CONSERVATION IMPLICATIONS OF ILLEGAL BIRD TRADE AND DISEASE

RISK IN PERU

A Dissertation

by

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ABSTRACT

       Trade in wild-caught animals as pets is a global conservation and animal-welfare concern. Illegal and poorly-regulated legal wildlife trade can threaten biodiversity, spread infectious diseases, and result in considerable animal suffering and mortality. I used illegal wildlife trade in Peru, specifically native bird trade, as a case study to explore important aspects and consequences of the trade for domestic markets. With data collected from a five-year market survey and governmental seizure records, I applied a statistical modeling approach to investigate the influence of Peru's legal export quota system on the country's illegal domestic bird trade. I used an infectious-disease mathematical modeling approach to analyze how illegal harvest influenced disease dynamics in a wild parrot population. Finally, I used qualitative research methods to investigate the role of non-governmental organizations (NGOs) and their members' philosophical perspectives toward wildlife in combating illegal trade. I found that Peru had a thriving illegal trade in native birds (mostly parrots) for domestic consumers; 150 species were recorded in markets and/or seizures with over 35,250 individuals offered for sale (2007–2011). Peru's current legal export quota system did not influence avian abundance in markets, but historic export trade did. Because authorities frequently release confiscated birds without health evaluation, infectious pathogens may be introduced into wild populations. I determined that the hypothetical release of white-winged parakeets infected with Newcastle disease would provoke a disease outbreak with considerable mortality in a susceptible population. Higher rates of illegal harvest dampened the magnitude of the outbreak, but the combined effects of high harvest and disease-induced mortality may threaten population survival. According to interviewees, Peru's government was considered lax in combating illegal wildlife trade and as such, many NGOs supplemented the government's efforts. The five NGOs most dedicated to decreasing illegal wildlife-pet trade in Peru had strong, dual philosophical perspectives that prioritized both wildlife populations and individual wild animals. In conclusion, there is considerable avian trafficking for Peru's domestic consumers that (1) is

independent of Peru's export market, (2) provides a mechanism to introduce harmful infectious diseases into wild population, and (3) is combated most by dual-perspective NGOs.

DEDICATION

To Robin Andrews, my first mentor, who set me on this path.

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NOMENCLATURE

CITES	Convention on International Trade in Endangered Species of Wild Fauna and Flora
DFE	Disease-free equilibrium
IUCN	International Union for Conservation of Nature and Natural Resources
ND	Newcastle disease
NGO	Non-governmental organization
ODE	Ordinary differential equation
VIF	Variance inflation factor
WCS	Wildlife Conservation Society

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

Illegal wildlife trade is a well-documented conservation and animal-welfare concern. Numerous scientific articles have described the scale of the trade, critiqued legislative enforcement efforts, and debated best economic policy responses (Moyle 1998; Warchol 2004; Rosen & Smith 2010; Bennett 2011; Lyons & Natusch 2011; Biggs et al. 2013; Reuter et al. 2015). Most scholarly research has broadly focused on regulation and the supply-side of wildlife trade. Only recently have investigations extended to include the demand-side of the trade, for example, to understand social drivers of wildlife trade (Gratwicke et al. 2008; Wasser & Bei Jiao 2010; Drury 2011), the structure of trade chains (Tieguhong et al. 2006; Nguyen 2008; Wyatt 2009), and the effectiveness of interventions (Lee et al. 2005; Nijman et al. 2011a; Wyatt 2013b; Lam et al. 2014). The aim of this dissertation is to improve understanding of an illegal wildlife trade system to ultimately help improve mitigation. I used illegal wildlife trade in Peru as a case study, specifically native bird trade for the domestic pet market, to explore three facets of the trade: (1) the interaction between legal and illegal wildlife trade, (2) disease risks associated with the trade, and (3) the role of organizations working within the country to combat the illegal domestic trade. The following literature review provides background information for these three topics.

Literature review

Illegal wildlife trade

Illegal wildlife trade is a broad and complex societal problem that intertwines biodiversity conservation, animal welfare, and judicial concerns. Illegal and poorly regulated wildlife trade can result in over-harvest and threaten populations and species survival (Nekaris et al. 2010; Shepherd 2010; Sung et al. 2013). Illegal trade can also undermine natural resource management (Broad et al. 2003), foster corruption and

violence (Warchol 2004; Kakabadse 2011; Ratchford et al. 2013), and facilitate spread of infectious, sometimes zoonotic, diseases (Karesh et al. 2007; Smith et al. 2009; Hueston et al. 2011; Karesh et al. 2012) and invasive species (Carrete & Tella 2008; Westphal et al. 2008; García-Díaz et al. 2014). In addition, the considerable suffering and mortality of wild-caught animals caused by illegal pet trade has received recent scientific attention (Cantú et al. 2007; Baker et al. 2013; Sollund 2013; Warwick 2014).

In many parts of the world, such as Asia and the Middle East, demand for wildlife and their derivatives appears to be growing (Bailey 2011; Drury 2011; Nijman et al. 2012; Bush et al. 2014; Giangaspero & Al Ghafri 2014). Several reasons for increased trade have been suggested, including improved transportation and communication infrastructure (Giovanini 2006; International Fund for Animal Welfare 2008; Wu 2010; Basu 2014), opening of borders (Zhang et al. 2008), growing popularity in exotic pets (Bush et al. 2014) and most importantly, economic growth (Robinson & Bennett 2002; Milner-Gulland & Bennett 2003; World Bank 2005; Drury 2009; Harris et al. 2013). Annual estimates of legal trade in (live) wild animals range from $400–800 million (Broad et al. 2003; Engler & Parry-Jones 2007). Illegal wildlife trade is difficult to quantify in economic or biological terms, but published reports estimate it at a fourth to a third the value of legal trade (Cook et al. 2002; Ratchford et al. 2013).

Illegal wildlife trade, with help from the media, frequently congers images of slaughtered rhinos and burning towers of confiscated ivory smuggled to fulfill demand from international markets (e.g., Davies 2005; Anon. 2014; Narula 2014). The egregious slaughter of charismatic megavertebrates represents just one aspect of illegal wildlife trade—international smuggling of wildlife products. During the past decade, the scientific community has raised awareness of another side of illegal smuggling—trade in live wild-caught animals for the booming global exotic pet industry, including highly coveted rare species and color mutations by collectors and breeders (Webb et al. 2002; Rosen & Smith 2010; Bush et al. 2014; Harrington 2015). Illegal trade in wild-caught animals for *domestic* consumers receives less media attention, although recent studies have documented the magnitude of illegal domestic trade, particularly involving avian

species (Drews 2001; Shepherd 2006; Cantú et al. 2007; Gastañaga et al. 2010; Alves et al. 2012).

Trade in wild-caught birds

Birds are popular pets in many countries throughout the world. Wild-caught birds have a long history of being traded as pets, both legally and illegally for international markets (Banks 1970; Inskipp 1979; Inskipp et al. 1988; Thomsen et al. 1992). In the early 1970s, international trade was estimated at 7.5 million exotic birds annually, many of which were parrots (Clapp 1975; Inskipp 1979). A global pandemic of Newcastle disease (1968–1973), largely blamed on the pet bird trade, caused many countries to introduce importation regulations, which caused the first dramatic reduction in legal international trade (Utterback 1973; Clapp 1975; Lancaster 1976; Inskipp 1979). In 1975, the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) entered in force to "ensure that international trade in specimens of wild animals and plants does not threaten their survival" (CITES 2014c). Due to strong international demand for parrots and the threat of over-harvest, most psittacines were listed by 1981 on either CITES Appendix I or II to stop or better regulate international trade (CITES 2013), although smuggling into the United States (and likely elsewhere) continued (Nilsson 1989).

Bird imports into the United States decreased further after the U.S. Congress passed the Wild Bird Conservation Act in 1992, which banned importation of all CITES-listed birds (WBCA 1992; Wright et al. 2001), following calls of concern from the scientific community regarding over-exploitation of wild populations (Beissinger et al. 1991). In 2005, another global infectious disease outbreak, highly-pathogenic H5N1 avian influenza, raised public and animal health fears in addition to conservation and animal-welfare concerns about international bird trade (World Parrot Trust 2004b; Appenzeller 2005). Following pressure from conservation and animal-welfare organizations, the European Union passed a blanket importation ban of all wild-caught birds (European Commission 2007), which effectively closed the largest legal import bird market. It is not yet clear the impact this ban has had on global bird trade, but it is

reasonable to assume that it has declined (Shepherd 2006; Nijman 2010).Thus, global trade in wild-caught birds peaked in the 1970–1980s (Inskipp 1979; Thomsen & Mulliken 1992), and subsequently declined largely due to international trade treaties and import bans (Beissinger 2001; Wright et al. 2001; Pain et al. 2006), along with captive-breeding of many popular pet species (Clubb 1992; Jepson & Ladle 2009; Li & Jiang 2014).

Despite the decline in international trade, Birdlife International (2012) reported almost 40% of at-risk birds (i.e., avian species with a conservation status other than least-concern on International Union for Conservation of Nature and Natural Resources (IUCN) Red List), are threatened by over-exploitation from hunting and/or pet trade. Much of today's demand for illegally-captured birds comes from domestic pet markets in source countries, such as in the Neotropics, where international trade regulations have little influence on domestic trade (Drews 2001; Wright et al. 2001; Herrera Scott 2004; Cantú et al. 2007; Herrera & Hennessey 2007; Gastañaga et al. 2010; Asmussen et al. 2011; Alves et al. 2012). Although the history of domestic bird trade in source countries is not as well documented as international trade, it is likely that many domestic wildlife markets were established in the 1960s and 1970s secondary to high international exports. Once domestic markets were established, many have remained active despite decline in global trade. One recent survey of Peruvian animal markets estimated 80,000–90,000 wild-caught parrots were sold yearly (Gastañaga et al. 2010). A nationwide survey in Costa Rica found 18% of the 1,021 households surveyed had illegally wild-caught parrots (Drews 2001). A conservative estimate of the captive population of native parrots in Costa Rica was 151,000 individuals with a yearly extraction rate of 25,000–40,000 individuals. Illegal trade in wild-caught songbirds for singing contests in Brazil has been a recognized conservation problem for decades (Levinson 1987) and continues in many parts of the country (Alves et al. 2010; Alves et al. 2012; Regueira & Bernard 2012). Interestingly, perhaps because Brazil has prohibited commercial export of native wild-caught birds since 1967 (Thomsen & Mulliken 1992), the songbird trade in South

America appears to have developed and remained primarily for Brazil's domestic consumers.

Psittacidae is one of most threatened bird families in the world, with 152 of the 350 extant species (43%) listed in a threatened category on the IUCN Red List (i.e., critically endangered, endangered, vulnerable, or near threatened; Butchart et al. 2004; BirdLife International 2015). Many parrot species are susceptible to exploitation because of their low reproductive rates, late age of first reproduction, and limited access to nest sites (Beissinger 2001; Wright et al. 2001; Cornelius et al. 2008). Destruction of suitable habitat, particularly nesting sites, and over-harvest for the pet trade are considered the primary threats facing wild parrot populations (Collar 2000; BirdLife International 2012). Clarke & de By (2013), however, suggested that that poaching and habitat loss were at least equal causes of parrot decline in the Neotropics, with poaching possibly being a stronger threat. From 1991–1996, 1.2 million parrots were legally traded globally, the majority originating from the Neotropics (Beissinger 2001). This number was considered an underestimation of the actual amount taken from the wild because it did not include domestic and/or illegal parrot trade. More realistically, 400,000–800,000 parrots may have been captured from the wild annually for the pet trade (Beissinger 2001). Several Neotropical countries that have problems with illegal domestic parrot trade, and native bird trade in general, also have limited legal international trade, which may complicate law enforcement and fuels debate over the perceived factors contributing to illegal trade (Fischer 2004; Kirkpatrick & Emerton 2010; Beckert & Wehinger 2012).

Legal and illegal wildlife trade

A common, yet overly simplified, criticism of legal wildlife trade is that it facilitates illegal trade by the mere existence of its legality. Opponents of legal trade frequently call for a complete trade ban or at the very least a ban on the transport and import of wildlife or wildlife products claiming that a ban is the easiest measure to implement (World Parrot Trust 2004b; Gilardi 2006; Homberger & Beissinger 2006). The European Union recently adopted this strategy by banning the import of all wild-

caught birds, regardless of their conservation status in the exporting country of origin (European Commission 2007). The interaction between legal and illegal wildlife trade is far from definite—more clearly defined are individual elements of the pro-trade and pro-ban arguments.

Advocating bans

In many cases, pro-ban advocates prefer blanket import bans over export bans because import bans are claimed to be easy to implement for border personnel, deter smugglers and ultimately decrease demand (World Parrot Trust 2004b; Homberger & Beissinger 2006). Import bans are also touted as being more realistic and effective than export bans or trade regulated by exporting countries such as required by CITES, because many exporting countries inadequately regulate their exports (Shepherd et al. 2004; Carpenter et al. 2005; Gilardi 2006; Shepherd & Nijman 2007; Nijman & Shepherd 2010; Nijman et al. 2012; Shepherd et al. 2012; Lyons & Shepherd 2013). Pro-ban advocates argue that conditions in wildlife exporting countries, which are typically economically underdeveloped, facilitate illegal trade because they are (1) plagued by corruption, (2) unable or lack political will to adequately enforce national wildlife legislation let alone fulfill international requirements for non-detriment findings of harvested CITES-listed species, and (3) have too few adequately trained inspectors to control exports, detect forged documents, and correctly identify traded species (World Parrot Trust 2004b; Smith & Walpole 2005; Nguyen 2008; Wyatt 2009; Bennett 2011; Kakabadse 2011).

