other heavily traded taxa such as reptiles, where the trade of most species (>75 %) is not regulated by CITES and only 10% of them involve captive-bred individuals (Marshall et al., 2020). After the US and EU bans to the import of wild-caught birds, the captive breeding market has flourished (Cardador et al., 2019), built on stocked wild individuals from past international trade. Parrot breeders have successfully managed to breed 80% of all existing species, which has led to the replacement of millions of wild-caught birds by captive-bred ones in the international markets. Moreover, this replacement is much higher than that reported by CITES records. On the one hand, Inskip (1979) estimated that about 7.5 million wild-caught birds were annually traded worldwide in the 1970s, before CITES regulations. On the other hand, the actual volume of captive-bred traded parrots is also much higher than that reported by CITES. This is because four of the most commonly captive-bred and worldwide traded species (*Agapornis roseicollis*, *Melopsittacus undulatus*, *Nymphicus hollandicus*, and *Psittacula krameri*) are currently not listed in an appendix of CITES, and thus recording their exports is not required, and an important volume of captive-bred parrots is freely traded between EU countries (Cardador et al., 2019) without needing CITES authorizations.

Our results show that captive breeding is positively related to the conservation status of a species. Thus, captive breeding may help to halt the international trade of wild individuals in the long-term, relieving harvesting pressure on most parrot species. For example, wild-caught African grey parrots (encompassing both Psittacus species) were exported in high numbers (reaching several years > 50,000 individuals) before international bans (especially the EU ban). However, nowadays all legal exportations comprise captive-bred individuals and even exceed the annual numbers of previously exported wild-caught individuals. Upgrading the CITES status of the species (Appendix I) combined with captive breeding may relieve poaching pressure of their wild populations in a near future. Moreover, and contrary to previous concerns (Rivalan et al., 2007; Conrad, 2012), seizure data indicate that illegal international trade of parrots did not increase after trade bans nor after including African grey parrots in Appendix 1.

Despite the existence of a consolidated captive-bred market, the international illegal trade of certain parrot species still represents a serious conservation issue (Martin et al., 2018). Several species are not easily bred in captivity due to their small captive stocks, low reproductive rates, delayed maturity, or low survival prospects in captivity (Silva, 2018), causing rare species to enter international markets from illegal sources (e.g., Barbosa & Tella, 2019). Moreover, some highly-demanded species are subject to both legal and illegal trade, being even exported declared as captive-bred from countries lacking commercial-scale breeding facilities (BirdLife International, 2019). However, despite the negative effects posed by illegal international trade for certain species, domestic illegal trade is a more pervasive threat for parrots in certain regions (Berkunsky et al., 2017; Aloysius et al., 2020), showing large hotspots in the Neotropics. In this vast region, there is a rooted tradition to keep wild animals as pets, mainly parrots (Ortiz-von Halle, 2018; Romero-Vidal et al. 2020), and increments in human population size may have increased the volume of the illegal domestic trade to the point that tens of thousands of parrots are annually sold at illicit markets across the Neotropical region (e.g., Gastañaga et al., 2011; Daut et al. 2015; Pires et al., 2016). These figures underestimate the actual poaching pressure since a large, although still poorly known, proportion of parrots are caught by people living in rural areas to be kept as their own household pets or to be sold locally without entering markets (Romero-Vidal et al., 2020; Sánchez-Mercado et al., 2020; Biddle et al., 2021). This widespread poaching activity, in the absence of organized networks (Pires 2015; Romero-Vidal et al., 2020), makes the control of domestic illegal trade extremely difficult by authorities. Moreover, in these areas, captive breeding of native species is anecdotic, few exotic species are bred in captivity (Daut et al., 2015; Romero-Vidal et al., 2020), and their prices can exceed up to six times the prices of illegally caught parrots (Cantu et al. 2007). Together with law enforcement and awareness campaigns, promoting the breeding in captivity of exotic parrot species under strict sanitary controls to avoid the spread of diseases to native species could lower their prices and contribute to reducing the domestic illegal trade (Romero-Vidal et al., 2020).

Although difficult to separate from other potentially synergic threats such as habitat loss or direct prosecution (Olah et al., 2016; Olah et al., 2018; Berkunsky et al., 2017; Vergara-Tabares et al., 2020, Barbosa et al., 2021), illegal trade, mainly domestic illegal trade, represents a large problem for the conservation of parrots worldwide, mainly in the Neotropics. Comparative studies, based on field data, are needed to understand the relative contribution of these factors in the conservation status of parrots, establish effective actions and counteract the decreasing population trends experienced by the vast majority of parrots worldwide.

4.2 The hidden face of parrot poaching: local demand of pets largely outnumbers domestic and international trade on parrots

Daily surveys performed at Los Pozos market show the important role played by domestic illegal parrot trade in the Neotropics, shedding a figure of 375,000 parrots sold annually to fulfil the local pet demand of urban areas of Bolivia. Similar numbers arise from studies conducted in other main wildlife markets in the Neotropics, as in Peru or Brazil, with thousands of individuals sold each year (Gastañaga et al., 2011; Daut et al., 2015). However, pet surveys conducted across different municipalities which are common places of origin for the parrots sold in Los Pozos, allowed us to estimate that annual figures of Los Pozos market represents only 2.4% of the total poached parrots in the country, representing the astronomic figure of 1,5 million parrots poached each year.

Ages of dead, escaped or sold parrots provided by the owners during the informal interviews conducted in Bolivia allowed us to estimate a median survival age of 2 years. Having in mind that these values are underestimated, as most of the available data corresponds to long-live species (Young et al.), the real median value could be lower. In fact, median age of individuals dead, escaped or sold was 1, and 0.8 for individuals alive at the moment when surveys were carried, showing that most parrots detected during the surveys were recently obtained by the owners. The low survival probability observed may be due to the precarious conditions to which parrots are exposed, being poorly fed with inadequate food (human food remains, as chicken or rice; author observations) and being keep in a way that facilitates predation by domestic animals, as dogs or cats (19% of dead pets died because of dog/cat predation). Considering that most of the owners renovate their pets when their die, escape or are sold, according to informal interviews performed with local people, that almost 50% of the families had 2 or more pets, and that around 60% of interviewed people knows somebody who have/had native parrots as pets in the area, the turnover of parrots kept as pet in Bolivia is concerning.

The exhaustive sampling effort made at Los Pozos verifies that illegal domestic parrot trade constitutes a potential risk for parrot conservation, comparable to international trade. Moreover, the data obtained during pet surveys at different bolivian municipalities rises the alarm on an even more underestimated threat for Neotropical parrots, local poaching to supply local demand which does not enter the trade channels. The figures obtained for Bolivia in one year exceed by far the number of parrots traded at Los Pozos market in the 5-year period, but also the total figures of legal exports and confiscations for all history of Bolivia since CITES regulations come into force. The enormous number of parrots poached locally, together with the high turnover possess an important threat for several Neotropical parrot species, which are already under threat or with decreasing population trends due to other factors as habitat loss or transformation (Berkunsky et al., 2017; Vergara-Tabarés et al., 2020). Although the problem of international illegal trade should not be neglected, as still to represent a serious threat for certain taxa, focus should be put on domestic illegal trade and local poaching, before consequences are irreversible.

4.3 Opportunistic or Non-Random Wildlife Crime? Attractiveness rather than Abundance in the Wild Leads to Selective Parrot Poaching

4.3.1. Parrot Poaching Is not an Opportunistic, but a Selective Wildlife Crime

Wildlife trafficking is increasingly recognized as both a specialized area of organized crime and a significant threat to many plant and animal species (Maxwell et al., 2016; Sodhi et al., 2004; Ortiz-von Halle, 2018). However, due to its intrinsic illegal nature, it is difficult to fully know its actual extent and consequences for wildlife (Esmail et al., 2020; Tittensor et al., 2020]. Here, we provide the first reliable and simultaneous large-scale estimation of poaching pressure and abundance in the wild of a community of parrot species, showing that poachingof this taxonomic group is not opportunistic, but largely focused on species with particular traits that make them more attractive to people. Following the CRAVED model approach (Pires & Clarke, 2012), our data would have suggested that parrot poaching is an opportunistic crime, as the numbers of poached parrots per species positively correlates with numbers recorded in the wild (Kendall's Tau-b = 0.33, p = 0.018, N = 27). However, this slight trend, which is markedly influenced by two parakeet species (which jointly made up >80% and > 45% of the individuals recorded in the wild and as poached pets, respectively), turns out to be non-significant when they are removed from the analysis (Kendall's Tau-b = 0.23, p = 0.125, N = 25).

Moreover, as recognized by authors using the CRAVED model (Pires & Clarke, 2012), conclusions derived from simple univariate analyses could change when simultaneously testing the effects of other variables, such as species attractiveness in multivariate models. This possibility was later confirmed when reanalyzing the same parrot poaching data from Mexico using generalized linear models: attractive species were more poached than expected when controlling for the number of years they were allowed to be legally trapped (Tella & Hiraldo, 2014).