Legal wildlife trade has many risks and negative consequences according to pro-ban advocates. Legal trade provides a pathway to launder illegally-harvested goods such as what was found with domestic trade in tiger pelts in China (Environmental Investigation Agency 2013), reptiles (Shepherd & Nijman 2007; Lyons & Natusch 2011; Nijman et al. 2011b; Sung et al. 2013), birds (Alves et al. 2012; Shepherd et al. 2012) and other species (Brooks et al. 2010; Gomes Destro et al. 2012). Trade in wild-caught animals for the pet trade risk introducing infectious diseases (Smith et al. 2009) and invasive species (Carrete & Tella 2008), and causes considerable animal suffering and

high mortality along the trade chain (Cantú et al. 2007; Sollund 2013). With the risk of poorly controlled legal trade and potential over-harvest, less wildlife would remain in native ranges, which could otherwise provide non-extractive economic opportunities that benefit local communities such as from ecotourism (Brightsmith et al. 2008; Steven et al. 2013; Welford & Barilla 2013). Fewer wild-caught animals for sale in the market (i.e., resulting in less competition) would provide entrepreneurs opportunities to develop or expand captive-breeding operations that could be certified to minimize laundering (Jepson & Ladle 2009) and would benefit species conservation (World Parrot Trust 2004b; Damania & Bulte 2007). Finally, legal trade in controversial products, especially from endangered species such as ivory, reduces consumer stigma, which may subsequently increase demand and poaching (Heltberg 2001; Vasquez 2003; Fischer 2004; Stiles & Stiles 2004). Pro-ban advocates argue that when trade bans are consistently enforced over time, such as India's ban on ivory trade, they help conserve endangered species (Environmental Investigation Agency 2013).

Advocating trade

On the other side of the wildlife trade argument, pro-trade advocates question much of the anti-trade rationale. For instance, effective enforcement of trade bans may not be any easier than regulating trade because trade bans require demand-reduction campaigns that are expensive and have largely proven ineffective (Biggs et al. 2013). Pro-trade advocates are also skeptical that an international trade ban would decrease demand for wildlife and wildlife products (Cooney & Jepson 2006). Numerous bans or more strictly regulated trade have increased demand in specialty markets, particularly for products with inelastic demand such as for rhino horn and ivory (Cooney & Jepson 2006; Courchamp et al. 2006; Hall et al. 2008). In such cases, increasing penalties for illicit trade, including the death penalty, has not prevented poaching (Conrad et al. 2013). Inelastic demand with high profit potential was the first of five ingredients that Conrad (2013) suggested contributed to a "perfect storm" where a wildlife trade ban may have the unintended effect of increasing, rather than decreasing, illegal trade. The other four components were: (1) long history of trade and a strong cultural affinity for the

animal or animal product, (2) ambiguous property rights, (3) human-animal conflict causing negative incentives for conservation, and (4) inadequate enforcement.

Trade proponents describe many benefits from legal, well-regulated trade. Legal trade, for example, keeps the trade transparent instead of pushing it underground where it is more difficult to detect and increases the risk of introducing infectious diseases by bypassing health screening protocols (CITES 2007; Karesh et al. 2012). When managed properly, legal trade can reduce prices and out-compete illegal sources (Hutton & Webb 2002; McAllister et al. 2009). Legal trade can also provide revenue for conservation, offer economic opportunities to the poor, and incentivize local communities—who are most effective at preventing poaching and protecting habitat—to conserve their natural resources (Cooney & Jepson 2006; CITES 2007; Roe 2008; Weber et al. 2015). Trade advocates point out that most legal international trade involves abundant species, not threatened by trade in their source countries, such as West African finches (CITES 2007). By eliminating a legal supply of common, non-threatened species, basic economic logic suggests that the value of these common species would increase, thereby creating opportunities for smugglers (Moyle 1998, 2005). Furthermore, pro-trade advocates argue that captive breeding may not be able to meet demand (Clayton et al. 2000), or in some circumstances consumers may prefer wild-caught animals or products (Gratwicke et al. 2008; Phelps et al. 2014). For instance, demand remains high in Brazil for some wild-caught song birds because they are considered better singers (Levinson 1987).

Complexity and enforcement

While both sides of the wildlife trade debate provide compelling arguments, consensus is a distant prospect and in the meantime, global trade remains complex and filled with many uncertainties (Damania & Bulte 2007; Wiersema 2013). It is unclear, for example, whether communities benefit more from non-extractive uses of wildlife or from legal wildlife trade. No scientific evidence has demonstrated that a blanket trade ban is more cost-effective and easier to implement than regulated legal wildlife trade. The conservation benefit of controlled legal trade or trade bans, especially in endangered

species products such as ivory and rhino horn, remains unanswered. What is clear is that international wildlife trade, just like other aspects of biodiversity conservation, is context dependent and the pros and cons of each trade system should be evaluated independently to understand the drivers and dynamics of the trade and to determine the best policy response (Fischer 2004; Fischer 2010; Lindenmayer & Hunter 2010). The same is true for situations of overlapping legal and illegal markets and for domestic wildlife trade, which occurs largely independent of international markets where traditional mechanisms to regulate wildlife trade, such as CITES, have little influence.

Only a few studies have investigated regulatory interventions in domestic wildlife markets. In an attempt to control illegal parrot trade, Mexico implemented a complete ban on the import, export, captive-breeding and commercialization of native psittacine species with apparent success (Neme 2012). Following the 2005 outbreak of avian influenza and subsequent new legislation, illegal trade decreased significantly in Vietnam's urban bird markets (Brooks-Moizer et al. 2009). Increased enforcement of wildlife legislation in Indonesia decreased trade in protected species for local markets during a two-year study period (Lee et al. 2005).

Poor enforcement of wildlife legislation and trade regulations in source countries is a legitimate concern (Keane et al. 2008; Bennett 2011; Lyons & Natusch 2011; Cottee-Jones et al. 2014). A potential disincentive to enforce legislation occurs when live animals are involved because enforcement usually requires confiscating the animals (IUCN 2002). Most developing countries are hampered by limited financial and technical resources to provide adequate husbandry for confiscated wildlife. The lack of housing options for confiscated parrots was considered one of the primary reasons why authorities rarely confiscated illegally-traded parrots in Peru (Ríos et al. 2008). Lack of rescue facilities likely influenced customs officials to inconsistently confiscate illegally-traded Barbary macaques (*Macaca sylvanus*) in Morocco and Spain (van Uhm 2014).

Wildlife rehabilitation centers and permanent-captivity facilities (zoos, aviaries) are scarce in most developing countries and they often have no space or desire to receive more individuals, especially of the most commonly traded species (Karesh 1995). In

Colombia, the most traded psittacine, the spectacled parrotlet (*Forpus conspicillatus*), was one of the least confiscated by authorities (Baquero & Baptiste 2004). Because authorities are reluctant to euthanize confiscated animals and have limited options to house them even temporarily, they frequently release the animals back to the wild without proper medical screening. Release often occurs without documenting the confiscation event and pertinent details to adequately monitor illegal trade, such as correct species identification (Karesh 1995; Troncoso & Naranjo-Maury 2004). Releasing individuals back to the wild under most circumstances is the least-recommended option for handling confiscated wildlife (IUCN 2002). One reason is because releasing confiscated wildlife without medical screening, similar to translocation of wild animals for conservation purposes, risks releasing novel and potentially harmful pathogens into susceptible wildlife populations (Snyder et al. 2000; Jiménez & Cadena 2004; Kock et al. 2010).

Disease and wildlife trade

Documenting that a disease was introduced into a wild population through illegal wildlife trade is problematic given the illicit nature of the trade. Infectious pathogens, on occasion, have been identified from confiscated animals smuggled internationally, which demonstrates illegal trade as a potential source for disease outbreaks. In 2004, two crested hawk-eagles (*Spizaetus nipalensis*) seized at the Brussels international airport were carrying a highly pathogenic H5N1 strain of the avian influenza virus (Van Borm et al. 2005). Raccoons (*Procyon lotor*), illegally imported into Norway were infected with a zoonotic nematode *Baylisascaris procyonis*. One of the raccoons escaped before confiscation and it is unknown if it was carrying the nematode (Davidson et al. 2013). More commonly, legal or accidental movement of wild animals harboring infectious pathogens have provoked disease outbreaks (Woodford 2000; Williams et al. 2002; Chipman et al. 2008; Kock et al. 2010). In 1985, raccoons translocated from Texas to West Virginia to supplement the local hunting stock were considered to have introduced parvoviral enteritis, previously absent in West Virginia and now enzootic (Kock et al. 2010). Many amphibian species worldwide are now threatened or extinct due to

chytridiomycosis, a fungal disease spread, in part, through the pet trade (Fisher & Garner 2007; Skerratt et al. 2007). In other cases, infectious pathogens were identified in time to prevent the spread of disease. In 2004, a highly pathogenic paramyxovirus was identified in a legal shipment of wild-caught and captive-bred birds imported for the pet trade from Pakistan to Italy; all 4,000 imported birds were euthanized in quarantine (World Parrot Trust 2004a). The introduction of a novel *Mycoplasma* spp. into a healthy population of wild pancake tortoises (*Malacochersus tornieri*) was averted when the confiscated individuals were examined prior to release (Karesh 1995).

Epidemiology of introduced infectious diseases in wildlife populations is challenging because rarely is a disease identified early in an outbreak, and may only be noticed after causing considerable mortality or after the disease becomes endemic (Hudson et al. 2002). Field studies are logistically difficult and, along with diagnostic testing, often prohibitively expensive. Without basic knowledge regarding the infectious pathogen, such as how it spreads and how effectively it infects a host, and fundamental host demographic data, it can be difficult predicting how a disease will respond in a wild animal population. Mathematical modeling allows us to use the information available about an infectious pathogen and the host population and, by accounting for uncertainty in the data, project how the pathogen will likely progress (i.e., will it go extinct or remain endemic and possibly impact the long-term stability of the host population). Models also provide a framework to help evaluate and compare potential interventions, such as vaccination programs (Keeling et al. 2003; Sterner & Smith 2006). Deterministic compartmental models are frequently used to depict wildlife disease outbreaks where transition rates from one class of the population to another are mathematically expressed as derivatives in continuous time (Anderson & May 1991; Hudson et al. 2002).

Epidemiological modeling typically is based on one of two theoretical concepts: threshold theory and fadeout theory (Swinton et al. 2002). The basic reproduction number (R_0) is the foundation of the threshold theory and defines the conditions for a pathogen to invade, specifically when $R_0 > 1$. Fadeout theory is founded on what happens, for example, if a highly infectious pathogen runs out of susceptible hosts and

subsequently goes extinct. R_0 is defined as is the average expected number of secondary infections produced by one typical infectious individual introduced into a fully susceptible host population (Heesterbeek 2002). It usually is estimated because rarely are all of the parameters known to calculate R_0 from actual epidemiological data (Heesterbeek 2002). The force or speed with which susceptible individuals become infected, the per capita rate, is called the force-of-infection. R_0 and the force-of-infection are influenced by the form of pathogen transmission between infected and susceptible individuals. Density-dependent transmission implies that R_0 is proportional to the size of the host population and that there exists a threshold host density or population size below which the pathogen cannot invade. Frequency-dependent transmission implies that R_0 is independent of the population size and has no effect on the pathogen's ability to invade the population (McCallum et al. 2001; Swinton et al. 2002; Lloyd-Smith et al. 2005).

The use of simulation modeling to estimate or mimic the spread of infectious diseases affecting agriculture animals is fairly common (Harvey et al. 2007). The agriculture industry is most concerned about highly infectious diseases that can provoke substantial morbidity, mortality and/or economic losses such as foot-and-mouth disease, swine fever, and highly-pathogenic avian influenza (Bates et al. 2003; Keeling et al. 2003; Bolzoni & de Leo 2007; Karsten 2007; Paarlberg et al. 2007). Model predictions for these high-risk diseases are increasingly being used to inform policy decisions (Guitian & Pfeiffer 2006) and guide response strategies (Harvey et al. 2007; Brooks-Pollock et al. 2014). Less common are simulation models that evaluate the "what if" scenarios of introducing an infectious disease into a susceptible wildlife population; although, discrete-time stochastic models were developed to investigate enzootic conditions for *Batrachochytrium dendrobatidis*, an often fatal fungal disease devastating many amphibian populations (Briggs et al. 2005; Skerratt et al. 2007; Briggs et al. 2010). It is more common that wildlife disease models are developed to investigate different management strategies to mitigate the spread or impact of a disease such as culling

(Wonham et al. 2004; Cox et al. 2005; Donnelly et al. 2006; Foley et al. 2011; Brooks-Pollock et al. 2014) or vaccination (Sterner & Smith 2006; Panjeti & Real 2011).

With respect to illegal wildlife trade, simulation models provide a method to explore potential consequences of pathogen introduction via illegal trade and disease dynamics in exposed and harvested host populations. Wild animal populations are at risk from introduced diseases by contacting confiscated individuals that were infected with an infectious pathogen while in captivity, and then subsequently released by authorities or escaped back to the wild. Minimizing the risk of introducing infectious diseases would require either euthanizing the confiscated animals, which is often the preferred and most responsible option (IUCN 2002), or improving confiscation management to include, for example, quarantine and proper health screening prior to release (Woodford 2000; IUCN 2002). In developing countries, quarantine and medical screening are problematic because husbandry and diagnostic expenses are typically beyond what governments can provide (Karesh 1993, 1995). For example, the minimum 60-day quarantine suggested for high risk species of infectious diseases such as Newcastle disease, would tax most governments' resources (Woodford 2000). Even most wildlife rehabilitation centers may not have the financial resources to care for and test individuals prior to release (Karesh 1995). The most direct approach to minimize the risk of disease introduction through illegal trade would be to decrease the illegal trade.

Non-governmental organizations

Historically, conservation and preservation groups have been the entities to raise alarm about international wildlife trade. One of the earliest anti-trade campaigns, started in the mid-1800s in the United States and England, confronted the perceived cruel and excessive slaughter of plume birds to harvest feathers for the fashion industry (Doughty 1975). The "plumage campaigns" used both conservation and animal-welfare arguments to influence the consuming public and politicians to decrease demand and increase commercial regulation. Since these earliest campaigns, conservation organizations have continued to tackle wildlife trade issues, while animal-welfare groups, until recently, have focused mostly on domestic and farm animals. Starting in the 1960s, conservation

non-governmental organizations (NGOs) grew into major actors on the international environmental stage. They were the driving force behind the development of key multilateral agreements in the 1970s such as the Convention on Wetlands of International Importance (Ramsar), the Convention of Migratory Species (CMS), and CITES (Cobb et al. 2007; Prideaux 2014). After establishment of CITES, NGOs adopted "the role of guardians of the spirit and purpose of CITES by monitoring both compliance and enforcement" (Sands & Bedecarré 1990: pg. 779).

In developing countries, increasingly powerful global conservation NGOs have established close relationships with governments and today drive much of the conservation policy (Duffy 2006; Brockington & Scholfield 2010a). Governments in many developing countries do not prioritize wildlife conservation and/or rarely have funding for conservation efforts (Lowther et al. 2002; Balmford et al. 2003; Balmford & Whitten 2003; Bruner et al. 2004; Nurse 2011; Shanee 2012; Miller et al. 2013). To compensate for governmental gaps, NGOs assist with wildlife management and policy development, and often directly support efforts to combat illegal wildlife trade (White 2012; Boehmelt et al. 2013; Nurse 2013; The Last Great Ape Organization 2013; Eilstrup-Sangiovanni & Bondaroff 2014). Conservation NGOs typically prioritize combating illegal trade of endangered species, which is consistent with the original edict for biodiversity conservation (Soulé 1985). Animal-welfare NGOs, on the other hand, when active against illegal trade, usually consider all wild animals regardless of their conservation status (Singer 1975; Irwin 2003).

Efforts to combat illegal wildlife trade range widely from broad indirect initiatives involving international policy, to supporting local demand-reduction interventions, and rehabilitation of confiscated wildlife (Lee et al. 2005; Brooks-Moizer et al. 2009; Humane Society International 2011; World Wildlife Fund / Dalberg 2012; Jiang et al. 2013; Challender & MacMillan 2014; Challender et al. 2015). Nurse (2011) categorized NGOs involved in combating wildlife crime as: (1) campaigning, (2) law enforcement, or (3) political-lobbying NGOs. Public-awareness campaigns and political lobbying have long been the cornerstones for both conservation and animal-welfare

NGOs (World Wildlife Fund / Dalberg 2012; African Wildlife Foundation 2013; Conservation International 2013b; Humane Society International 2013). Improving wildlife law enforcement has received international attention recently following egregious poaching of rhinos and elephants (Anon. 2014; Narula 2014). Strengthening enforcement was also the first of three recommendations made by the U.S. President's Advisory Council on Wildlife Trafficking, in addition to reducing demand for illegally traded wildlife, and expanding international cooperation and commitment (McHale & Hayes 2014). Large international initiatives involving conservation NGOs, such as the Freeland Foundation and TRAFFIC, helped create the Association of Southeast Asian Nations' Wildlife Enforcement Network (ASEAN-WEN), considered the world's largest regional wildlife law enforcement network spanning across ten countries (ASEAN-WEN 2014). Locally, NGOs have helped train wildlife authorities and provide salary and equipment (Holmern et al. 2007; Freeland Foundation 2013; International Fund for Animal Welfare 2013; The Last Great Ape Organization 2013; Wildlife Conservation Society 2013; Wyatt 2013a). The outcomes of the various NGOs' efforts to combat illegal wildlife trade have not been systematically evaluated.

Research objectives and dissertation outline

The goal for my dissertation research was to improve understanding of illegal wildlife trade, particularly native bird trade, for the domestic pet market in Peru. My dissertation is divided into four primary chapters designed for publication; each chapter addresses different research objectives:

(1) Establish the relationship between Peru's legal export quota system and illegal domestic trade in native birds. (Chapter II)

(2) Evaluate how illegal harvest and the potential introduction of the infectious pathogen, Newcastle disease virus, interact to affect a susceptible population of white-winged parakeets. (Chapter III)

(3) Explore the role of transmission threshold values when predicting disease epidemics associated with potential pathogen introduction via wildlife rehabilitation. (Chapter IV)

(4) Examine NGOs and the influence of different philosophical perspectives toward wildlife on their effort to decrease illegal wildlife-pet trade in Peru. (Chapter V)

I end with a summary chapter including recommendations and opportunities for future research. (Chapter VI)

Study area

Peru, located on South America's central Pacific coast, is roughly the size of Alaska with 1,300,000 km^2 and is bordered by Bolivia, Brazil, and Chile to the east and south, and Colombia and Ecuador to the north. The current human population is almost 31 million (INEI 2014). Geographically, Peru is divided into three natural regions; the western coastal lowlands, the Andes Mountains and the eastern Amazonian lowlands that cover over 50% of the nation's territory. Politically, Peru is divided into 24 *departamentos* (provinces); provincial capitals are important transport links and wildlife trade sites. Lima, the capital, is the largest city (~ 9 million inhabitants) and the country's largest consumer base for wildlife (INEI 2014). Traditional animal markets were surveyed in Lima and eight other cities (Fig. 1).

Peru offered a unique opportunity to explore illegal wildlife-pet trade issues because (1) it has a long history of legal export trade with limited quotas still regulated for many native species, in contrast to most neighboring countries (Dourojeanni 1985; Falero & Sánchez 1990; Thomsen & Mulliken 1992), (2) illegal wildlife-pet trade for the domestic market is ubiquitous, and demand for unusual pets may be growing along with Peru's improved economy (TRAFFIC 2008; Castano 2011; Vera & Yu 2013), (3) infectious diseases such as Newcastle disease are endemic in poultry, offering opportunities for transmission between domestic and wild animals via illegal trade (The Poultry Site 2009), and (4) many conservation and animal-welfare NGOs are in Peru and could potentially be working to decrease the illegal wildlife-pet trade.

CHAPTER II

ILLEGAL DOMESTIC BIRD TRADE AND THE ROLE OF EXPORT QUOTAS IN

PERU

Synopsis

Legal international trade of wild animals is controversial because some experts speculate that it facilitates illegal domestic trade in source countries. Wild-caught birds are commonly traded as pets, both legally and illegally, for international and domestic markets. I used Peru's native bird trade as a case study to explore the relationship between legal international and illegal domestic trade. Peru's current quota system started in 2001 and is designed to permit limited export of wild-caught birds, while domestic trade is largely prohibited. I evaluated survey data from 40 markets in nine cities (March 2007–July 2011), tabulated government seizure records and export quotas, and compared proportions of native birds with and without quotas in markets and seizures. Sixteen independent variables were evaluated using generalized linear models to explain native bird abundance in the markets and government seizures. I observed a thriving illegal domestic market with 130 native species (n = 35,279 birds) offered for sale. Parrots were the most abundant birds. I found no evidence that Peru's current quota system facilitated illegal domestic trade; authorities confiscated birds regardless of their quota status. While the current quota system did not influence market abundance, historic export trade did. Peru's domestic market, and likely other illegal Neotropical bird markets, developed as a consequence of high historic exports and now appears driven, in part, by tradition and which birds harvesters are accustomed to trapping. Improved enforcement of Peru's wildlife legislation, including species-identification and records-management training, would likely be more effective in decreasing illegal domestic trade than eliminating quotas.

Introduction

Exotic animals are popular pets in many parts of the world. Growing consumer demand for these novel creatures drives a complex, lucrative, and often illicit international trade in wild-caught animals (Christy 2008; Laufer 2010; Bush et al. 2014). Legal and illegal trade of the same or similar species frequently occurs simultaneously for national and international markets (Cheung & Dudgeon 2006; Lyons & Shepherd 2013). Intertwined legal and illegal markets complicate trade regulation, and fuel debate regarding the perceived costs and benefits of wildlife trade. On the one hand, legal sustainable trade can provide important economic benefits for rural communities and developing nations while conserving wild populations (Broad et al. 2003; Carpenter et al. 2005; Cooney & Jepson 2006). On the other hand, illegal or poorly regulated trade of wild-caught animals can result in over-harvest and threaten populations and species (Nekaris et al. 2010; Shepherd 2010; Sung et al. 2013).

Enforcement of wildlife trade legislation varies among countries, but typically is insufficient in developing source nations (Brack & Hayman 2002; Bennett 2011; World Wildlife Fund / Dalberg 2012), and where control is complicated by the intersection of legal and illegal markets (Fischer 2004; Zhang et al. 2008). Some have suggested the existence of legal international trade, such as an export quota system, can enable illegal domestic trade in wild-caught animals in source countries (Herrera & Hennessey 2007; Gastañaga et al. 2010; Pires & Clarke 2011). A legal quota system may facilitate illegal trade, in part, through falsification of permits, deliberate or accidental misidentification of species, and corruption of wildlife officials. While authors debate the pros and cons of international wildlife trade and trade bans (e.g., World Parrot Trust 2004b; Burton 2006; Cooney & Jepson 2006; Gilardi 2006; Roe 2006; CITES 2007), few have evaluated the influence of legal export quotas on illegal domestic markets.

Wild-caught birds are commonly traded as pets, both legally and illegally, for international and domestic markets (Wright et al. 2001; Tieguhong et al. 2006; Herrera & Hennessey 2007; Alves et al. 2012; Shepherd et al. 2012). Despite declining international trade largely due to trade treaties, import bans, and captive-breeding

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(Wright et al. 2001; Jepson & Ladle 2005; Pain et al. 2006), almost 40% of threatened birds experience over-exploitation from hunting or pet trade (BirdLife International 2012), and illegal domestic trade of native birds still flourishes in many countries (Shepherd 2010; Regueira & Bernard 2012). Legal and illegal trade in wild-caught birds are likely to continue because demand for pet birds remains strong (Jepson & Ladle 2005; RSPCA 2006; AVMA 2012), and wild-caught birds are inexpensive options for international markets and domestic consumers (Cantú et al. 2007; Alves et al. 2012).

Peru has among the highest avian diversities in the world (n = 1,780 species, BirdLife International 2014a), and many species have legal export quotas and/or are traded illegally for the domestic pet-bird market (Ríos et al. 2008; Shanee 2012). Domestic demand for wild-caught native birds is high, in part, because they are often less expensive than locally captive-bred ornamental species. Because no captive-bred or legally-harvested native bird options exist, native birds are captured from the wild and illegally offered for sale in traditional animal markets throughout Peru (González 2003; Ríos et al. 2008; Gastañaga et al. 2010). Trafficked birds range from common species, such as *Brotogeris versicolurus*, to threatened endemics (e.g., *Forpus xanthops*) (BirdLife International 2014d), and globally endangered species (e.g., *B. pyrrhoptera*) (BirdLife International 2014b). Gastañaga et al. (2010) estimated that 80,000–90,000 wild-caught parrots were illegally sold annually to domestic consumers in Peru. Authors noted that seven of the most commonly traded parrot species had export quotas (Gastañaga et al. 2010; Pires 2014). Better understanding of the relationship between legal and illegal markets should provide valuable insight into whether legal wildlife export quotas facilitate illegal domestic trade.

I used the native pet-bird trade in Peru as a case study to evaluate the relationship between a legal quota system and illegal domestic trade. I first evaluated the numbers of birds recorded in the domestic pet trade through a five-year survey of animal markets and government seizure records (2007–2011). To assess the role of export quotas, I explored differences in proportions of native birds with and without quotas recorded in markets and seizures. I hypothesized that if the quota system facilitated illegal domestic

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trade, birds with quotas would be (1) more abundant in the markets, and (2) less abundant in government seizures. I then used regression models to evaluate the influence of current export quotas and 15 other factors on avian abundance in the markets and seizures.

Methods

Export quota system and wildlife commercialization legislation

Peru became a Party to CITES in 1975 (CITES 2014a) and published its first commercial avian harvest-export quotas in 2001 (INRENA 2001). The commercial quota system was designed to permit limited legal export of wildlife and wildlife products. The Ministry of Agriculture (MINAG), Peru's CITES Management Authority, regulates wildlife commercialization and publishes an annual calendar of commercial export quotas for native wildlife (MINAG 2001a). The number of avian species with export quotas nearly doubled from 56 in 2001 to 100 in 2011, but the maximum number of potential exports decreased by 7%, from 86,600 to 80,555 individuals over the same period.

During the study period, wildlife commercialization for the domestic market was largely considered illegal because it typically was performed without appropriate permits and licenses (Daut et al. 2015). The Forestry and Wildlife Law regulations (MINAG 2001a) stated that legal trade required a commercial hunting license and annual authorizations that specified the permitted species, number of specimens, time, location and method of harvest, and fees/taxes to be paid according to a published annual commercial calendar (e.g., MINAG 2011). A transport permit was required for internal movement of wildlife, including a list of the unique tags/bands used to identify each specimen being transported. Regulations also stipulated that a wild animal may only be kept as a pet if it was a permitted (quota-listed) species, the specimen originated from an authorized management area, breeding facility, or a temporary custodial center, and must be properly identified with a tag/band and registered with MINAG. The commercial sale of wildlife was prohibited in public spaces or places not authorized for that purpose,

which included all markets surveyed during the study (Congreso de la República 2000). As a result, all domestic native-bird trade monitored during this study was illegal for one or more reasons.

Market survey

Forty animal markets in nine cities were surveyed for pet birds for sale at varying frequencies between March 2007 and July 2011, excluding March–June 2010 (see Fig. 1 for map). These nine cities represent roughly 73% of Peru's human population (INEI 2014) and seven of the country's 24 political departments. Because the primary objective for the market visits was to survey wild animals for infectious diseases, not all markets were visited regularly; markets with large numbers of wild animals were prioritized to maximize sample collection. Annual market visits varied from a low in 2007 (n = 51) to a high in 2009 (n = 516), totaling 994 visits. Most markets were located in Lima (n = 25), with 1–3 in the other eight cities. Markets varied from informal roadside stands to permanent stalls reminiscent of pet stores. Given the fluid and often illegal nature of animal markets, many closed, moved, or became inactive during the study. New markets were investigated when they were identified.

During market visits, Peruvian technicians recorded the avian species and number of birds offered for sale in each vendor's stall. Wild-caught Peruvian species (native), South American native species not found in Peru (regional), introduced exotic birds, and captive-bred ornamental birds were recorded. Most individuals were identified to species, but otherwise to genus or family. Identification of native species followed Schulenberg et al. (2007) and nomenclature was updated according to del Hoyo et al. (2014). When possible, the asked selling price was recorded.