To identify selection, it is not only important to assess resource availability, but also be able to calculate its statistical significance. Here, we provide direct estimates of parrot availability and poaching and a key analytical advance, the application of the Savage selectivity index (Manly et al., 2007) to quantitatively measure poaching selection. To our knowledge, this is the first time that a selectivity index is used to statistically evaluate whether any given species is positively, negatively, or not selected at all. A further advantage of this index is that it can be used as a continuous response variable to ascertain drivers of poaching selection. In this sense, we found that 63% of the variance in parrot poaching selection is explained by the attractiveness of the species, thus confirming that poaching is not a taxonomically random, but a species-specific activity that preferentially focuses on the most attractive species for people (Tella & Hiraldo, 2014).

Attractiveness in this taxonomic group has been found related to body size and coloration, which determines for instance which species are kept in zoos (Frynta et al., 2010). Meanwhile, the ability to imitate human speech can be particularly appealing when parrots are kept as pets at close contact with people (Silva, 2018). Thus, the combination of these traits can describe species attractiveness and, therefore, predict their selection as pets and their prices (Tella & Hiraldo, 2014). As found in other countries (Tella & Hiraldo, 2014; Wright et al., 2001; Herrera & Hennessey, 2007), in Colombia macaws and amazons were much more expensive than other poached parrot species.

We also show that higher prices in the domestic pet trade are not related to the rarity of a species in the wild, but strongly related (65% of the variance explained) to its attractiveness. While both rarity and physical attractiveness influence the prices of internationally traded birds (Vall-llosera & Cassey, 2017), our results show that local demand focuses on attractive rather than on rare parrot species.

The quantitative measurement of poaching selection also allows deeper investigation of the unexpected preference of some species and additional cultural drivers of selection. For example, the high positive selection of the scarlet macaw *Ara macao* among Colombian people is surprising (Table 3.3.2), while its attractiveness is not much higher than that of similar macaw species (Figure 3.3.6). Local knowledge provided us with the answer: people explained to us that this species is sought after because its plumage resembles the Colombian national flag, hence its local name "guacamayo bandera" (flag macaw). Moreover, they also described that the Colombian guerrillas (revolutionary armed forces) persecuted its capture and use as pets because it was considered as unpatriotic; thus, poaching pressure on this species has increased since the guerrillas ceased their warlike activities. As this species became extremely rare because of overharvesting (Rodríguez-Mahecha & Hernández-Camacho, 2002), poachers seemed to switch efforts towards the similarly sized and colored green-winged macaw *Ara chloropterus* (Figure 3.3.6) as a substitute species, thus also explaining its outstanding selection (Table 3.3.2). Another case that merits attention is the positive selection of the blue-crowned parakeet *T. acuticaudatus* (Table 3.3.2), despite its low attractiveness rating (Figure 3.3.6). This species is restricted to very dry forests of the Guajira region, where the most preferred species such as macaws and amazons are absent (Rodríguez-Mahecha & Hernández-Camacho, 2002), and thus it is the largest and most colorful species available. Other potential covariates of poaching selection could be assessed in further studies, such as the accessibility of nests and life expectancy of parrot species as pets.

4.3.2. Conservation Implications of Selective Parrot Poaching

The colorful plumage of parrots and their ability to imitate human speech have made them highly popular as pets (Silva, 2018), thus leading to the international trade of at least 259 species of parrots, involving millions of individuals in recent decades (Bush et al., 2014; Beissinger & Bucher, 1992; Cardador et al., 2017]. In the near absence of long-term monitoring programs of wild populations (Marsden & Royle, 2015) and analyses of sustainable harvesting (Beissinger & Bucher, 1992; Valle et al., 2018), international trade of wild-caught individuals may constitute a threat to many parrot species worldwide (Tella & Hiraldo, 2014; Olah et al., 2016; IUCN, 2019). A concerning example is the African grey parrot *Psittacus erithacus*, considered the best at imitating human speech among all extant parrot species (Silva, 2018). Overharvesting due to trapping for the international trade has caused large range contractions and decimated the populations, to the point that the species was included in Appendix 1 of CITES in 2017, prohibiting international trade on wild specimens for commercial purposes, and was listed as globally Endangered by IUCN in 2018 (Martin, 2018). Although international bans have largely reduced the legal trade on parrots (Cardador et al., 2017; Cardador et al., 2019) and the upsurge of captive-breeding (Silva, 2018; Cardador et al., 2019) has reduced the demand of wild-caught traded birds, illegal trade is still active (Ribeiro et al., 2019), although at much lower volumes, including illegal trade on African grey parrots (Martin et al., 2019). Nonetheless, while international trade is a matter of concern, less attention has been paid to the conservation impact of domestic trade on parrots, even though it is known to occur in different regions of the world, such as Madagascar (Reuter et al., 2019), Asia (Sodhi et al., 2004), and all across the Neotropical region (Cantú et al., 2007; Luna et al., 2018; Ortiz-von Halle, 2018; Wright et al., 2001; Herrera & Hennessey, 2007; Regueira & Bernard, 2012; Alves et al., 2013; Daut et al., 2015; Biddle et al., 2020; Sánchez-Mercado et al., 2020). Due to its illegal nature, the true scale and impact of parrot poaching are often underestimated (Sodhi et al., 2004) and based mainly on counts from pet markets (Regueira & Bernard, 2012; Daut et al., 2015; Harris et al., 2015), government seizures, or other information sources difficult to verify (Cantú et al., 2007; Ortiz-von Halle, 2018; Regueira & Bernard, 2012).

In the Neotropics, expert knowledge indicated that 68% of the studied parrot populations are threatened due to their capture for the domestic pet trade (Berkunsy et al., 2017). However, it is unknown whether and to what extent poaching threatens these species differentially. Based on conclusions obtained through the CRAVED model, parrot poaching would mostly affect common species the most, thus aleviating concerns on its conservation impacts (Pires & Clarke, 2012; Pires, 2015; Pires & Moreto, 2011) since harvesting individuals of common species could be even considered as sustainable resource use (Daut et al., 2015; Robinson & Bennett, 2004; Fryxell et al., 2010). Our results lead to the opposite conclusion: the two most common species are poached half as much as expected based on their availability in the wild, while a few, highly attractive species are poached in larger numbers than expected according to their abundance and are likely to be overharvested. Pet owners indicated that these still abundant parakeets are poached as substitutes of more preferred species, when the former are not available because of their scarcity in the wild and/or their high prices. Therefore, our concern is not the absolute number of individuals poached of a given species but the proportion of the wild population size. In fact, the poaching of as few as 70 individuals per year constitutes a major threat to the Critically Endangered red siskin *Spinus cucullatus* in Venezuela (Sánchez-Mercado et al., 2020). The trade of some attractive parrot species has been shown to cause negative population trends and affect their conservation status (Tella & Hiraldo, 2014). A proper test of the overharvesting effects of parrot poaching would be to relate the selection on each species to their population trends. While detailed information on population trends is not available for Colombian parrots, they could be estimated through expert knowledge (Harris et al., 2015). However, there is evidence that poaching has caused large population declines and range contractions of the yellow-crowned amazon *Amazona ochrocephala*, considered as the species that best imitates human speech in Colombia (Rodríguez-Mahecha & Hernández-Camacho, 2002), and of the highly demanded scarlet macaw, while species we identified as less preferred or not selected at all by poachers have not suffered large declines in Colombia (Rodríguez-Mahecha & Hernández-Camacho, 2002). It is worth mentioning that the scarlet macaw was considered the most abundant macaw species in the region in the 1950s, in contrast with its current rarity (Rodríguez-Mahecha & Hernández-Camacho, 2002; this study).

Although adult parrots are also eventually trapped (Pires et al., 2018), parrot poaching mostly focuses on nestlings (Wright et al., 2001; Pires et al., 2018; Carrascal et al., 2013) as hand-reared chicks make better pets than birds caught as adults in terms of docility and ability to learn human speech (Silva, 2018). This has different implications on the population dynamics of the poached species (Pires et al., 2018), as lifespan generally increases with the size of parrot species (Young et al., 2012). Nest poaching of the largest species like amazons and large macaws could alleviate concerns about its impact as they have the longest lifespans among parrots (at least 34-63 years in captivity; Young et al., 2012), and thus small reductions in their breeding success due to poaching could have less impact on their population dynamics compared to small, short-lived species. However, we learned from local people that the last remaining nests of the preferred amazon and macaw species are located and poached year after year, often for decades. Indeed, local poachers compete for the same nests to the point that nests are surveyed daily to avoid robbing by others. Therefore, breeding pairs may occupy the same areas for decades, giving the wrong impression of apparent population stability to local people acting as regular or occasional poachers, birdwatchers, and wildlife managers. Ultimately, if current poaching pressure is not halted, the remaining populations will collapse due to the senescence and death of breeding adults in the absence of population recruitment.

4.3.3. Ecological Implications of Selective Parrot Poaching

Selective parrot poaching severely affects the conservation of the preferred species, as well as the ecosystem services they provide. Parrots have been long considered as plant antagonists, given their undoubted role as seed predators (Toft & Wright, 2015). However, they also provide several ecological functions (Blanco et al., 2018) within an antagonist-mutualism continuum (Montesinos-Navarro et al., 2017). Particularly, parrots can act as effective seed dispersers through complementary mechanisms, such as stomatochory (Baños-Villalba et al., 2017; Luna et al., 2018; Tella et al., 2015; Tella et al., 2019; Blanco et al., 2019; Tella et al., 2020), endozoochory (Blanco et al., 2020; Blanco et al., 2017; Bravo et al., 2020), and epizoochory (Hernández-Brito et al., 2021), further facilitating secondary seed dispersal by a variety of other species (Sebastián-González et al., 2019). Altogether, they may play an important role in the structure of networks, communities, and ecosystems (Blanco et al., 2015; Baños-Villalba et al., 2017; Montesinos-Navarro et al., 2017). Poaching reduces the population size of parrots, thereby quantitatively reducing and threatening their ecological functions. In fact, the selective poaching of the largest species (amazons and macaws) may have the strongest impact, as these species are the main—and sometimes the only—effective long-distance seed dispersers of palms and trees with large-sized fruits, which are biomass-dominant and key species in several ecosystems (Baños-Villalba et al., 2017; Tella et al., 2019; Blanco et al., 2019; Tella et al., 2020). The defaunation of these large-sized parrot species, which could be considered as megafauna attending to a new functional definition (Moleón et al., 2020), further reduces the dispersal of large-fruited plants that previously was only attributed to the decimated large-sized mammals and those extinct in the Pleistocene in South America (Blanco et al., 2019). The dispersal of some of these tree and palm species has already been disrupted after the large-scale extirpation and population declines of some amazon and macaw species (Tella et al., 2016; Barbosa & Tella, 2019).

4.3.4. Suggested Conservation Actions

Keeping parrots as pets in Colombia, as in other Neotropical countries, seems to be ancestrally rooted (Rodríguez-Mahecha & Hernández-Camacho, 2002). This cultural tradition could has been sustainable in the past but not today, given the large human population and economic power increase in recent decades (DANE, 2020). These two factors have increased the demand for pets while promoting habitat loss, also affecting parrot populations (Rodríguez-Mahecha & Hernández-Camacho, 2002). Therefore, conservation actions are urgently needed to halt parrot defaunation. Based on the conclusions derived from CRAVED model analyses, conservation actions should focus on the most heavily poached species by protecting and preventing poaching in their breeding areas (Pires & Clarke, 2012; Pires, 2015; Pires & Moreto, 2011). In Colombia, this would mostly apply to two parakeet species with a wide distribution (Rodríguez-Mahecha & Hernández-Camacho, 2002), thus making the protection of breeding sites unfeasible. Moreover, these species have large, non-threatened populations (Rodríguez-Mahecha & Hernández-Camacho, 2002), and thus their conservation should be not a priority. Our results on selective poaching provide a completely different conservation management scenario, as actions must focus on the most preferred, currently overexploited species. The protection of breeding sites to avoid nest poaching (Pires & Clarke, 2012; Pires, 2015; Pires & Moreto, 2011) may be efficient in the case of species with restricted breeding ranges (Tella et al., 2013; Barbosa & Tella, 2019; Brightsmith et al., 2008), but it is not feasible for Colombian macaws and amazons, with large distribution ranges and low population densities (Rodríguez-Mahecha & Hernández-Camacho, 2002; this study). The attraction of ecotourism and the creation of eco-lodges may increase local incomes and reduce poaching (Pires & Moreto, 2011), and favor research and the conservation of large parrots and macaws (Reuter et al., 2017). Colombia has great potential and should promote these conservation-friendly economic activities, but these local activities cannot prevent parrot poaching at a national scale. Paradoxically, in the absence of law enforcement in Colombia, we found tourist establishments displaying captive macaws to attract tourists.

As in other Neotropical countries (Reuter et al., 2017), we learnt from pet owners that parrot poaching in Colombia is generally not an organized crime, but is performed by local people to obtain their own pets or supply pets to neighbours and relatives. A large proportion of the population (c. 60%) is involved in the illegal activity of keeping native parrots as pets, often acting simultaneously as poachers and consumers, and this activity is widespread across the country. Law enforcement and reducing the demand are two strategies to reduce wildlife poaching that must be balanced in terms of cost-effectiveness, especially when conservation resources are limited (Holden et al., 2019). Police control should be strengthened to dissuade people from keeping pets at least of overexploited species, while educational campaigns for public awareness on the consequences of poaching should reduce the demand (Tella et al., 2013). Alternative sources can also be offered to satisfy the cultural tradition of owning pet parrots. Breeding parrots in captivity is well established (Silva, 2018), and can successfully supply the previous demand for internationally traded wild parrots (Cardador et al., 2019). Thus, breeding native parrots for local sale (Cantú et al., 2007) could reduce the pressure on wild populations. However, the low-reproductive rates of preferred species (amazons and macaws) in captivity (Silva, 2018) make it difficult to supply enough individuals and at prices low enough to counteract poaching. Moreover, this activity is prone to fraud, as chicks of preferred species could be poached and sold as captive-bred (see Nijman et al., 2018 for traded Asian songbirds). The genetic control of supposedly captive-bred individuals (Coetzer et al., 2017) requires great surveillance efforts, the development of genetic markers, and the availability of molecular laboratories

(Hogg et al., 2018), which are difficult to implement at a large scale in countries such as Colombia.

An alternative is to supply the pet demand with captive-bred exotic parrot species that are easier to reproduce (Silva, 2018), can be bought at competitive prices, and show low risks of invasion when they are accidentally released to the wild (Carrete & Tella, 2017; Abellán et al., 2017). A combination of these actions seems to have been successful at halting parrot poaching in a small Colombian region, within the Andean distribution of the yellow-eared parrot *Ognorhynchus icterotis*, a globally endangered species for which conservation programs and awareness campaigns were implemented over decades (Botero-Delgadillo & Páez, 2011). In this area, most people have non-native pet parrots, such as budgerigars *Melopsittacus undulatus*, cockatiels *Nymphicus hollandicus* and lovebirds *Agapornis spp*., often after the seizure of their native pets by the police, and are very aware of the illegal nature of this activity. Wildlife authorities should realize that law enforcement and demand reduction must be urgently extended to the whole country to avoid, at least, the predicted population collapse of overexploited species. Considering cost-effectiveness (Holden et al., 2019), law enforcement is probably the most effective action at a national scale, since police are widespread across the country and should simply apply current laws without the need for additional economic costs. However, the seizure of all parrot pets is unfeasible due to the economic costs of creating and maintaining wildlife rescue centers (Ortiz-von Halle, 2018; Carrascal et al., 2013) to hold them. In fact, seized birds are often returned to the wild to reduce costs and to create space for newly confiscated individuals, in the absence of reintroduction programs (Ortiz-von Halle, 2018). Thus, seizures should focus on overexploited species and should be combined with well-designed awareness campaigns (Botero-Delgadillo & Páez, 2011; Thomas-Walters et al., 2020) to reduce demand. On the other hand, captive breeding of exotic parrots to supply the demand should also be promoted, but under strict sanitary control, as exotic parrots can carry pathogens (e.g., Morinha et al., 2020) that could spread and negatively impact native populations.

4.3.5. Further Prospects for Assessing Selective Harvesting

Solving the dichotomy between opportunistic or selective poaching has profound conservation implications, since the overexploitation of preferred species may be causing their decline, pushing their populations toward regional (Tella & Hiraldo, 2014; Harris et al., 2015) and global (Nijman et al., 2018) extinctions. Several lines of evidence show that any form of harvesting (including legal fishing and hunting) is selective toward individuals of a certain sex, size, morphology, or behavior, with long-term population and evolutionary consequences [Harris et al., 2002; Coltman et al., 2003; Allendorf et al., 2008; Allendorf & Hard, 2009; Mysterud, 2011; Segura et al., 2019; Corlatti et al., 2019). However, to our knowledge, the hypothesis of selective harvest at the community level (i.e., on species with particular characteristics over others) has not yet been properly tested, mainly due to the difficulty of assessing their availability in the wild. The application of a selectivity index allows a quantitative measure and statistical test of harvesting selection in both intra- and interspecific studies. Therefore, it is a powerful tool for assessing selection and investigating the factors driving it, not only in other poached parrot communities and heavily traded birds, such as Asian songbirds (Harris et al., 2015; Nijman et al., 2018; Heinrich et al., 2020; Marshall et al., 2020), but also in other animal and plant species harvested, for example, through deforestation, fisheries, game hunting, or bush-meat exploitation.