Figure 1. Map of Peru; cities included in the market survey (2007–2011) are indicated by a black dot.

Quota and seizure data

I compiled avian commercial export quotas from annual calendars published by MINAG (e.g., MINAG 2007b) for all years of our study period except 2010 when no quotas were published. Data included the species permitted for harvest and extraction period per geographic location. Government seizure records of native birds (2007–2011) were compiled from reports published by the National Police and MINAG, and information requested from regional offices of the Technical Administration of Forestry and Wildlife (ATFFS) through Peru's Transparency Law (Congreso de la República 2002). I recorded the confiscated species (or most specific taxonomic level provided), number of individuals, year, and political department or governmental region where individuals were confiscated.

Biological and trade variables

I identified 16 variables that could influence abundance of the 150 avian species found in animal markets and/or government seizures. Eight variables represented biological factors related to avian species (region, range size, abundance, conservation rank, capture, body mass, color, and voice), and eight variables were related to bird trade (current quota, past quota, total quota, quota years, U.S. import, CITES permit, price, and CITES status) (Table 1; for more detailed descriptions see Appendix A).

Table 1. Description of 16 independent variables included in the analysis of avian abundance in Peruvian animal markets and in governmental seizure records (2007–2011). See Appendix A for detailed descriptions.

Variable name	Variable type	Description
Biological factors		
Region	Nominal	1 of 4 major biogeographic regions in Peru
Range size	Continuous	Estimate of wild-range size (km^2)
Abundance	Ordinal	3-point scale; 1 = uncommon, 2 = fairly common to common, 3 = abundant
Conservation rank	Ordinal	2-point scale; 1 = least concern, 2 = near threatened, vulnerable, or endangered
Capture	Ordinal	3-point scale; 1 = easy, 2 = moderate, 3 = difficult
Body mass	Continuous	Body size (gm)
Color	Continuous	Composite value: number of contrasting colors x percent body coverage
Voice	Ordinal	3-point scale; 1 = poor talking ability or simple/harsh vocalizations, 2 = medium talking ability or semi-pleasing vocalizations, 3 = excellent talking ability or pleasing singing vocalizations
Trade factors		
Current quota	Continuous	Commercial harvest/export quota (2007–2011)
Past quota	Continuous	Commercial harvest/export quota (2001–2006)
Total quota	Continuous	Commercial harvest/export quota (2001–2011)
Quota years	Continuous	Number of years with published quota (2001–2011)
U.S. import	Continuous	U.S. Import of avian species from Peru (1970–1974 and 1980–1989)
CITES permit	Continuous	CITES export permit for avian species from Peru (1975–1979 and 1990–2006)
Price[a]	Continuous	Average market selling price during study period (U.S. dollar)
CITES status	Nominal	2-point scale; 1 = not listed on any Appendix, 2 = listed on either Appendix I or II

[a] Included only in parrot-subset models.

Analyses

To minimize duplicate market-survey counts of the same individual bird from frequent visits to the same market, I removed species' duplications < 10 days apart for each market stall. I used a 10-day interval based on estimated turnover rates suggested by vendors. During the study period, 115,409 birds were recorded for sale in markets. Following removal of 22,648 potential duplicate counts, 92,761 birds and 947 market visits were used for analyses. To evaluate market-survey effort, I constructed an accumulation curve of the native avian species identified at the 40 markets surveyed across 577 market-visit days.

I used generalized linear models to evaluate the influence of current export quotas and 15 other variables (Table 1) on the number of individuals of native species in (1) animal markets and (2) government seizures, assuming a normal distribution for the response variables. A parrot-only subset of the global markets model was also evaluated and was the only group of models to include price. Suitable transformations were performed to fulfill assumptions (Appendix A). Residuals of the statistical models followed a normal distribution and residual plots were randomly distributed. I used variance inflation factors (VIF) to identify multi-collinearity among explanatory variables, and where necessary (VIF > 5; O'brien 2007), included only the variable that contributed most to the model (Appendix A). For example, the four quota variables (current quota, past quota, total quota, and quota years) were highly collinear (VIF > 5), so I retained only one of these four variables (quota years). Therefore, 12 variables were retained for the market and seizure model sets and 11 in the parrot-only market subset.

I used an information-theoretic approach employing Akaike's information criterion corrected for small sample sizes (AICc) to identify plausible models (Burnham & Anderson 2002). For the two model sets and one subset, I began with the global model including biologically relevant twofold interactions and progressively dropped non-significant terms until the most parsimonious model with significant terms was obtained. All analyses were conducted using JMP Pro 11.0 (SAS Institute, North Carolina, USA).

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Results

Diversity and numbers in markets and seizures

There were 92,761 birds counted for sale during 2007–2011; 38% (n = 35,279) were wild-caught native species belonging to 41 families, 97 genera, and 130 species (Appendix B). The remaining individuals were captive-bred ornamental, regional or exotic species. An accumulation curve for native species stabilized at approximately market-visit day 500 (Fig. 2). Parrots made up 76% of the native market (n = 26,661) and was the family with the largest number of species (n = 34; 65% of Peru's psittacines), followed by Thraupidae (n = 16) and Columbidae (n = 11). The 12 most abundant native species represented 81% of all native birds observed, but only 9% of species diversity (Table 2).
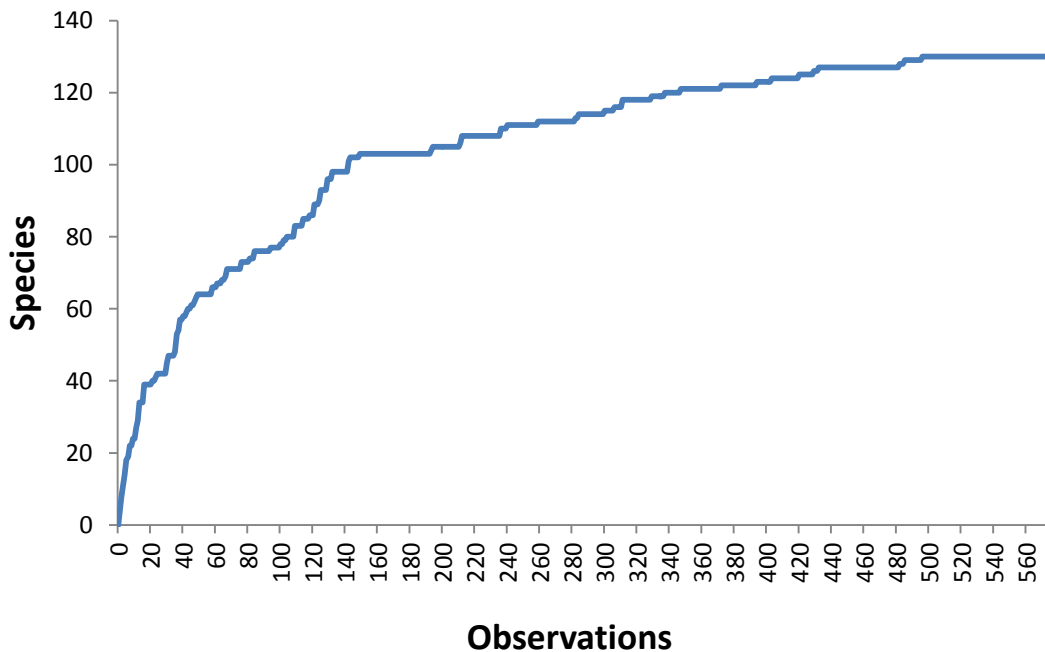
Figure 2. Accumulation curve for native avian species (n = 130) based on observations made during 577 market-visit days in nine Peruvian cities (2007–2011). Market-visit days include multiple visits to different markets on the same day.

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Authorities registered 21,745 confiscated birds during the study; 31% (n = 6,656) were identified to species (n = 64). In most cases, individuals were listed as a generic "bird" (n = 13,285, 61%; Appendix B). The 39 genera identified included 17 raptor and eight parrot species. Most individuals (92%) identified to family were parrots. Forty-three (68%) of the confiscated native species were also recorded in the market survey. Nine of the 12 most frequently recorded species in the markets and seizure records were the same (Table 2). Avian market and seizure data were moderately correlated ($r_s = 0.19$, $p < 0.02$, n = 150).

Export quotas

Commercial export (harvest) quotas were published for 103 avian species with a maximum potential export of 24,005 individuals (2007–2011; Appendix B). The actual number of exported birds is unknown because, despite multiple requests, I was unable to obtain those data from the Peruvian government. The number of species with quotas varied annually from seven in 2009 to 100 in 2011 (Table 3). The family Thraupidae had the highest number of quota species (n = 42), followed by Columbidae (n = 9), Fringillidae (n = 7), Icteridae (n = 8), and Psittacidae (n = 7) together representing 71% of all quota-listed species. The majority of *species* recorded in the market survey and/or in government seizures did not have published export quotas; however, the majority of *individual* birds did (Table 3). Seven of the 12 most abundant native species observed in the markets had quotas published three or four years of the study (Table 2).

Table 2. Twelve most abundant native birds observed for sale in Peruvian animal markets and in government seizure records (2007–2011). Quota is the sum of published export quotas.

Genus species	Market counts	% of market	Quota	Seizure counts	% of seizure
Brotogeris versicolurus	12,093	35.3	5,000	5,012	77.1
Forpus coelestis	3,504	10.2	600	70	1.1
Brotogeris cyanoptera	2,568	7.5	5,000	54	0.8
Dives warszewiczi	2,041	6	0	0	0
Sicalis flaveola	1,741	5.1	11,000	441	6.7
Brotogeris sanctithomae	1,349	3.9	4,350	36	0.5
Psittacara erythrogenys	1,072	3.1	0	73	1.1
Amazona amazonica	1,027	3	0	111	1.7
Psittacara leucophthalmus	775	2.3	0	146	2.2
Aratinga weddellii	609	1.8	5,000	160	2.4
Sporophila luctuosa	569	1.7	10,500	0	0
Amazona festiva	520	1.5	0	22	0.3
Total	27,868	81.4		6,151	93.8

Table 3. Number of native avian species (n) recorded in published export quotas, markets, and government seizures, and percent of quota-listed species and individuals in markets and seizures in Peru (2007–2011).

Year	Quota species	% in markets	Market species	% with quotas		Seizure species	% with quotas	
					Individuals			Individuals
2007	(62)	32.2	(58)	34.5 (20)	73.6 (2,025)	(3)	66.7 (2)	99.5 (193)
2008	(58)	41.4	(91)	26.4 (24)	71.4 (6,024)	(38)	18.4 (7)	85.5 (1,008)
2009	(7)	100	(81)	8.6 (7)	60.5 (7,769)	(41)	17.1 (7)	70.1 (1,234)
2010	(0)[a]	0	(48)	0	0	(26)	0	0
2011	(100)	20.0	(54)	37.0 (20)	59.6 (4,335)	(40)	17.5 (7)	88.1 (973)

[a] No quotas were published in 2010, but 2,944 individuals were observed in markets (excluding March–June) and 2,314 in seizures.

Market and seizure abundance

U.S. import, CITES permit, voice, body size and region and a twofold interaction term (CITES permit*body mass) were included in the most plausible model explaining abundance of *avian species in markets* (Table 4). According to evidence ratios, the second most supported model differed only marginally from the best by an additional interaction term. Together these two models comprised the 95% confidence set.

For the subset model, *parrot species in markets*, the best approximating model included U.S. import, voice, range size, price and quota years along with interaction price*quota years (Table 4). Because price and body mass were highly correlated (VIF = 9.96; $r = 0.84$, $p < 0.0001$, n = 34), they should be considered surrogates when comparing *avian* and *parrot species in markets* models. The second most plausible model included CITES permit and received only marginally less support than the best model (Table 4). CITES permit, along with U.S. import and voice, were also included in the most plausible *avian species in markets* model. The remaining models in the 95% confidence set contributed little to explaining parrot abundance in the markets.

For *avian species in seizures,* U.S. import, CITES permit, voice, range size, and quota years and a twofold interaction term (CITES permit*range size) were included in the best approximating model (Table 4). The second most plausible model also included body mass plus an interaction term (US import*body mass), and received only marginally less support than the best model. The summed weight (w_i) for the top two models was 0.65 (Table 4). Different combinations of these effects were retained in the next two best plausible models of the 95% confidence set, with evidence ratios < 3.8. The remaining models in the 95% confidence set had little support, meaning the top model was almost ten times better than the fifth (Table 4).

Table 4. Model selection results for all native avian and parrot (subset) species (n) observed in market surveys and recorded in governmental seizures in Peru, 2007–2011. Models were ranked by Akaike's Information Criterion with small-sample correction (AIC_c). Statistics include: number of parameters including intercept (K), twice the negative log-likelihood (-2l), difference between AIC_c of each model and the best model (ΔAIC_c), Akaike model weight (w_i), evidence ratio (w_i/w_1), and R^2. Models listed under each heading include the 95% confidence set (+1 for *avian species in markets*).