4.4 Selective poaching as the main pet source in Peru and Ecuador: warns on the unsustainable domestic demand for preferred parrot species

4.4.1 Unraveling domestic illegal trade

Illegal pet trade is considered among the major threats for birds in the Neotropics (Dayer et al. 2020), and much information on species poached, their origin, and the actors involved in this activity came from the analysis of open-air markets in Peruvian cities (Gastañaga et al. 2011, Daut et al. 2015a, Pires 2015a, 2015b, Leberatto 2016a). Although extremely valuable, these studies lack a wider approach, which we overcome here by including a large scale census of household pets across small towns and rural areas in Peru and Southern Ecuador, showing a new scenario with different kinds of trade. Our results show that markets provide only a small fraction of pets (ca. 14%), whereas most of them were poached by pet owners or neighbours who sold the poached parrots in the same or close localities. This poaching and trade system predominates in the Andean valleys and the arid regions of Tumbes (Peru) and Guayas (Ecuador), and most poached parrots remain in the same areas. Contrarily, parrots poached in Amazonian areas inhabited by people remain as local pets but also are traded to other areas. Finally, we confirmed that parrots poached in remote Amazonian areas by indigenous people are transported by middlemen through rivers to the main Amazonian markets (González 2003). There, parrots are bought by local people, distributed to other villages, or transported to markets of coastal cities such as Lima to mostly supply the urban demand (very few parrots are redistributed from coastal urban areas to other urban areas). This domestic parrot trade has been documented in Peru since pre-Columbian times, following routes from Amazonian regions to Andean mountains or even coastal areas (Guaman Poma de Ayala 1615) similar to those reported nowadays for parrots and other traded taxa such as primates (Shanee et al., 2017).

4.4.2 Differences in poaching pressure and transport among species

Information obtained from illicit markets has built the idea that parrot poaching is an opportunistic activity mainly focused on common and non-threatened species (Leberatto 2016, Dayer et al. 2020, Pires 2015b, Daut et al 2015a). However, when measuring the relative abundance of species in the wild and as household pets, the scenario changes dramatically toward the selective poaching of the most attractive species (Romero-Vidal et al. 2020; present results). Amazon parrots and large macaws are the most preferred species due to their size, coloration, and mimicry ability (Tella & Hiraldo 2014, Romero-Vidal et al. 2020), and were poached much more than expected and reached higher prices than the rest of the species. The scarcity of preferred species often provokes their replacement by less attractive ones (Luna et al., 2018) such as small parakeets, which are locally abundant and more affordable. These species appear in larger numbers than preferred species both in our survey of household pets and in previous market surveys (Pires 2015a, Daut et al 2015), but much less than expected attending to their wild abundances. Moreover, some species are persecuted as crop pests (Barbosa et al. 2020) and thus are killed but also live-trapped for selling (Herrera and Hennessey 2008). We found that in the Andean valleys of Peru and Ecuador, where agriculture is the main subsistence economic activity (Quintana et al., 2019), some unattractive and common species are trapped by farmers both to protect their crops and get additional incomes by locally selling them as pets (author's pers. obs.).

Poached species were neither randomly transported. As we expected attending to their attractiveness (Tella & Hiraldo 2014, Romero-Vidal et al. 2020), preferred species were transported far from their distribution ranges, covering large distances and even crossing country boundaries. However, once moved from their distribution ranges, the distance at which preferred species were displaced was not explained by its selection index. This result can arise due to our conservative distance measurements. First, we measured the shortest distances through the whole road net, while traffickers could actually cover much longer distances through impassable roads to minimize seizure risks. Second, we measured the shortest road distances to the hypothetical distribution ranges of species, when we learned from our field surveys and conversations with people that the most preferred species are already absent from large areas due to overharvesting (Merkford et al. 2009), and thus their current distributions are different (i.e., constrained to more remote areas) than those reflected in IUCN maps.

4.4.3 Unsustainability of parrot poaching

Our survey increases previous concerns on the impacts of domestic parrot trade in the Neotropics (Wright et al. 2001; Berkunsky et al., 2017). By surveying rural areas, we found that 45% of surveyed people kept or have recently kept parrots as pets, most of them poached locally and only a small percentage bought in markets. Therefore, the tens of thousands of parrots sold in these markets (Pires et al. 2015a, Daut et al. 2015a) represent a small fraction of all parrots annually poached, even more taking into account the high mortality rates reported during harvesting (González 2003; Baños-Villalba et al. 2020).

Our results show that local poaching is widespread across Peru and Ecuador (see also Romero-Vidal et al. 2020 for Colombia) and that preferred species are demanded from areas far from their distribution ranges, with distances much larger than those previously estimated using straight-line buffers around markets (Pires et al 2015a). Therefore, selective poaching is not only affecting population trends of restricted-ranged endemics (*Ara ambiguus guayaquilensis*, *Amazona lilacina*; Biddle et al. 2020) but also of species with broad distributions given the large spatial scales of poaching and demand from farther areas. The effects of selective poaching of amazons and large macaws on their population trends are likely concomitant with habitat loss (Berkunsky et al. 2017), which causes the scarcity of large trees needed for nesting, and facilitates poaching by allowing the location of these nests easily. Moreover, the life-history traits of these species (i.e., longevity, low productivity, and large generation times, Romero-Vidal et al. 2020) make them particularly vulnerable to extinction, as shown for Amazonian mammals hunted for bushmeat in Peru (Bodmer et al. 1997). However, we did not find a relationship between poaching pressure (measure through the selectivity index of each species) and the global conservation status of the species may be due to the large –although wrong- distribution ranges of many of them that reduce their threatened status by the IUCN. This aspect should be urgently reviewed, given the unnoticed range contractions of most parrot species and the relationship between population decline and poaching reported here.

Concern should be also extended to the long-term sustainability of non-preferred, still common species. Peru has established harvest quotas for the legal international trade of some species, which varied with years attending to sustainability criteria (Salinas 2014). However, numbers of these species illegally sold in domestic markets largely exceed these quotas (Daut et al. 2015a) and are even higher when considering the large local poaching and trade in rural areas, out of markets. In fact, we have found that two of the species with harvest quotas are already poached more than expected attending to their abundance in the wild.

4.4.4 Challenging conservation actions

Although domestic wildlife trade is prohibited in all Neotropical countries since decades ago, parrot trade is still flourishing in large Peruvian cities (despite thousands of parrots are annually seized by authorities; Daut et al. 2015) and, to a lesser extent, in Ecuador (where law enforcement seems to be stronger; Mestanza-Ramón et al. 2020). Law enforcement is important to halt wildlife trade (Holden et al. 2019), and it can be effective mainly in large cities and when it is geographically predictable, such as happens with markets. However, our results show that local poaching and domestic trade are widespread in rural areas, where only a very small fraction of pet parrots come from markets. Pet keeping seems to be a rural tradition similar to bushmeat consumption, another harvesting activity that translates to cities, where it declines with urban development and generations (Chaves et al. 2020). This rooted tradition, together with the low investment and the high corruption in the governmental agencies (Daut et al. 2015b; Shanee et al. 2017), makes it extremely difficult to effectively prosecute illegal wildlife trade in rural areas. Moreover, the few rescue centers available are insufficient to hold all seized parrots (Leberatto 2016), so they are usually released by authorities into the wild without considering their condition, even potentially causing translocations to non-native ranges and disease transmission to wild populations (Daut et al. 2015). It is worth mentioning that several conservationist NGOs have been dealing with the pet trade, at least in Peru, but they share the general idea that poaching is not a conservation issue as it is mainly directed to common, more abundant species (Daut et al. 2015b). This perspective arises from their focus on city markets, which are a skewed sample of the actual pet trade, at least with parrots. Thus, government laxity is not counteracted by non-governmental organizations or the scientific community, which underestimate the role played by illegal pet trade on the long-term persistence of wild populations.

Several complementary actions are needed to reduce the parrot pet trade in Peru and Ecuador, which can be extended to other Neotropical countries that experience a similar situation. As for subsistence hunting (Bodmer and Pezo-Lozano 2001), which is often interconnected with domestic trade (Sánchez-Mercado et al. 2016), rural development actions to compensate for the economic benefits of parrot poaching should be put into practice. Ecotourism has proven to be effective in Peru (Brightsmith et al. 2006). In fact, most of the preferred parrot species we recorded in the wild were within or close to ecotourist and protected areas, and parrot poaching is reduced in areas under protection (Wright et al. 2001). Besides, programs to compensate for losses due to crop damage (Barbosa and Tella 2019) could also reduce trapping for trade as a by-product of parrot persecution. However, pet-keeping is a trans-cultural rooted tradition (Tella and Hiraldo 2014, Romero-Vidal et al. 2020) difficult to manage, so urgent actions directed at changing people behavior to reduce the demand for wild parrots, and wildlife in general, are needed (Dai and Zeng 2020; Sánchez-Mercado et al. 2020). Captive-bred exotic parrots could substitute native ones (Romero-Vidal et al. 2020) and a few species are yet widely available in large cities of Peru and Ecuador (Daut et al. 2015a; authors pers. obs.), although not in rural areas (based on our data, exotic parrots are only the 2% of all household pets). Though, these exotic species can spread several diseases such as the Beak and Feathers Disease Virus (BFDV), the Avian Polyomavirus (APV), the Avian Bornavirus (ABV), or the bacteria *Chlamydia psittaci*, which are among the most common infectious agents in captive parrots (Friend et al. 2001; Wellehan et al. 2016). Perhaps more efficiently, awareness campaigns should be promoted to reduce demand through cultural change in the medium-long term. For instance, schooling has proved to be effective to fight against wildlife hunting in the Bolivian Amazon (Luz et al. 2015). However, this may be a difficult task too. After three decades of closely working with communities to halt the illegal harvesting of a threatened amazon in Venezuela, Sánchez-Mercado et al. (2020) found that people negatively perceived selling but not poaching individuals for their personal use pets. Attending to this complex scenario, greater efforts on law enforcement and from the emerging field of conservation social science (Dayer et al. 2020) are urgently needed to reduce parrot overharvesting before the collapse of several species populations. These actions would also help to reduce the illegal trade of many other taxa (Shanee 2012, Daut et al. 2015a), as Peru and Ecuador are within the major global hotspots of wildlife trade worldwide (Scheffers et al. 2019).

4.5 Deforestation or overharvesting? Pet-keeping cultural burden rather than habitat transformation causes selective parrot defaunation in Costa Rica

Costa Rica has been at the forefront of tropical forest conservation and a large proportion of the country's land area is currently under some form of protection (Robalino and Villalobos, 2015). However, habitat transformation out of these protected areas is still important, whereas poaching by local communities (mainly illegal hunting for bushmeat but also market purposes) is a problem of great concern even within some protected areas (Molina-Murillo and Huson, 2014). Here, using field data, we assess the role played by habitat transformations and poaching on parrots, one of the groups of wild birds most appreciated as pets due to its colorful plumage and ability to imitate human speech (Grahl, 1990; Olah et al., 2016; Romero-Vidal et al., 2020). Our results show that while parrots seem to tolerate a rather high range of habitat transformations in Costa Rica, poaching is heavily affecting some particular species which, despite their rarity in the wild, are still kept in captivity as pets. This result is in line with previous findings showing that poaching for the local pet trade is a non-random but a species-specific, unsustainable activity that may be threatening parrots across their Neotropical distribution range (Berkunsky et al., 2017; Romero-Vidal et al., 2020).

4.5.1. Habitat characteristics and parrot communities

Habitat characteristics related to the degree of human transformation seem to not strongly affect parrot communities in Costa Rica. Moreover, in some biomes, the abundance and richness of species are even higher in villages than in more natural areas. Parrots are successful urban adaptors, with many species naturalized across the world living in cities (Lever, 2005; Carrete et al., 2021). In their native areas, there are also species which have expanded their range to make use of new food and nesting resources provided by urban areas, which are also used for communal roosting (Fitzsimons et al., 2003; Matuzak et al., 2008; Davis et al., 2012; Tella et al., 2014) or as refugees from overharvesting (Luna et al., 2018). This ability of parrots to thrive in human-modified habitats to exploit exotic and cultivated plant species is particularly important having in mind that large areas of the Neotropics are converted from native habitats to more transformed, humanized landscapes.

Intensive agriculture has been claimed as one of the main threats for avian communities in Costa Rica (Karp et al., 2012; Hendershot et al., 2020) and parrots, in general, in the Neotropics (Olah et al., 2016; Berkunsky et al., 2017). However, we did not find a significant effect of agriculture on parrot communities. This result should be carefully interpreted as these variables encompasses a wide variety of crops, some of which are highly used as food resources such as mangos. Moreover, most croplands crossed during our census were interspersed with forests, did not covering the so large areas typical of most intensive agricultural lands in South America (Soares-Filho et al., 2006). Parrots have high dispersal abilities, so even if not using these crops for feeding, they may cross them during their foraging trips (Karp et al., 2012). It is worth mentioning that in the few cases where large monocultures of banana, pine apple, oil palms and sugar cane were crossed, we did not count any parrot species. Moreover, at small spatial scales, we detected negative effects of the distance to populations, human offspring index, and forest cover, suggesting that parrots may be using with more intensity areas of intermediate levels of perturbation, typical of the periphery of small village. Besides, although we were not able to detect marked effects of agriculture on parrot communities, it is possible that the full effects of habitat conversion may not be realized for decades or centuries (Vellend et al., 2006; Gibson et al 2013; Essl et al., 2015) owing to, among others, extinction debts (Tilman et al., 1994; Hylander and Ehrlén, 2013).

Models performed to test the influence of habitat characteristics on parrot communities at the point-level showed a strong positive effect of the autocorrelation component, supporting a spatial aggregation of individuals and species that can arise from a combination of endogenous (e.g. dispersal, gregarious behaviour) and exogenous (e.g. aggregated environmental conditions) factors (Van Teeffelen and Ovaskainen, 2007). Parrots show complex social structures implying aggregation to forage and roost to reduce predation risk (Seibert, 2006; Salinas-Melgoza et al., 2013; Hobson et al., 2014). Habitat heterogeneity, clearance of forests, and human cultures (mainly exotic trees with fruits and seeds available in large quantities and during periods in which natural forest are less productive; Matuzak et al., 2008) may reinforce parrot tendency to aggregate (Gilardi and Munn, 1998; Salinas-Melgoza et al., 2013; Hobson et al., 2014), while nest-site availability may promote aggregation through different, complementary processes (Salinas-Melgoza et al., 2009; Lopes et al., 2018). On the one side, small parrot species can use a wide range of cavities, which may allow aggregation even when habitat is altered, while the largest species, mainly of the genus Ara and Amazona depend on big trees with specific cavities for nesting (Salinas-Melgoza et al., 2009; de la Parra-Martínez et al., 2015) that may be aggregated at large scale due to the patched distribution of well-conserved habitats with some large trees remaining.

Parrot presence, abundance, and richness were not affected by the distance to the nearest protected area. This result, which seems surprising at first glance, can be better understood when considering that most of the protected areas are located at montane highlands. Thus, despite the well-preserved forests of these areas (Sanchez-Azofeifa et al., 2001), the number of parrot species present at high elevation habitats (up to 1500 m) is reduced (Herzog et al., 2005; Rahbek, 1995), which explains the lower abundance and richness in the Highlands biome (Blake and Loiselle, 2000; Herzog et al., 2005).

4.5.2. Non-random poaching pressure of parrot species for the local pet trade

Our results suggest that habitat transformation by itself can hardly explain the marked decline experienced by some parrot species, which have been almost driven to extinction in Costa Rica (Brightsmith et al., 2005; Vaughan et al., 2005). Deforestation and selective logging of big trees may surely threaten parrot species by reducing the availability of breeding places and food sources (Cornelius et al., 2008; Maron, 2005). However, poaching has been very intense in Costa Rica in the past and is probably the main reason for the situation of highly preferred native species, such as Ara macao and A. ambiguus (Vaughan et al., 2005). Of greatest concern, our results from informal inquiries, and the reports of park guards and seizures (Vaughan et al., 2003; data shown here) point that poaching is still operating and can be the main determinant of parrot decline and extirpation from some areas.

Our data show that a large number of native parrots are illegally kept as pets throughout the country. However, poaching pressure is not taxonomically random but directed toward particular species, which show a high positive selectivity index. Understanding if poaching is species-specific (i.e., focused on species with particular characteristics) or opportunistic (i.e., taking advantage of the most abundant or easily available species) is key to derive conservation consequences. The most concerning situation involves the yellow-napped amazon, which has been frequently detected as pet but is present at worrying low abundances in the wild. Wright et al. (2018) have shown that populations of this species are very small and fast declining in the country, a tendency supported by our census data. However, it was the third most abundant species illegally kept in captivity, the fourth more confiscated by Costa Rican authorities, and the most geographically widespread pet, even though its native area is limited to the Tropical Dry forest (Forshaw, 2010; Wright et al., 2018). The ability to imitate human speech may make this species particularly appealing (Wright et al., 2018), as it has been shown for other amazon parrot species in Colombia (Romero-Vidal et al., 2020). In contrast, the orange-fronted parakeet was the most abundant species kept as a pet, and most individuals were located inside its distribution range, the Tropical Dry biome. This species often approach populated areas looking for food and suitable places to breed, so that they are easy to be caught by professional poachers and local people (Dahlin et al., 2018). Because it is relatively abundant in the wild according to our census, the selectivity index shows a negative Savage selectivity index indicating a lesser preference as a pet.