Model	K	-2l	AIC_c	ΔAIC_c	w_i	w_i/w_1	R^2
Avian species in markets (129)							
US import + CITES permit + voice + body mass + region + CITES permit*body mass	9	226.27	245.79	0	0.537	1	0.59
US import + CITES permit + voice + body mass + region + US import*CITES permit + CITES permit*body mass	11	222.02	246.27	0.487	0.421	1.276	0.60
US import + CITES permit + voice + body mass + US import*CITES permit + CITES permit*body mass	10	231.25	253.11	7.325	0.014	38.96	0.55
Parrot species in markets[a] (34)							
US import + voice + range size + price + quota years + price*quota years	9	30.87	56.37	0	0.519	1	0.81
US import + CITES permit + voice + range size + price + quota years + price*quota years	10	28.34	57.91	1.538	0.24	2.158	0.82
US import + voice + range size + price + quota years + US import*voice + price*quota years	13	15.92	60.12	3.746	0.08	6.506	0.83
US import + voice + range size + price + quota years	7	42.7	61.01	4.637	0.051	10.159	0.75
US import + voice + range size + price + quota years + US import*voice	11	27.38	61.38	5.014	0.042	12.266	0.80
US import + CITES permit + voice + range size + CITES permit*range size	8	40.68	62.44	6.067	0.025	20.769	0.74

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Table 4. Continued

Model	K	-2l	AIC$_c$	ΔAIC$_c$	w_i	w_i/w_1	R^2
Avian species in seizures (63)							
US import + CITES permit + voice + range size + quota years + CITES permit*range size	9	68.47	89.86	0	0.419	1	0.55
US import + CITES permit + voice + body mass + range size + quota years + US import*body mass + CITES permit*range size	12	60.69	91.06	1.195	0.231	1.817	0.66
US import + CITES permit + voice + body mass + range size + quota years + CITES permit*range size	10	68.16	92.48	2.616	0.114	3.698	0.63
US import + CITES permit + voice + range size + quota years + CITES permit*range size + range size*quota years	11	65.37	92.54	2.679	0.109	3.818	0.60
US import + CITES permit + voice + quota years + US import*CITES permit	8	75.73	94.39	4.531	0.043	9.638	0.59
US import + voice + CITES status + quota years	6	81.53	95.03	5.17	0.032	13.26	0.57

[a] CITES-status variable was not included because all parrots are listed on either Appendix I or II; abundance and region variables were re-scaled due to small sample size (Appendix A).

Conservation

Individuals of threatened species were rarely recorded in the market study or in government seizures. Thirteen market species (10%) and 2,034 individuals (6%) were listed as threatened on the International Union for Conservation of Nature and Natural Resources Red List (IUCN; 2013b), Peru's list of threatened species (MINAG 2004), or both (Table 5). Three species made up the vast majority of threatened individuals in the markets (n = 1,808; 89%, i.e., *Psittacara erythrogenys*, *Amazona festiva*, and *B. phyrroptera*). A higher diversity of threatened species was confiscated than recorded in the markets. Nineteen of the 64 confiscated species (30%) and 211 individuals (3%) were listed in a threatened category (Table 5). Fifty-seven market species (44%) and the majority of confiscated species, (n = 51; 80%) were listed on either CITES Appendix I or II largely due to the family group listings including parrots and raptors (Appendix B).

Ornamental, regional, and exotic birds

Captive-bred ornamental cage birds were frequently recorded in the market study. Over 57,000 individuals were observed for sale (62% of market), representing 14 species in three families and outnumbering native birds in six of the nine cities surveyed (Appendix B). *Melopsittacus undulatus* was the most commonly recorded ornamental species (n = 43,521), representing 76% of ornamental birds and 47% of the entire market. Native and ornamental bird species were observed for sale together at most markets surveyed (n = 35; 88%). Four regional species (*A. aestiva, B. chiriri, Myiopsitta monachus, Paroaria coronata*), and one exotic species (*Passer domesticus*) were recorded in low numbers (n = 322, 0.4%; Appendix B).

Table 5. Conservation status of native species and counts recorded in the market survey and seizure records in Peru (2007–2011).

Genus species	Common name	IUCN status[a]	Peru status[a]	Market counts	Seizure counts
Amazona festiva	Southern Festive Amazon	NT	NT	520	33
Andigena hypoglauca	Grey-breasted Mountain-toucan	NT	NT		2
Ara chloropterus	Red-and-green Macaw		VU	82	10
Ara macao	Scarlet Macaw		VU	47	15
Ara militaris	Military Macaw	VU	VU	7	4
Brotogeris pyrrhoptera	Grey-cheeked Parakeet	EN	EN	216	4
Buteogallus solitarius	Black Solitary Eagle	NT			1
Falco peregrinus	Peregrine Falcon		NT	3	15
Forpus xanthops[b]	Yellow-faced Parrotlet	VU	VU	24	22
Harpia harpyja	Harpy Eagle	NT	VU		1
Mitu tuberosum	Razor-billed Curassow		NT	21	
Patagioenas oenops	Peruvian Pigeon	VU	VU	4	
Phalacrocorax bougainvilliorum	Guanay Cormorant	NT	EN		2
Phoenicopterus chilensis	Chilean Flamingo	NT	NT		1
Pionites leucogaster[c]	White-bellied Parrot	VU		17	7
Pseudastur occidentalis	Grey-backed Hawk	EN	EN	2	
Psittacara erythrogenys	Red-masked Parakeet	NT	NT	1072	73
Pyrilia barrabandi	Orange-cheeked Parrot	NT		19	
Ramphastos ambiguus	Yellow-throated Toucan	NT	NT		1
Rhamphastos toco	Toco Toucan		NT		1
Spheniscus humboldti	Humboldt Penguin	VU	EN		9
Sula variegate	Peruvian Booby		EN		1
Vultur gryphus	Andean Condor	NT	EN		9

[a] NT = near threatened, VU = vulnerable, EN = endangered.
[b] Endemic species.
[c] Currently called *P. xanthomerius,* Black-legged Parrot, and is listed as Least Concern.

Discussion

       My study demonstrates that a large number of Peru's native birds, predominantly psittacines, are captured from the wild and illegally offered for sale in animal markets to domestic consumers. I found that Peru's current legal quota system, which started in 2001, had little influence on avian species abundance in domestic markets. I anticipated that if the quota system facilitated illegal domestic trade, birds with export quotas would make up a higher proportion of birds in the markets and a lower proportion of birds in seizures because they would be considered more "legal" by authorities. I found, however, that the majority of individual birds observed in both the markets and in seizures, representing 44 of 150 species, had export quotas (Table 3). This pattern indicates that Peru's domestic market was dominated by a few popular species that have export quotas, but their quota status did not facilitate illegal domestic trade or deter confiscation (Table 2). Authorities confiscated birds that were commonly available in the markets, regardless of their quota status, meaning risk to vendors was no less for selling quota-listed birds. Further, relatively few species (~ 1/3) observed in the markets had export quotas (Table 3), suggesting that harvesters and traders were not taking advantage of the potential "cover" offered by the legal export quotas.

       My regression analyses demonstrated that high historic export trade influenced avian species abundance in Peru's illegal domestic markets, but not the current quota system (Table 4). Interview data suggest that high exports to the United States and elsewhere, especially during the 1970s and 1980s, helped establish the domestic market because surplus birds, or those not selected for export, were then sold nationally (Daut et al. 2015). Much of Peru's domestic bird trade appears to be a consequence of tradition— dependent on which birds harvesters are accustomed to capturing—regardless whether the species has a quota or not. For example, all of the top 12 most abundant species in the markets (Table 2) were heavily exported from 1970–2001 ($\bar{x}$ = 10 years, SE = 6.5). Correspondingly, nine of the top 12 species were common to abundant in a 1989 market study in Lima, meaning 30–60 to > 60 individuals, respectively, were observed per visit (Begazo 1989).

Other factors associated with increased avian abundance in Peru's domestic market included originating from the Amazon or coastal regions and having a larger body size and a pleasant singing voice or "talking" abilities (Table 4). Songbirds, and especially species with aesthetically-pleasing songs popular for singing competitions, were most abundant in markets in Taiwan (Su et al. 2014) and Brazil (Alves et al. 2012). Talking ability was also associated with higher parrot poaching in Mexico (Pires & Clarke 2011), and when combined with bright colors and large size to represent parrot species' attractiveness, resulted in disproportionate selective poaching (Tella & Hiraldo 2014). In Peru, neither color nor large size influenced the parrot market; in fact, smaller body mass (i.e., lower price), was associated with higher market abundance.

Parrot abundance, unlike the full bird market, was influenced by both Peru's current quota system (i.e., more years with a published quota, 2001–2011), and historic trade (Table 4). In Mexico, parrot species with longer legal trade similarly correlated with higher poaching (Pires & Clarke 2011). The reason why the quota system influenced parrot abundance and not the full bird market was likely because parrots that were commonly exported in the past, and already popular in Peru's domestic markets, were assigned formal quotas in 2001 (Table 2). Having a formal export quota did not suddenly increase their market abundance (Begazo 1989); just as eliminating the quotas did not decrease market abundance. For example, two species, a parrot (*P. erythrogenys*), and a songbird (*Dives warszewiczi*), had quotas for only two years under the current quota system (2002–2003), but were still among the top 12 most abundant species in the market surveys (2007–2011). Furthermore, while Peru's historic domestic market was supplied with surplus birds harvested for a strong export market, contemporary international demand is not filling Peru's quotas. From 2001–2011, exports of the eight quota-listed parrots were only 43% of the published quotas. This implies that eliminating the quota system would not stop domestic trade and emphasizes the importance of domestic consumer demand and the influence of historic trade and traditional harvest, which have been recognized as important drivers of wildlife trade elsewhere (Cantú et al. 2007; Mancini et al. 2011; Cao Ngoc & Wyatt 2013).

Larger geographical ranges were also associated with higher parrot abundance (Table 4). Pires and Clarke found that larger ranges with overlapping human populations increased accessibility and contributed to higher poaching in Mexico (2011), Bolivia and Peru (2014). While this study did not investigate overlapping human population, it is reasonable to assume that a larger geographical range would provide greater accessibility for harvesters, particularly opportunistic villagers that poach nestlings during breeding seasons (Pires & Clarke 2011).

Government seizure records offer an independent perspective of Peru's illegal domestic bird trade and provide insight into what authorities consider worthwhile confiscating. Avian seizure and market abundances were explained by many of the same factors, including high historic trade levels, a pleasant singing voice or "talking" abilities, and small body size as seen with the parrots-only subset (Table 4). Confiscated birds also paralleled parrot abundance by having larger ranges and more years with a published quota. Similarity between abundance in confiscations and the parrot market was unsurprising given that 77% of all confiscations were *B. versicolurus*, a quota-listed parrot and the most abundant native species in the markets (Table 2). Removing this species from the seizure regression models did not change the variables in the most plausible model. Why authorities confiscated so many *B. versicolurus* may be, in part, because vendors appear less concerned about losing this inexpensive species compared to others, as *B. versicolurus* are often transported and displayed in large numbers at markets making them more difficult to hide from authorities. Having an export quota certainly did not protect *B. versicolurus* from confiscation compared to non-quota-listed species (Table 2).

Brotogeris versicolurus deserves further discussion given its high market and seizures abundance (this study; Ríos et al. 2008; Gastañaga et al. 2010), second only to captive-bred *M. undulatus* for the entire bird market (Appendix B). This small (75 gm, Dunning Jr. 2008), mostly green parakeet with average talking ability, is fairly common within its relatively average-sized geographical range in Amazonian Peru (Schulenberg et al. 2007). It does not represent the highly-attractive (large and colorful) psittacines

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disproportionately poached in Mexico (Tella & Hiraldo 2014). However, *B. versicolurus* nestlings are particularly easy to take from their nests in arboreal termite mounds close to the ground, and even though the capture variable was not retained in the most plausible models (Table 4), it was considered important for parrot poaching in Mexico (Pires & Clarke 2011). Two additional, yet potentially important, factors that I did not consider in the regression analyses were adaptability and hardiness. *Brotogeris versicolurus* readily adapts to secondary habitats, such as those close to urban areas, making them accessible to harvesters (Forshaw 2010). Furthermore, this parakeet was considered by local veterinarians and owners to be hardy and able to survive the stress of captivity better than other species (E. Daut, unpublished data).

It was encouraging that captive-bred ornamental birds were offered as legal pet options for Peru's domestic consumers (Appendix B). Ornamental birds made up more than half of the entire bird market and their market appears to be growing. Conversations with pet-store owners and veterinarians indicated that ornamental birds were now commonly available in Amazonian cities, when ten years ago, the only pet-bird options were wild-caught native birds (E. Daut, unpublished data). Reports from Southeast Asia, a region with high illegal bird trade, indicated that captive-bred ornamental birds likewise comprised substantial portions of bird markets (Shepherd et al. 2004; Jepson & Ladle 2005; Brooks-Moizer et al. 2009).

Although most of the native birds in markets and seizures were not threatened, 2,222 birds (n = 23 threatened species) were illegally taken from the wild (Table 5). Of particular concern were the six globally and/or nationally endangered species, including iconic species such as *Vultur gryphus* and *Spheniscus humboldti*. Authorities confiscated a greater diversity of threatened species than what was observed in the markets (Table 5). This could be explained by where authorities typically confiscate animals—at highway control posts versus crowded markets that are notoriously dangerous. The relatively low number of threatened species in the markets could be due to the growing use of the internet and *entrega directa*—home-delivery service—which bypasses the risk of confiscation from displaying individuals in the markets (Ríos et al. 2008; Gastañaga

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et al. 2010). This implies that there could be considerable hidden and specialized bird trade in Peru for domestic consumers and/or for smuggling internationally.

Peru's economy is strong and as it continues to grow (Vera & Yu 2013), it may drive trade in rarer species as status symbols (Shepherd et al. 2004; Courchamp et al. 2006). Households owning threatened avian species in Indonesia, for example, were richer and better educated (Jepson & Ladle 2005). Moreover, a stable economy has spurred Peru's domestic and international tourism, which may increase demand for native birds at "rescue centers" to display for tourists (Daut et al. 2015). Authorities have also commented that the frequency of wildlife confiscations from tourists has risen at Lima's international airport in recent years (P. Mendoza, Wildlife Conservation Society (WCS), unpublished data). The potential for increased trade targeting wealthy consumers and tourists calls for greater vigilance to enforce wildlife legislation by Peru's authorities, whom typically do not prioritize wildlife (Shanee 2012; Daut et al. 2015). Better training and capacity building of authorities should improve enforcement (Bennett 2011). Interview data indicated there was high turnover for wildlife officials (e.g., often every 3–6 months), and limited knowledge regarding details of Peru's quota system (Daut, unpublished data). Because only 30% of confiscated birds were identified to species, training should include species identification and record management—banal suggestions, yet critical steps—to improve the ability to monitor the illegal trade and develop targeted interventions (Brooks-Moizer et al. 2009; World Wildlife Fund / Dalberg 2012).