Although keeping parrots as pets is a widespread and illegal activity in Costa Rica, it is and has no strict control from governmental authorities. Indeed, most pets recorded during our fieldwork were exposed (64% of all pets detected) and could be easily detected from the streets or roads. People living closer to important touristic areas were more suspicious and reluctant to provide us information about parrots kept in captivity. However, the proportion of exposed pets, as well as their abundance and richness were not affected by the distance to the nearest protected area or the visitors they received. This suggest that the presence of environmental police in the surrounding of protected can persuade people to have the rarest species, such as macaws or amazons which are seized, but not other parrot species. Similarly, the number of tourists visiting these protected areas has a negative relationship with the Savage selectivity index of parrot species kept as pets, which could be related to the fact that more touristic areas have more police presence. As a consequence, people living close to touristic areas can avoid keeping parrot species that can be seized or are extremely reluctant to show them. In fact, almost all the people asked during our inquiries were worried about the danger of owning species such as macaws because of government control. Nevertheless, data supplied by environmental authorities for seven years of parrot confiscations showed that these species are still poached in high numbers across the country. Of special concern are some species such as the macaws or the yellow-napped amazon. While different conservation actions are performed for the macaws in Costa Rica (Vaughan, 2019), our results, other recent studies, and the last IUCN report (BirdLife International, 2017; Wright et al., 2018) indicate that the yellow-napped amazon is approaching a critical conservation situation requiring rapid actions by government authorities to avoid extinction due to the pet trade. It is very alarming that 50% of the roost counted by Wright et al. (2018) had less than 20 individuals and that in our census, comprising 539 kilometres of road survey inside its distribution area, we only recorded 22 individuals. Considering the low rates of reproduction of these species, the scarcity of available breeding sites and their delayed breeding (González, 2003; Snyder, 2000), halt poaching should be priority to attempt avoid the extinction of this species.

4.5.3. Synthesis and applications

Our results highlight the importance of defaunation through selective poaching for pets instead of habitat transformation as a main factor of endangerment for parrots in Costa Rica. Actions to effectively halt poaching should be urgently implemented. However, the rooted culture of having pets, in particular parrots, is widespread across many cultures. Pet-keeping has been found to be largely a product of social learning and imitation-based cultural evolution, which create the desire to live with specific types of animals (Herzog, 2014). Thus, it should be tackled using different fronts. On the one side, prosecution should be more effective, and not skewed towards certain species which may redirect people to keep others as pets. Complementarily, educational campaigns and local enhancement of people are also important (Sánchez-Mercado et al., 2020). To be more successful, these campaigns should not only ask people to simply stop keeping wild pets but include the promotion of acceptable alternatives (Thomas-Walters et al., 2020). In this sense, encouraging captive breeding of parrots can help suppling individuals for the local demand, reducing the pressure on wild populations. However, the low-reproductive rates of amazons and macaws, which are the most selected species, make it difficult to provide enough individuals and at prices low enough to counteract poaching. Moreover, chicks of preferred species could be poached and sold as captive bred, which could be extremely difficult to discern if not through complex genetic procedure difficult to monitor. Changing people preferences toward captive-bred exotic parrot species can be a good option to satisfy the local pet market. Some species are easy to reproduce (Silva, 2018) and can be bought at competitive prices. Importantly, these captive-bred individuals have a low risk of establishing invasive populations when accidentally released into the wild (Carrete and Tella, 2008; 2015; Abellán et al., 2017). All these actions combined have been successful at halting parrot poaching in a small Colombian region, within the Andean distribution of the yellow-eared parrot

Ognorhynchus icterotis (Botero-Delgadillo and Páez 2011), where most people now have non-native pet parrots, such as budgerigars Melopsittacus undulatus, cockatiels Nymphicus hollandicus and lovebirds Agapornis spp. Further efforts should be devoted to extend this experience to other Neotropical areas. In this regard, Costa Rica is a good candidate to prove the feasibility of these actions at relatively large spatial scales due to its compromises with biodiversity conservation.

4.6 Cities may save some threatened species but not their ecological functions

4.6.1. Large-scale parrot population declines

Our large-scale field survey, conducted at the end of the breeding season (Latta et al. 2006) when parrot population sizes are expected to be the largest due to the recent recruitment of fledglings, shows an extremely low abundance of the two parrot species endemic to Hispaniolan Island in their natural habitats. Their scarcity in the wild is striking when compared to the abundances of congeneric species we obtained following the same methodology in other Neotropical habitats. The relative abundance of Hispaniolan parakeets in natural habitats (Table 3) resulted one order of magnitude lower than that of blue-crowned parakeets (*Tecthocercus* (=*Psittacara*) *acuticaudatus*, with an abundance x47 times higher) and mitred parakeets (*Psittacara mitratus*, x25.8 times higher) in Bolivian Andean dry forests (Blanco et al. 2015), and white-eyed parakeets (*Psittacara leucophthalmus*, x57.8 times higher) in Brazilian Atlantic forests (Tella et al. 2016b). On the other hand, the relative abundance in natural habitats of the Hispaniolan amazon resulted one to two orders of magnitude lower than that of two amazon species also listed by IUCN as Vulnerable, the red-spectacled amazon (*Amazona pretrei*, x109 times higher) and the vinaceus amazon (*Amazona vinacea*, x23 times higher), in the Atlantic Brazilian forests (Tella et al. 2016b). Even the blue-fronted amazon (*Amazona aestiva*) living in the inter-Andean valleys of Bolivia, where populations are suffering from strong poaching pressure for the domestic pet trade (Pires et al. 2016), showed a relative abundance 3.3 times higher (Blanco et al. 2015) than the Hispaniolan amazon.

The current low abundance of Hispaniolan parrots cannot be attributed to island versus continental environmental conditions, as densities of bird species are often higher on islands than on the mainland (Newton 2003), but rather to a long-term process of human-induced population decline. Hispaniolan amazons and parakeets were known to form flocks of hundreds and thousands, respectively, until 1930, with the recent decline attributed to habitat loss, hunting and trapping for the pet trade (Latta et al. 2006). It is worth noting that the low abundances we obtained in natural habitats cannot be explained by habitat loss, since they were mostly obtained within protected and remote areas where the habitat still is reasonably well conserved. On the other hand, hunting and trapping have been at play for centuries. The Amerindians already trapped parrots for household pets and hunted them as they were highly appreciated as a food source, and Spanish colonists also hunted and traded parrots to the point of causing the extinction of one species (Wiley & Kirwan 2013).

As a matter of concern, hunting and trapping are still threatening parrot populations. Both species of parrots formed large flocks in the past that probably moved through the island while tracking food resources (Latta et al. 2006). According to our conversations with local people, they were often killed for food during the post-breeding season coinciding with the massive hunting of very large flocks of pigeons, which gathered in coniferous forests during pine fructification. The access to modern guns probably accelerated the decimation of both parrots and pigeons; in fact, we only observed seven of the ten pigeon species occurring in Hispaniola Island, and always in very low numbers. Moreover, the loss of natural habitats by agriculture may have increased crop damage by parrots and thus motivated the shooting and trapping of parrots in agricultural lands. This may explain their lowest abundance in rural habitats, despite the high food availability in the form of cereal crops and fruiting trees surrounding small villages.

Parrots are long-lived species with slow reproduction rates (Young et al. 2012), and thus the overharvesting of adults (through hunting and trapping) has a higher impact on population dynamics than nest poaching (Pires et al. 2016; Valle et al. 2018). Nest poaching to supply the pet trade has ancestral cultural roots in Hispaniola Island (Wiley & Kirwan 2013; White et al. 2011). However, the human population and economic growth in recent decades may have increased its intensity and contributed to the decimation of wild parrot populations. Information provided by local people supports the results of our field survey: they indicated local extinctions and population reductions in natural areas, with the last wild populations currently restricted to the protected and more inaccessible areas to which poachers are now forced to travel to obtain chicks for illegal trade. The fact that the pet trade is still a thriving activity, despite the rarity of parrots in the wild and its prohibition since 2000, may be explained both by cultural influences maintaining a high demand for pets (White et al. 2011) and by the lucrative benefits. Poachers may take risks since just two nests of amazons can yield monetary rewards equal to the average wage per month in the country (259 USD, http://www.salaryexplorer.com/salary-survey.php?loc=61&loctype=1#disabled).

Our baseline survey suggests that the conservation status of the endemic Hispaniolan parrots is worse than previously thought (Latta et al. 2006, BirdLife International 2016a, b), and that these species could enter a vortex of extinction in the wild if current threats are not halted. We hope this work will encourage further, more detailed conservation-aimed research on the remaining wild populations, as well as the enforcement of current laws against hunting and parrot poaching and the creation of education and conservation programs, ideally involving local residents (White et al., 2011).

4.6.2. Cities as conservation hotspots

The scarcity of Hispaniolan parrots in natural habitats contrasts with their relatively high abundances in the two larger cities. Parrots are known to be good natural colonizers of urban habitats (Carrete & Tella 2011), and the presence of urban parrots in the largest city (Santo Domingo) is known for at least three decades (Carlos Cano, com. pers. 2017). We found that cities offer sufficient resources, such as food (including a variety of native and exotic plants), nesting sites (cavities in trees and historic buildings) and safe roosting sites, allowing parrots to develop their complete annual cycles within urban areas. After initial urban colonization, ecological conditions differing between natural and urban habitats should explain the largest abundance of parrots in cities. Predation release (i.e., the generally lower abundance of avian predators in urban habitats, Díaz et al. 2013) has been shown to explain the positive population growth of a bird species in the city up to much higher densities than in the surrounding natural habitats (Rebolo-Ifrán et al. 2017). In the case of Hispaniolan parrots, the few avian predator species are scarce and mostly prey on small birds (Latta et al. 2006), and thus humans can be considered as the main "predators" of parrots through hunting and trapping of adults and nest poaching. These illegal activities are undoubtedly hampered in populated cities, where moreover people may be more prone to conserving parrots. The same predator-release mechanism could explain the proliferation in cities of an introduced exotic pigeon (Luna et al. 2018), in contrast to the poor conservation status of native pigeons due to hunting (Latta et al., 2006). In addition to natural colonization and intrinsic growth of predator-free urban populations, the release of parrots in cities may be reinforcing them; some pets could escape from cages, and 28 Hispaniolan parrots and 132 Hispaniolan parakeets seized by the police have been released in Santo Domingo since 2011 after being recovered in the city's zoo (Marielis Sánchez, com. pers. 2017).

Whatever the mechanisms for explaining urban parrot populations, large cities now constitute key conservation hotspots for these two endemic globally threatened parrots. Particularly, Santo Domingo could hold the largest world population of Hispaniolan parakeets, which we estimated at c. 1,600 individuals after censusing the only known communal roost that most likely concentrates all parakeets living in the city. As recently claimed for several threatened Australian species (Ives et al., 2016), national conservation policies should integrate urban populations when planning for and managing these threatened parrots. Conservationists and policymakers need to understand the opposing trends of natural and urban populations, since the flourishing urban populations may mask the poor conservation status of the species in the wild.

4.6.3. Conserving species and their ecological functions

The importance of not only saving species but also their ecological functions from extinction is gaining increasing support (Valiente-Banuet et al. 2015), to the point that some have claimed that rewilding management actions should include the introduction of non-native species that are functionally similar to extinct ones (Corlett 2016). The conservation value of some non-native urban populations of threatened parrots (Gibson & Yong 2017; Mori et al. 2017) has been recently highlighted, as they can be viewed as genetic and population stocks for conservation programs rather than just as invasive species (Gibson & Yong 2017). This is a valuable conservation argument but does not take into account that ecological functions of parrots may be lost in nature if they are confined to cities, both within and outside of their native ranges. This is likely because their ecological functions, other than their role as plant antagonists, have been largely overlooked until recently (Blanco et al. 2018).

Despite the short-term nature of our baseline survey, we were able to demonstrate that Hispaniolan parrots are legitimate long-distance seed dispersers of most of their food plant species, as they frequently transport fruits to distant perching trees where they discard undamaged seeds after fruit consumption. These results should be taken with caution, since most seed dispersal records were obtained from food plants growing in urban habitats. Unfortunately, to our knowledge there are no studies focusing on the diet and foraging behaviour of these species in the wild. However, it is reasonable to expect Hispaniolan parrots are also acting as frequent seed dispersers in natural habitats, as we have recently shown for other parrot-plant systems (Blanco et al. 20015, 2018; Tella et al. 2015, 2016a, 2016b; Baños-Villalba et al. 2017; Montesinos-Navarro et al. 2017). Notably, parrots are also covering an important ecological function in urban environments, but with the undesirable side effect of often spreading exotic plant species (see Table 4). On the other hand, it is worth noting that we only focused on the easily observed external dispersal (stomatochory), while internal dispersal through the ingestion and defecation of small viable seeds (endozoochory) is also expected to occur as in other parrot species (Blanco et al. 2016). Other mutualistic functions of Hispaniolan parrots can be also expected, such as pollination, food wastage that facilitates secondary dispersal and food for terrestrial animals, and the consumption of plant parasites (Montesinos-Navarro et al. 2017; Blanco et al. 2018).

Parrots have been shown to be key dispersers of some plant species in contrasting ecosystems (Boehning-Gaese et al. 1999; Blanco et al. 2015; Tella et al. 2016a, 2016b; Baños-Villalba et al. 2017), and their regional or global extinction may disrupt ecological processes with uncertain consequences (Blanco et al. 2018). One of the ecological functions most affected by the decline of plant-animal mutualisms is seed dispersal (Howe & Smallwood, 1982), in the way that the disruption of disperser-plant interactions can trigger declines in plant diversity (Cordeiro & Howe, 2003), seedling recruitment (Terborgh et al. 2008), and gene flow in fragmented landscapes (González-Varo et al. 2017). Disruptions of seed dispersal by habitat loss and defaunation can be more dramatic in the case of islands (Traveset et al. 2012; Fontúrbel et al. 2017), given a generally lower species diversity than in the mainland (Newton 2003) and thus a higher probability of losing functionally non-redundant species (Valiente-Banuet et al. 2015). In the case of Hispaniola Island, the only large-sized species feeding on fruits are one trogon and two crow species, which are scarce and threatened, while the rest are small passerines (Latta et. al 2006). These smaller-sized species are expected to only disperse tiny seeds through endozoochory, and thus parrots are probably the only species capable of dispersing the seeds of plants producing large fruits and seeds through stomatochory (see Blanco et al 2016). Therefore, the loss of rare species performing rare functions, as may be the case of Hispaniolan parrots, may have a stronger impact on ecosystem functioning (Violle et al. 2017). Unfortunately, the regional and global extinction of these parrot species are not a mere possibility, but a likely fact. Parrot populations began a strong decline in the Caribbean islands upon European colonization due to habitat loss, hunting and the pet trade (Wiley, 1991), to the point that endemic macaws inhabiting up to 11 islands were all extinct by the 1850s (Wiley & Kirwan 2013), as well as subspecies of the Hispaniolan parakeet endemic to Puerto Rico (by 1900), the Guadeloupe amazon (*Amazona violacea*) and the Martinique amazon (*Amazona martinicana*) were extinct as a result of hunting (by the end of the 18th century), while 10 out of the 13 extant Caribbean parrot species are globally threatened (IUCN 2017).

4.6.4. Conclusions

If current trends continue, approximately 5 billion of the world’s 8 billion residents will live in cities by 2030, with projections of nearly 6 million square kilometers of land converted to urban areas (Seto et al. 2012). This global urbanization process will increase the negative impacts on biodiversity through habitat loss (Seto et al. 2012; Newbold et al. 2015), but also the role of cities as conservation hotspots for a number of threatened species that perform better there than in their natural habitats (Rebolo-Ifrán et al. 2017). Our example using Hispaniolan parrots as a case study may reflect many others, currently overlooked or expected in the near future, given the widespread human impact on parrot populations through habitat loss and overharvesting (Tella & Hiraldo 2014; Olah et al. 2016; Berkunsky et al. 2017). On the other hand, the role of Hispaniolan parrots as seed dispersers should not come as a surprise, given the variety of ecological functions of parrots that have gone unrecognized until recently (Blanco et al. 2017). Therefore, although conservation planning should seriously consider the value of urban populations of parrots and many other threatened taxa (Ives et al. 2016; Gibson & Yong 2017), it should not distract efforts to restore their populations in natural habitats to conserve their ecological functions. In fact, the loss of ecosystem functions and services through local biodiversity loss should be given as much attention as the rate of species extinction in the current scenario of global change (Newbold et al. 2012).

4.7 The widespread poaching of wild pets as an overlooked risk of zoonosis in the Neotropics

4.7.1 Markets and people-to-people trade

Chinese wet markets exploded over social media after the emergence of different respiratory diseases in humans, mainly the current COVID-19 (SARS-CoV-2). However, wet markets are found all over the low and middle income countries. Millions of low-income households across Asia, Africa, India, and Latin America rely heavily on wet markets for affordable fresh food. Although it is not something that can be generalized, most wet markets in poor areas lack basic sanitary conditions to ensure the hygiene of food. A study of markets in Dhaka, Bangladesh, found that fecal bacteria from humans and animals were commonly detected on produce that is eaten raw, such as carrots and tomatoes (Harris et al., 2018). More concerning, some wet markets sell wild animals for meat or as pets. Buying, selling, and slaughtering wild animals for food is one way an animal-borne disease may infect people, and viruses can spread more easily if animals in markets are sick or kept in dirty, cramped conditions, such as in stacked cages. Animals, especially wild ones, can carry lots of diseases that are fatal to them but ineffective when they come into contact with humans. But once in a while, a virus would be able to mutate and ‘jump’ from one species to another—sometimes another animal, and sometimes a human (spillover). Therefore, many global health leaders advocate for bans on wildlife trading at wet markets as a defense against potential future zoonotic outbreaks. It is worth noting that most of these animals are illegally sold (national laws are prohibiting their capture, possession in captivity, and selling), so more than a ban what is needed is stronger controls.