In conclusion, my results show no evidence that the quota system, facilitated illegal domestic trade, and it is doubtful that eliminating the quotas would stop the domestic trade in the short term. It was the historic export trade that helped create Peru's domestic bird market and shaped the current species composition—a scenario likely repeated elsewhere in the Neotropics. While improving enforcement of Peru's wildlife legislation should be encouraged, I recognize that enforcement is just one aspect of combating illegal wildlife trade (Challender & MacMillan 2014). Better understanding of consumer demand and the effectiveness of strategies to raise public awareness,

modify consumer behavior, and promote market substitutions would provide much needed information to develop an integrated approach to help decrease illegal native bird trade in Peru (Challender et al. 2014).

CHAPTER III

INTERACTING EFFECTS OF NEWCASTLE DISEASE TRANSMISSION AND

ILLEGAL TRADE ON A WILD POPULATION OF WHITE-WINGED PARAKEETS

IN PERU: A MODELING APPROACH

Synopsis

Illegal wildlife-pet trade can threaten wildlife populations directly from over-harvest, but also indirectly as a pathway for introduction of infectious diseases. This study evaluated consequences of a hypothetical introduction of Newcastle disease (ND) into a wild population of Peru's most trafficked psittacine, the white-winged parakeet (*Brotogeris versicolurus*) through release of infected confiscated individuals. I developed two mathematical models to describe ND transmission and the influence of illegal harvest in a homogeneous (model 1) and age-structured population of parakeets (model 2). Infection transmission dynamics and harvest were consistent for all individuals in model 1, which rendered it mathematically more tractable compared to the more complex, age-structured model 2 that separated the host population into juveniles and adults. I evaluated the interaction of ND transmission and harvest through changes in the basic reproduction number (R_0) and short-term host population dynamics. My findings demonstrated that ND introduction would provoke considerable disease-related mortality, up to 24% population decline in two years, but the magnitude of the outbreak would be dampened by high harvest rates. Model 2 produced moderate differences in disease dynamics compared to model 1 ($R_0 = 2.66$ and 3.63, respectively), and highlighted the importance of adult disease dynamics in diminishing the epidemic potential. Therefore, I suggest that future studies should use a more realistic, age-structured model. Finally, for the presumptive risk that illegal trade of white-winged parakeets could introduce ND into wild populations, my results suggest that while high harvest rates may have a protective effect on the population by reducing virus

transmission, the combined effects of high harvest and disease-induced mortality may threaten population survival. My results capture the complexity and potential consequences of the interaction between ND transmission and harvest in a wild parrot population and highlight the importance to protect these populations from illegal trade in the first place.

Introduction

Illegal wildlife trade and infectious diseases are recognized conservation threats affecting wildlife populations (Daszak et al. 2000; Fèvre et al. 2006; Rosen & Smith 2010). Illegal and poorly regulated wildlife trade can result in over-harvest and threaten population and species survival (Nekaris et al. 2010; Nijman et al. 2012; Shepherd 2012; Sung et al. 2013). Introduced infectious diseases have been linked to major declines of wildlife populations (Daszak et al. 2003; Smith et al. 2006; Frick et al. 2010), and even species extinctions (Warner 1968; Wyatt et al. 2008). The influence of *legal* harvest or culling on disease dynamics in wildlife populations has been examined (Wonham et al. 2004; Choisy & Rohani 2006; Woodroffe et al. 2006), but the influence of *illegal* wildlife trade on the introduction and spread of infectious diseases has rarely been investigated (but for related topics see: Brooks-Moizer et al. 2009; van den Berg 2009; Gilbert et al. 2012). The risks of introducing infectious diseases are particularly high in developing nations where illegal wildlife trade for domestic consumers flourishes and law enforcement and disease surveillance are lacking (Karesh 1995; Keane et al. 2008; Bennett 2011; Karesh et al. 2012). As a case study, I used simulation modeling to evaluate a hypothetical introduction and outbreak of Newcastle disease (ND) in a population of Peru's most trafficked psittacine, the white-winged parakeet (*Brotogeris versicolurus*) (Table 2, Chapter 2; Ríos et al. 2008; Gastañaga et al. 2010). Threat of infectious disease and illegal harvest of wildlife should be of concern for Peru because it is a megadiverse country and a high priority area for biodiversity conservation (Myers et al. 2000).

The white-winged parakeet is a small, non-threatened, highly gregarious species that is common throughout most of its Amazonian range (Schulenberg et al. 2007; Birdlife International 2014c). Peruvian authorities consider domestic trade of the white-winged parakeet and other native birds illegal because harvest and commercialization are conducted without proper licenses and authorizations (Chapter 2). During a five-year market survey in Peru, supply of white-winged parakeets was surprisingly constant throughout the year, which may stem from the dual harvest techniques employed (E. Daut, unpublished data). These two techniques include taking nestlings from easily accessible nests located in arboreal termite mounds during the breeding season, and capturing adult parakeets throughout the year using mist nets at roost and feeding sites (Begazo 1989). It is impossible to determine whether harvest is sustainable (Beissinger & Bucher 1992), but local experts assume current harvest rates do not negatively influence abundance (J. Álvarez, *Dirección General de Diversidad Biológica*, personal communication).

Newcastle disease is a highly infectious and fatal viral disease caused by avian paramyxovirus serotype-1 that affects many avian species including parrots and poultry (Leighton & Heckert 2007). Large epidemics have occurred in poultry operations (Walker et al. 1973; Kinde et al. 2005), racing pigeons (Alexander et al. 1986), and free-ranging double-crested cormorants (Kuiken 1999). The frequency of such epidemics in free-ranging populations appears to be increasing (White et al. 2015). Even though vaccination programs have largely prevented recent outbreaks in commercial flocks, ND is still a serious problem in backyard poultry in rural areas throughout the developing world and in the pet trade (Awan et al. 1994; Spradbrow 2005; Jibril et al. 2014). In 2004, ND virus was isolated in a shipment of imported parrots and other species from Pakistan to Italy (World Parrot Trust 2004a).

The ND virus spreads horizontally between healthy and infected birds through direct contact with bodily secretions from infected birds (Alexander 2009). Crowded confinement typical of poultry houses or large breeding rookeries provides ideal conditions for virus transmission (Alexander 2009). Disease in parrots is suspected to

result from contact with infected poultry, particularly at animal markets (Kaleta & Baldauf 1988; Hines & Miller 2012). Wild-caught parrots smuggled into the United States in the 1970s were suspected to have acquired ND while at animal markets in South America (Walker et al. 1973; Kaleta & Baldauf 1988; Panigrahy et al. 1993). Subsequent outbreaks of ND in chickens cost the U.S. poultry industry millions of dollars (Panigrahy et al. 1993). The most common clinical signs in captive psittacine species were respiratory, but ranged from lethargy to limb paralysis (Erickson et al. 1977; Clubb et al. 1980; Hirai 1981; Bruning Fann 1992). Mortality can reach as high as 100% (Panigrahy et al. 1993), but typically ranged from 20 to 80% (Grausgruber 1972; Erickson et al. 1977; Clubb et al. 1980).

White-winged parakeets are susceptible to ND. During an outbreak in Austria, 53% (n = 32) of parakeets died from ND following importation (Grausgruber 1972). In the early 1980s, ND was diagnosed in importation lots of white-winged parakeets from Argentina and Bolivia four times according to United States Department of Agriculture (USDA) quarantine records (Nilsson 1985). Newcastle disease is considered endemic in Peru. Twelve outbreaks were reported to the World Organization for Animal Health (OIE) during 2008–2011 in unvaccinated backyard (*criollo)* chickens and fighting cocks (e.g., The Poultry Site 2009). In animal markets throughout Peru, it is common to observe wild-caught parrots alongside *criollo* chickens (E. Daut, personal observation), thus providing the opportunity for cross-species ND transmission. Authorities frequently confiscate white-winged parakeets (Chapter 2) and immediately release these individuals into the wild (González Medina 2004), typically without health evaluation because they do not have financial or diagnostic means to conduct medical screening (Karesh 1995; Jiménez & Cadena 2004; Marini & Garcia 2005; Zhang et al. 2008; Godoy & Matushima 2010; Gomes Destro et al. 2012). Although ND has not been identified in the limited studies of psittacines in the wild to date (Johnson et al. 1986; Goodman & Hanson 1988; Gilardi et al. 1995; Karesh et al. 1997; Deem et al. 2005), I expect that illegal trade provides a mechanism for ND to reach susceptible wild white-winged parakeets due to the release of confiscated individuals infected at animal markets.

Infectious disease modeling is a useful tool for conservationists and epidemiologists to evaluate potential synergistic effects of illegal trade and disease on wildlife populations and to compare mitigating strategies (Dubé et al. 2007). The influence of illegal trade—specifically harvest—on pathogen transmission can be evaluated by comparing the pathogen's basic reproduction number (R_0) at different harvest rates (Heesterbeek 2002). R_0 is the average expected number of secondary infections produced by one typical infectious individual introduced into a fully susceptible host population (Heesterbeek 2002), and is often used as a threshold value to determine whether or not a pathogen can invade and persist in the population i.e., when $R_0 \geq 1$, or fades out ($R_0 < 1$).

Under certain density-dependent pathogen transmission conditions, harvest can decrease transmission and is the reason for culling to prevent disease spread (Wobeser 2002; Haydon et al. 2004). In other cases, where a host population is under strong density-dependence that stimulates natality, harvest can increase the number of susceptible individuals, disease prevalence and disease-induced mortality (Choisy & Rohani 2006). Because harvest is often selective for specific age groups, and diseases can disproportionately affect some age groups, age structure can be an important demographic component in mathematical models. Recent studies have demonstrated that incorporating age structure into disease modeling can have strong, yet often unpredictable, influences on wildlife disease dynamics (Heisey et al. 2006; Brooks-Pollock et al. 2010).

I hypothesized that (1) introducing ND into a susceptible population of white-winged parakeets would result in an outbreak with considerable mortality and (2) increasing harvest would lower disease transmission and the magnitude of the outbreak. To evaluate these hypotheses, I developed two deterministic, continuous-time, mathematical models, with and without age structure, to assess whether predictions about ND dynamics would differ between a simplified model with a homogeneous bird population and a presumed more realistic, but less tractable, model with an age-structured host population. Both models were considered under different harvest

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scenarios and R_0 and disease-related mortality were assessed using a combination of analytical and numerical approaches. I conducted sensitivity and scenario analyses to evaluate the robustness of the models' results in the presence of uncertainty to individual parameters. Lastly, I discussed the limitations and implications of my results, including the conservation relevance of illegal trade and ND emergence in wild populations of white-winged parakeets.

Materials and methods

Model formulation

Because ND typically results in severe but short-lived epidemics in avian species, I focused my attention on short-term infection dynamics without including density-dependent responses from the host population to the disease-induced mortality (e.g., increased fecundity). Given the possibility of long-term chronic infections in parrots, I did consider an endemic state where ND persists in the population.

In model 1 (Fig. 3), I described the parakeet population as homogeneous where the SEI_AI_CR model assumed no differences in the infection–transmission dynamics and harvest among age groups. The host population was divided into susceptible (S), exposed (E), acutely-infected (I_A), chronically-infected (I_C) and recovered (R) classes (Anderson & May 1991). I included two infectious stages (I_A and I_C) because experimental evidence suggested two levels of severity of clinical signs, which I used as a proxy for viral shedding (Erickson et al. 1977; Erickson et al. 1978).
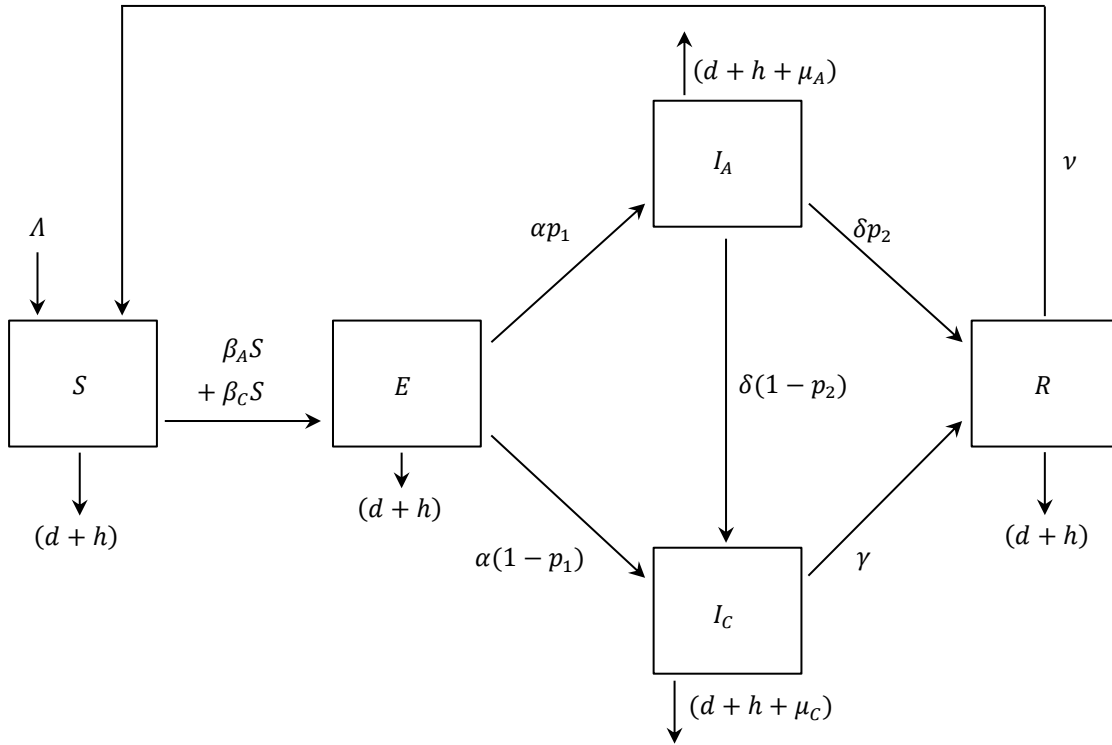
Figure 3. Compartmental diagram of model 1, the dynamics of Newcastle disease in a homogeneous population of white-winged parakeets. Five transition states include: susceptible (S), exposed (E), acutely-infected (I_A), chronically-infected (I_C) and recovered (R). See Table 6 for parameter descriptions.