In Neotropics, there are a large number of wildlife markets, especially in large cities and key areas where wildlife poaching is very intense (Herrera & Hennessey, 2007; Gastañaga et al. 2011; Pires & Clarke 2012; Regueira & Bernard, 2012; Daut et al., 2015; Shanee et al., 2017). Neotropical markets are quite similar to the Asian wet markets when applies to hygienic conditions (Weston & Memon, 2009) and wild animals are also sold for bushmeat consumption together with poultry or other human food (Bodmer & Lozano, 2001; Pilco Lozano, 2012; Mendoza et al., 2014). Moreover, large numbers of individuals are annually traded into these markets to supply the demand for pets. For instance, up to 50,000 birds were traded to a few markets of Brazil in just one year (Regueira & Bernard, 2012),around 24,000 birds were sold in just 40 markets of Peru during three consecutive years (Daut et al., 2015) and 4,063 monkeys in Pucallpa market in Peru during two consecutive years (Shanee et al., 2017). This volume only represents a fraction of the total amount of wildlife traded illegally at markets and real numbers may be significantly higher (Gastañaga et al., 2011) but difficult to estimate. However, most household pets in the Neotropics are not obtained from markets as in Asia but captured locally by people or by poachers who sell them out of commercial routes (i.e. only 0.4 % of wild pets were bought in markets in Colombia, and 3.48% in Peru). Local people know exactly the breeding cycle of common target species and, in many areas, they called the period during they poach animals “the harvest” (Romero-Vidal et al. 2020; authors personal observations). These wild animals are kept in private houses, in straight contact with poultry and people, and at very poor hygienic conditions, like a miniature replica of wet markets but replicated thousands of times all across the continent.

Despite several studies focus on the Asian wet markets and bushmeat consumption as risk factors in zoonoses spillover (Webster, 2004; Woo et al., 2006; Paige et al., 2014; Pernet et al., 2014; Kurpiers et al., 2016) only a few have treated the problem of wildlife pets as a source of diseases (Chomel et al., 2007; Jones et al., 2008; Green et al., 2020) and were mostly focused on international trade and pets keep at high income countries (Green et al., 2020; but see Chomel et al., 2007) However, domestic wildlife pets at the Neotropics (and African and Asian countries too) are not subject to any type of veterinary control and live in low hygienic conditions in close contact with people and domestic animals (Figure 3.7.2). Wildlife markets and bushmeat practices share with the tenure of wild pets the facilitation of contact between wildlife not subjected to any health regulation and humans, which can increase the risk of transmission of pathogens of animal origin to humans (Chomel et al., 2007; Pavlin et al., 2009). However, the nature of this contact is very different in both situations. While the contact in markets and bushmeat practices is in most cases reduced to a single and punctual event, the close contact with pets is prolonged over time, often over many years. Thus, prolonged contacts may influence the capability of zoonotic pathogens to shift to human hosts (Johnson et al., 2015), as it happens with domestic animals with several pathogens presenting wider host ranges (Wolfe et al., 2007). From an epidemiological point of view, this makes a big difference. Bushmeat practices and wildlife consumption represent a high risk for infection (Wolfe et al., 2005; Karesh & Noble 2009), but the number of people being involved may be significantly lower than with pets. In fact, when people in areas such Amazonia moves to cities from rural areas their bushmeat consumption gets reduced (Chaves et al., 2020), while the demand for wild pets still high in urban areas (Daut et al., 2015; Shanee et al., 2017). Regarding the magnitude of the illegal pet trade, the number of people exposed to prolonged and close contact with it, and the large likelihood of human-to-human transmission after spillover (Jhonson et al., 2015), the risk of the domestic wildlife pet trade in the Neotropics is concerning.

4.7.2. Pathogeography and pets: a movie with risky actors

Several studies point to the importance of wild animals, mainly mammals and birds, as a key source of endemic and emerging human pathogens (Taylor et al., 2001; Woolhouse & Gowtage-Sequeria, 2005; Jones et al., 2008; Allen et al., 2017). Their pathogenic agents, mainly RNA viruses that infect a wide variety of animal hosts, are likely to infect and be transmitted among humans, having a great potential to cause pandemics (Woolhouse et al., 2014). Thus, a key factor in predicting the emergence of zoonoses is viral richness found in natural reservoir species (Wolfe et al., 2005). This ‘‘zoonotic pool’’ (Morse, 1993) is still largely undetermined to science (Poulin, 2014), and their geographic distribution poorly or completely unknown (Hay et al., 2013). Thus, biogeographic pattern definition and process identification based on historical patterns of disease occurrence, recent emergence events, or proxy taxa such as mammalian or arthropod vector biodiversity may shed light and provide some early insights to predict areas where disease outbreaks are likely to occur (Murray et al., 2015).

Biogeographic and macroecological studies have found that species richness is greater at lower latitudes across a wide range of taxa (Stevens, 2004; Mittelbach et al., 2007; Adams & Hardly, 2013). As parasite richness is strongly correlated with host species richness in area-based studies (Kamiya et al., 2014), we might expect a similar latitudinal gradient for pathogens. Although data on latitudinal gradients in pathogens are conflicting and not accurate, recent studies show that disease richness (mainly human pathogens) decreases towards the poles (Guernier et al., 2004; Guernier & Guégan, 2009; Dunn et al., 2010; Cashdan, 2014; Stephens et al., 2016; Murray et al., 2018). Moreover, Cooper & Nunn (2013) mapped the areas likely to harbour undiscovered parasite diversity (based on primate species richness based on effort devoted to study primate parasites in various countries), predicting that central South America, along with some parts of Africa and Asia, hid the largest numbers of undiscovered primate parasite species and should be the focus of future parasite surveys.

Environmental changes experienced in the Neotropics during the last 30/50 years such as the increment in road networks, deforestation, species endangerment, and human population size can all combine to even increase the likelihood of zoonosis outbreak. More roads can broaden the geographic reach of pathogens by facilitating the movement of people and pets, and of insect vectors transported inadvertently in the goods they carry (Cashdan, 2014). Heard et al. (2013) also found that being threatened by any other factor (e.g. land-use change, invasive species, pollution) increases the risk of a host species (amphibian, bird, or mammal) also being threatened by disease and that parasite-related problems increase with host threat status.

4.7.3. Better prevent than cure

The Neotropics represent an ideal scenario for zoonosis outbreaks. However, despite the existence of laws in the Neotropics to control the wildlife trade, the truth is that they are not implemented (Maldonado et al., 2009; Regueira & Bernard, 2012; Goyes & Sollund, 2016; Shanee et al., 2017; Romero-Vidal et al., 2020). Actions to close wildlife markets and laws to punish wildlife trade, as the Chinese government implemented after the recent corona crisis (Li et al., 2020), seem practicable with markets because they have a specific location. However, they are almost impossible to implement at a large scale, out of the main cities, due to the extension of local poaching by people to satisfy their own demand for household pets, which can be included millions of rural houses, the lack of resources, and the rooted cultural tradition of keeping wild animals as pets. Other measures, such as the identification of wildlife pathogens likely to cause human diseases, are necessary to face future outbreaks (Anthony et al., 2013; Temman et al., 2014), but not realistic in the short term. Meanwhile, massive educational and sensibilization campaigns could help to cope with a problem difficult to solve otherwise, in a moment where all the world is ready to listen.

5. Conclusions

1. Illegal trade, mainly domestic illegal trade, represents a concerning threat for parrot conservation worldwide, with a special focus on the Neotropics. The present study clarifies the magnitude of the risk represented by this activity at a global scale, which has been largely overlooked.
2. Real figures on parrots illegally traded on the Neotropics at domestic level were severely underestimated. Previous estimations were based on markets counts, and did not account for the local trade which does not enter the markets that represents the largest part of illegal domestic trade.
3. Parrots kept as pet in the Neotropics have low survival, which in most cases do not overpass two years. The bad conditions on which animals are kept and the high predation rate by other domestic animals are responsible for the high mortality. The annual turnover is very high as most of the people replace their pets once they are lost, inducing to an annual repetition of these high figures of poached parrots.
4. Parrot poaching is not an opportunistic crime focused on more abundant and available species, but driven by people selection. Parrot species are selected according to their attractiveness features, being over-trapped regarding to their abundances in the wild. Species positively selected have also higher prices than not selected species.
5. Poached parrots can be moved hundreds of kilometres from their native ranges to be sold as household pets. Species positively selected are significantly moved more than negative or non-selected species. Once individuals are moved, distance is not influenced by selection.

6. Despite strong laws on habitat protection parrots still poached in high numbers, indicating that the preservation of natural habitats is only partially effective for parrot conservation, and must be complemented with other conservation actions against illegal trade.
7. Cities can act as a refugee for endangered parrot species against habitat-loss and poaching on their natural habitats, which can adapt to this human modify habitats. However, ecological functions of these species could disappear if only urban populations are preserved.
8. Domestic illegal trade on the Neotropics represents an important threat for human health. The combination of risk factors extant in this region creates the perfect environment for zoonoses spillovers.

6. References

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