In model 2, I divided the host population into juvenile and adult stages to account for age-related differences in harvest and disease transmission and severity (Fig. 4). While model 2 was demographically more realistic than model 1, it was also far more complex and less tractable, which makes its application by non-mathematicians more difficult and brings up a question of whether model 1 could be an acceptable alternative for studying interaction of infection and harvest in a wild bird population. To assure a fair comparison of results between both models, model 2 was structured to collapse into model 1 when the two age stages had the same parameter values. Both models included a baseline harvest rate (h_b) and I conducted scenario analyses to evaluate the interaction of ND dynamics and additional harvest ($h1$) on R_0 and host population size.
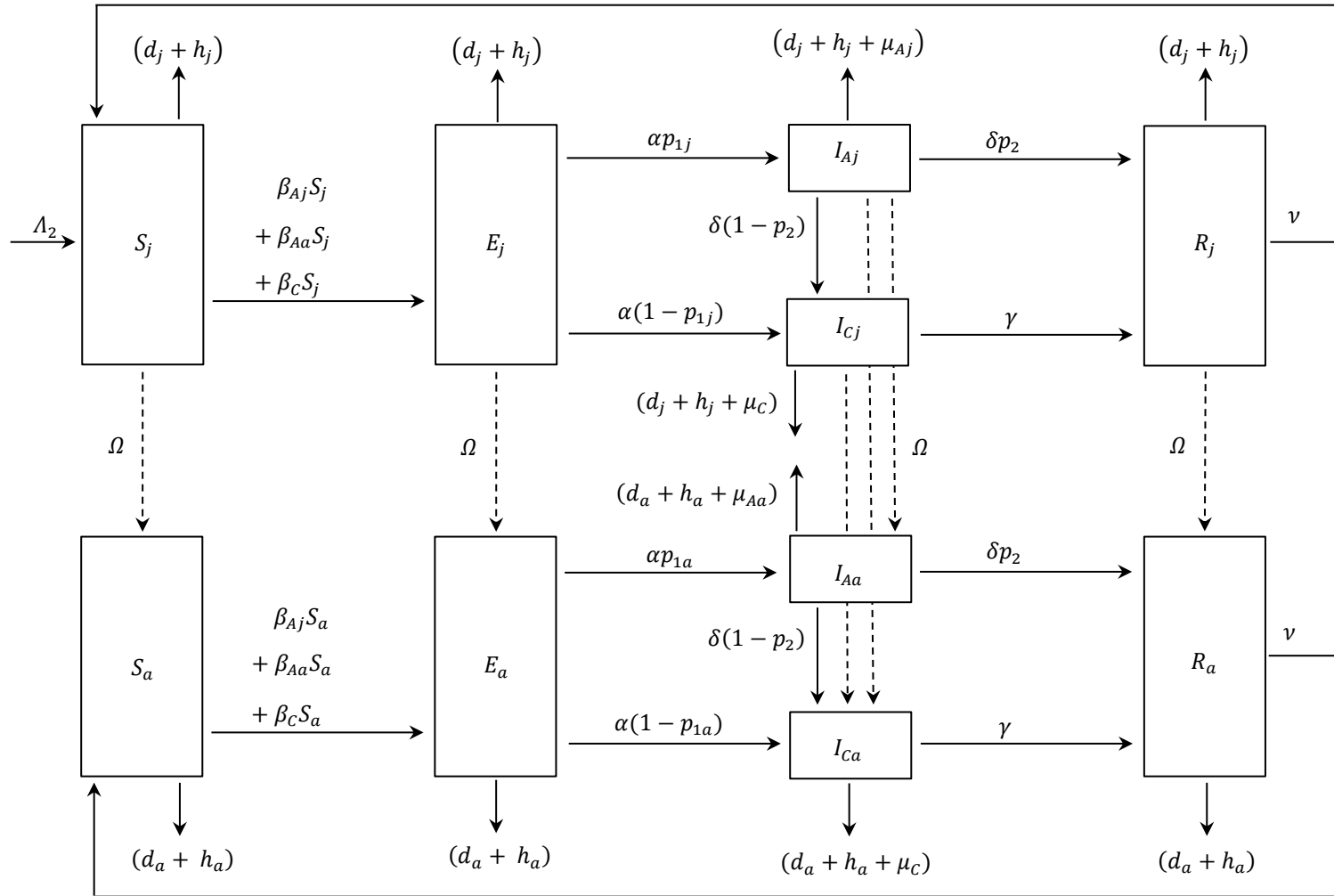
Figure 4. Compartmental diagram of model 2, the dynamics of Newcastle disease in an age-structured population of white-winged parakeets. Transition states for juvenile parakeets are: susceptible (S_j), exposed (E_j), acutely-infected (I_{Aj}), chronically-infected (I_{Cj}) and recovered (R_j) and for adult parakeets the states are: susceptible (S_a), exposed (E_a), acutely-infected (I_{Aa}), chronically-infected (I_{Ca}) and recovered (R_a). See Table 6 for parameter descriptions.

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My mathematical framework started with the following assumptions:

(1) The host population was a single, free-mixing population and individual parakeets were equally likely to encounter an infected individual. This was a realistic assumption given the gregarious nature of white-winged parakeets and the large number of individuals at communal roost sites.

(2) The host population was stable under initial conditions, closed to immigration and emigration, and the parakeet natality and mortality were not under the influence of density dependence. While these conditions may not always hold true, they were useful simplifying assumptions that helped isolate the evaluation of harvest and ND dynamics.

(3) At hatching, chicks were susceptible to ND virus, and both sexes were equally affected (Jibril et al. 2014).There is limited evidence that psittacine chicks can receive maternal antibodies through the egg (Lung 1996); however, no studies have evaluated whether protective maternal ND antibodies are transferred to psittacine chicks.

(4) Transmission of ND was density-dependent where the number of contacts per unit time was proportional to the number of individuals in the population (McCallum et al. 2001). Density-dependent transmission was a reasonable assumption and has been suggested for systems where the pathogen is transmitted through random contact among individuals and/or by aerial transmission (May & Anderson 1979; Anderson & May 1981). Airborne transmission was considered to contribute to spread of the ND virus near poultry facilities (Hugh-Jones et al. 1973; Li et al. 2009). In laboratory experiments involving two Neotropical psittacine species, 100% of contact-exposed individuals (those housed with aerosol-exposed birds), became infected (Erickson et al. 1977).

I used a system of ordinary differential equations (ODEs) to describe transmission of ND in white-winged parakeets for each model (equations (1–5) for model 1 and equations (6–15) for model 2).

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Model 1

$$dS/dt = \Lambda - (d+h)S - \beta_A S I_A - \beta_C S I_C + \nu R \tag{1}$$

Where $\Lambda = N(d+h)$ and N changes over time as $N(t) = S(t) + E(t) + I_A(t) + I_C(t) + R(t)$

$$dE/dt = \beta_A S I_A + \beta_C S I_C - (d+h+\alpha)E \tag{2}$$

$$dI_A/dt = \alpha p_1 E - (d+h+\mu_A+\delta)I_A \tag{3}$$

$$dI_C/dt = \alpha(1-p_1)E + \delta(1-p_2)I_A - (d+h+\mu_C+\gamma)I_C \tag{4}$$

$$dR/dt = \delta p_2 I_A + \gamma I_C - (d+h+\nu)R \tag{5}$$

Model 2

<u>Juvenile</u>

$$dS_j/dt = \Lambda_2 - (d_j+h_j+\Omega)S_j - \beta_{Aj}S_j I_{Aj} - \beta_C S_j I_{Cj} - \beta_{Aa}S_j I_{Aa} - \beta_C S_j I_{Ca} + \nu R_j \tag{6}$$

Where $\Lambda_2 = N(d_j+h_j+\Omega)(d_a+h_a)/(d_a+h_a+\Omega)$ and N changes over time as $N(t) = N_j(t) + N_a(t)$ where $N_j(t) = S_j(t) + E_j(t) + I_{Aj}(t) + I_{Cj}(t) + R_j(t)$ and $N_a(t) = S_a(t) + E_a(t) + I_{Aa}(t) + I_{Ca}(t) + R_a(t)$

$$dE_j/dt = \beta_{Aj}S_j I_{Aj} + \beta_C S_j I_{Cj} + \beta_{Aa}S_j I_{Aa} + \beta_C S_j I_{Ca} - (d_j+h_j+\Omega+\alpha)E_j \tag{7}$$

$$dI_{Aj}/dt = \alpha p_{1j}E_j - (d_j+h_j+\Omega+\mu_{Aj}+\delta)I_{Aj} \tag{8}$$

$$dI_{Cj}/dt = \alpha(1-p_{1j})E_j + \delta(1-p_2)I_{Aj} - (d_j+h_j+\Omega+\mu_C+\gamma)I_{Cj} \tag{9}$$

$$dR_j/dt = \delta p_2 I_{Aj} + \gamma I_{Cj} - (d_j+h_j+\Omega+\nu)R_j \tag{10}$$

<u>Adult</u>

$$dS_a/dt = \Omega S_j - (d_a+h_a)S_a - \beta_{Aa}S_a I_{Aa} - \beta_C S_a I_{Ca} - \beta_{Aj}S_a I_{Aj} - \beta_C S_a I_{Cj} + \nu R_a \tag{11}$$

$$dE_a/dt = \Omega E_j + \beta_{Aa}S_a I_{Aa} + \beta_C S_a I_{Ca} + \beta_{Aj}S_a I_{Aj} + \beta_C S_a I_{Cj} - (d_a+h_a+\alpha)E_a \tag{12}$$

$$dI_{Aa}/dt = \Omega I_{Aj} + \alpha p_{1a}E_a - (d_a+h_a+\mu_{Aa}+\delta)I_{Aa} \tag{13}$$

$$dI_{Ca}/dt = \Omega I_{Cj} + \alpha(1-p_{1a})E_a + \delta(1-p_2)I_{Aa} - (d_a+h_a+\mu_C+\gamma)I_{Ca} \tag{14}$$

$$dR_a/dt = \Omega R_j + \delta p_2 I_{Aa} + \gamma I_{Ca} - (d_a+h_a+\nu)R_a \tag{15}$$

For both models, the initial (time $t = 0$) susceptible population, $S(0)$, was set equal to the total population, $N(0)$, minus one individual, which represented an acutely-infectious parakeet introduced into the population, $I_A(0) = 1$ and $I_{Aa}(0) = 1$ for models 1 and 2, respectively. All remaining stages were set to zero. Additionally for model 2, the proportions of N_j and N_a were fixed according to disease-free equilibrium (DFE) conditions so that the initial age composition (i.e., the fraction of juvenile and adult parakeets) was the same across all iterations irrespective of the varying total population size (N). Model analysis was conducted in Matlab (MathWorks, USA).

Basic reproduction number (R_0)

To calculate R_0 for the systems of ODEs, I used the next-generation method (NGM; Diekmann et al. 1990; van den Driessche & Watmough 2002). See Appendix C for the full derivations of R_0. For model 1 the derived expression for R_0 (Eq. C1) was:

$$R_0 = R_{0A} + R_{0C},$$

The terms R_{0A} and R_{0C} represent the average number of secondary infections resulting from interactions between susceptible and acutely- and chronically-infected hosts, respectively. For model 2, the derived expression for R_0 (Eq. C2) was:

$$R_0 = \tfrac{1}{2}\left[R_{01} + R_{02} + \sqrt{(R_{01} - R_{02})^2 + 4R_{03}R_{04}}\right].$$

The terms R_{01} and R_{02} represent the average number of secondary juvenile or adult infections, respectively, produced by one exposed juvenile E_j during its entire infection period. The terms R_{03} and R_{04} represent the average number of secondary juvenile or adult infections produced by one exposed adult E_a during its entire infection period, respectively.

Parameter estimates

Parameter notations, definitions, mean values, distributions for sensitivity analyses, and sources of information are described below and in Table 6. All demographic parameters except population size were constant and disease parameters were allowed to vary around their corresponding baseline values.

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Table 6. Definitions and values of parameters for the model of Newcastle disease (ND) transmission in a homogeneous (model 1) and age-structured (model 2) population of wild white-winged parakeets.

Notation	Definition (unit)	Baseline value	Sensitivity analysis	5th and 95th percentiles	Model	Source
$N(0)$	Initial number of individuals of white-winged parakeets in a typical flock in Ucayali, Peru	200	Log-normal (ln(189), ln(1.4))	109, 329	1	(Shroads 1974; Forshaw 1989)
N_j, N_a	Initial number of individual juvenile (N_j) and adult (N_a) white-winged parakeets in a typical post-breeding flock in Ucayali, Peru	$N_j = 0.08N$, $N_a = 0.92N$			2	Estimated for D_d=5 years[a]
D_d	Life expectancy (year)	5.0[b]			1, 2	(Young et al. 2012)
d	Natural mortality rate (day^{-1})	$1/D_d$			1, 2	
D_Ω	Duration of juvenile stage (day)	135			2	Informed from: (Rowley 1983; Ritchie et al. 1992; Lindsey et al. 1994; Lung 1996; Salinas-Melgoza & Renton 2007; Denadai et al. 2010; Cox et al. 2014)
Ω	Rate of leaving juvenile stage (day^{-1})	$1/D_\Omega$			2	
d_j	Natural juvenile mortality rate (day^{-1})	$1/–D_\Omega/\ln(0.6)$[c]			2	(Sandercock & Beissinger 2002; Salinas-Melgoza & Renton 2007)
d_a	Natural adult mortality rate (day^{-1})	$1/(1/d–1/d_j)$			2	
h_b	Baseline harvest rate (year^{-1})[d]	1%			1, 2	P. Mendoza, WCS, unpublished data
$h1$	Additional harvest rate (year^{-1})[d]	0[e]			1, 2	
h	Total harvest rate (year^{-1})[d]	h_b+h1			1, 2	
h_j	Total juvenile harvest rate (year^{-1})[d]	$0.4h$			2	P. Mendoza, WCS, unpublished data

Table 6 Continued

Notation	Definition (unit)	Baseline value	Sensitivity analysis	5th and 95th percentiles	Model	Source
h_a	Total adult harvest rate (year^{-1})[d]	0.6h			2	P. Mendoza, WCS, unpublished data
β_A	Transmission rate from an acutely-infected parakeet (individual^{-1} day^{-1})	0.00107	Uniform (0.00107*0.5, 0.00107*1.5)	0.000601, 0.0016	1, 2	(Johnston 1992)
I_r	Infectiousness reduction coefficient for chronically infected parakeets	0.1	Uniform (0.05, 0.15)	0.055, 0.145	1, 2	Assumed
β_C	Transmission rate from a chronically-infected parakeet (individual^{-1} day^{-1})	$\beta_A I_r$			1, 2	
$c\beta_A$	Age-dependent acute transmission factor	0.25	Uniform (0.25*0.5, 0.25*1.5)	0.1375, 0.3625	2	Informed from: (Erickson et al. 1980; Alexander et al. 2004; Kapczynski et al. 2006)
β_{Aj}	Transmission rate for acutely-infected juvenile parakeet (individual^{-1} day^{-1})	$(1+c_{\beta A})\beta_A$			2	
β_{Aa}	Transmission rate for acutely-infected adult parakeet (individual^{-1} day^{-1})	$(1-c_{\beta A})\beta_A$			2	
D_α	Duration of infected but not yet infectious stage (day)	5.5	Exponential (1/5.5)	0.3, 16.5	1, 2	(Leighton & Heckert 2007)
α	Rate of becoming infectious (day^{-1})	$1/D_\alpha$			1, 2	
D_δ	Duration of acute-infectious stage (day)	30	Exponential (1/30)	1.5, 89.9	1, 2	(Erickson et al. 1978)
δ	Rate of leaving acute-infectious stage (day^{-1})	$1/D_\delta$			1, 2	
D_γ	Duration of chronic-infectious stage (day)	39	Exponential (1/39)	2.0, 116.8	1, 2	(Erickson et al. 1977)
γ	Rate of leaving chronic-infectious stage (day^{-1})	$1/D_\gamma$			1, 2	
D_v	Duration of immunity (day)	243	Uniform (120, 365)	132.25, 352.75	1, 2	(Erickson et al. 1977)
ν	Rate of losing immunity (day^{-1})	$1/D_\nu$			1, 2	

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Table 6 Continued

Notation	Definition (unit)	Baseline value	Sensitivity analysis	5th and 95th percentiles	Model	Source
p_1	Probability of acute infection	0.625	Uniform (0.5, 0.75)	0.5125, 0.7375	1	(Erickson et al. 1977)
p_2	Probability of recovery from acute infection	0.5	Uniform (0.375, 0.625)	0.3875, 0.6125	1, 2	Informed from: (Parede & Young 1990; Carrasco et al. 2009; Chukwudi et al. 2012)
p_{1j}	Probability of acute juvenile infection	0.75	Uniform (0.625, 0.875)	0.6375, 0.8625	2	Informed from: (Panigrahy et al. 1993; Kuiken et al. 1998b; Alexander 2009; Barman et al. 2010)
p_{1a}	Probability of acute adult infection	0.5	Uniform (0.375, 0.625)	0.3875, 0.6125	2	Informed from: (Panigrahy et al. 1993; Kuiken et al. 1998b; Alexander 2009; Barman et al. 2010)
pd_A	Probability of acute disease-related death	0.25	Uniform (0.1,0.4)	0.115, 0.385	1, 2	Informed from: (Grausgruber 1972)
μ_A	Disease-related mortality rate for acutely-infected parakeet (day^{-1})	pd_A/D_δ			1, 2	
pd_C	Probability of chronic disease-related death	0.075	Uniform (0.025, 0.125)	0.03, 0.12	1, 2	(Erickson et al. 1977; Erickson et al. 1978)
μ_C	Disease-related mortality rate for chronically-infected parakeet (day^{-1})	pd_C/D_v			1, 2	
c_m	Age-dependent acute mortality factor	0.25	Uniform (0.25*0.5, 0.25*1.5)	0.1375, 0.3625	2	Informed from: (Panigrahy et al. 1993; Kuiken et al. 1998b; Alexander 2009; Barman et al. 2010)

Table 6 Continued

Notation	Definition (unit)	Baseline value	Sensitivity analysis	5th and 95th percentiles	Model	Source
μ_{Aj}	Disease-related mortality rate for acutely-infected juvenile parakeet (day^{-1})	$(1+c_m)\mu_A$			2	
μ_{Aa}	Disease-related mortality rate for acutely-infected adult parakeet (day^{-1})	$(1-c_m)\mu_A$			2	

[a] Proportions of N_j and N_a were fixed according to disease-free equilibrium (DFE) conditions and remained constant for all iterations. When life expectancy D_d=2, N_j=0.22N, N_a=0.78N; and when D_d=9, N_j=0.05N, N_a=0.95N.
[b] Scenario analysis was conducted at 2, 5, and 9 years.
[c] 0.6 represents 40% mortality in the juvenile stage.
[d] Annual rates were prorated to daily rates.
[e] Scenario analysis was conducted at 0, 2, 5, and 10%.

Model 1

Host demography and harvest

Flocks of white-winged parakeets can range from 700 to 1,000 individuals (Forshaw 1989; Tossas et al. 2012), but flocks of 200 birds have been commonly reported (Shroads 1974; Forshaw 1989). Therefore, I defined the initial population of parakeets as ($N(0) = 200$), which included those birds roosting together at a communal site throughout the year, except during the breeding season when pairs separate for nesting. I set population recruitment (Λ) equal to the sum of natural mortality (d) and baseline harvest (h_b) to maintain a stable population in absence of additional harvest (hl), so that $\Lambda = N(d+h_b)$, as supported by local experts (see Introduction). Daily natural mortality was calculated as the inverse of the mean life expectancy ($D_d = 5$ years) from captive white-winged parakeets, so that $d = 1/D_d$ (Young et al. 2012). Baseline harvest of white-winged parakeets was set at a conservatively low constant daily rate for a cumulative total annual harvest of 1% ($h_b = 0.01/365$).

Transmission rate

Transmission coefficients (β) for ND in psittacines have not been published; therefore, I adapted a transmission probability published for backyard poultry that was considered to reasonably represented ND dynamics in wild white-winged parakeets. In a mathematical model describing density-dependent ND dynamics in a backyard chicken flock, Johnston (1992) estimated 3% infection probability during a 14-day period. I prorated this probability to a per day rate for the population size and used it as a baseline transmission rate for acutely-infectious individuals, so that $\beta_A = (3/14)200$ individual^{-1} day^{-1} (Table 6). Chronic ND transmission rate was assumed to be a fraction ($I_r = 10\%$) of the acute transmission rate, so that $\beta_C = \beta_A I_r$.

Infection stages

According to the standard assumption of exponentially-distributed periods of infection (Anderson & May 1991), the reciprocal values of the mean durations in days that a parakeet spends in the exposed (E), acutely-infected (I_A), chronically-infected (I_C), and recovered (R) stages were used as the daily rates α, δ, γ, and ν, respectively (Table 6; Fig. 3). The daily rate of becoming infectious, therefore, was the inverse of the duration of an average latent period reported for most studied avian species ($\alpha = 1/5.5$) (Leighton & Heckert 2007). I based the duration of the acute-infectious stage on the study by Erickson et al. (1978) where individual Neotropical psittacines (n = 48) shed ND virus on average for 30 days so that $\delta = 1/30$. Although some individuals continued to chronically shed for over a year, on average individuals had stopped shedding by 39 days post infection (Erickson et al. 1977), which represented the baseline recovery rate from chronic infection $\gamma = 1/39$ and was consistent with shedding duration observed in other avian species (Vickers & Hanson 1979; Kuiken et al. 1998a; Kapczynski et al. 2006). I used this same duration for individuals that became chronically infected directly following exposure and for those individuals transitioning from an acute infection (Fig. 3). I based the recovery rate on the average duration of effective ND antibody titers (> 1.2 log10; Alexander et al. 2004) in experimental infections so that the average daily rate of immunity loss was $\nu = 1/243$ (Erickson et al. 1977).

Acute and chronic infections

According to ND infection rates in psittacines in captive and experimental conditions, I assumed that all effectively contacted white-winged parakeets would become either acutely- or chronically-infected, with acutely-infected parakeets shedding more ND virus (Pearson 1976; Erickson et al. 1977; Clubb et al. 1980; Bruning Fann 1992). Following Erickson et al.'s (1977) experimental study, I considered that 63% (p_1) of newly infected white-winged parakeets would become acutely infected, and $1-p_1$ would become chronically infected (Fig. 3). After acute infection, parakeets could recover or become chronically infected where individuals continued to shed virus but at

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lower levels. Little has been published regarding recovery or progression to a chronic ND state; however, a chronic-like state is common following live ND vaccination and has been considered a concern for environmental contamination and consequent infection spread (Parede & Young 1990; Carrasco et al. 2009; Chukwudi et al. 2012). Therefore, I considered that 50% of acutely-infected individuals would recover (p_2), while the remainder ($1–p_2$) would become chronically infected.

Disease-related mortality

Mortality from ND was over 50% in captive white-winged parakeets (Grausgruber 1972). Under free-ranging conditions, I assumed that mortality would be lower, so considered that 25% of individuals would die from ND during the acute-infectious period (30 days) making the daily rate, $\mu_A = 0.25/30$ (Table 6). To obtain disease-related mortality in chronically-infected parakeets, I averaged mortality recorded in experimentally-infected psittacines during the nine days following the acute-infection period so that $\mu_C = 0.075/39$ (Erickson et al. 1977; Erickson et al. 1978).

Model 2

Host demography and harvest

I set the initial population size of the two age classes according to their distribution at the disease-free equilibrium with life expectancy (D_d), so that $N(0) = N_j + N_a$. For instance, when $D_d = 5$ years and $N(0)=200$, $N_j = 16$ (8%) and $N_a = 184$ (92%) (Table 6). I estimated the duration of the juvenile stage based on two factors: (1) the age when juveniles develop immune-competence, and (2) when their survival rate starts to increase. Development of immuno-competence in psittacines and other altricial species is poorly understood (Apanius 1980; Schat et al. 2013), but appears to occur between six weeks (Ritchie et al. 1992; Lung 1996) and five months (Denadai et al. 2010). Considering juvenile survival, it is widely recognized that juveniles of many avian species suffer their highest mortality during the first several months after fledging (Rowley 1983; Lindsey et al. 1994; Salinas-Melgoza & Renton 2007; Cox et al. 2014),

which for white-winged parakeets occurs at roughly six weeks of age (Shroads 1974). Combining these two factors I considered that juveniles transition to adults at $D_\Omega = 135$ days (4.5 months), meaning that the maturation rate was $\Omega = 1/135$.

I fixed juvenile mortality at 40% during the 135-day long juvenile period (Sandercock & Beissinger 2002; Salinas-Melgoza & Renton 2007). The corresponding juvenile population was modeled as an exponential decay $S_j(t) = S_j(0)e^{(-dj*t)}$ so that 60% of the population remained after the juvenile period. The daily natural mortality was then estimated as $d_j = 1/(-D_\Omega/\ln(0.6)) = 1/264$. Adult daily natural mortality (d_a) was calculated from the difference between the natural mortality already defined for model 1 (d) and the juvenile mortality (d_j), so that $d_a = 1/(1/d-1/d_j)$ (Table 6). According to market survey data in Peru, roughly 20% more adult white-winged parakeets were harvested annually than juveniles (P. Mendoza, WCS, unpublished data), therefore, I set 60% of the total harvest (h) to represent adults ($h_a = 0.6h$) and 40% juveniles ($h_j = 0.4h$).

Transmission rate

Transmission coefficients (β) for ND in juvenile or adult psittacines have not been published; however, acutely-infected juvenile chickens, pigeons, and other species were considered more infectious than adults (Erickson et al. 1980; Kuiken et al. 1998b; Rupiper 1998; Alexander et al. 2004; Kapczynski et al. 2006; Hoque et al. 2012). It is reasonable to assume that the same would be true for juvenile parakeets. For simplicity, I parameterized an acute-transmission factor ($c_{\beta A}$) to represent a 25% increase for acutely-infected juveniles over the baseline rate of transmission (β_A) in model 1, so that $\beta_{Aj} = (1+c_{\beta A})\beta_A$, and a 25% decrease for adult transmission below baseline so that $\beta_{Aa} = (1-c_{\beta A})\beta_A$ (Table 6; Fig. 4). I used the same chronic transmission rate (β_C) for juveniles and adults as in model 1. The transition rates for leaving infectious states, α, δ, γ, and ν, used in model 2 were previously defined for model 1 (Table 6).

Acute and chronic infections and disease-related mortality

In natural outbreaks and experimental studies, juvenile birds frequently disproportionately suffered acute clinical signs and high mortality following ND

exposure compared to adults (Panigrahy et al. 1993; Kuiken et al. 1998b; Alexander 2009; Barman et al. 2010). Therefore, I considered that 75% of juvenile white-winged parakeets would become acutely infected following exposure ($p_{1j} = 0.75$), while $1-p_{1j}$ would become chronically infected (Table 6; Fig. 4). For adults, I considered a 50% probability of becoming acutely or chronically infected, p_{1a} and $1-p_{1a} = 0.5$. The proportion of acutely-infected individuals that would recover (p_2) versus becoming chronically infected was defined as in model 1. I used an acute-mortality factor (c_m) to estimate a $\pm\ 25\%$ age-related difference so that disease-related mortality for acutely-infected juveniles was $\mu_{Aj} = (1+c_m)\mu_A$ and for adults, $\mu_{Aa} = (1-c_m)\mu_A$. Little is known about age-related mortality from chronic ND infection. I assumed that little difference existed among juveniles and adults and, therefore, used the parameter μ_C from model 1 for both.

Scenario analysis

Because life expectancy (D_d) is unknown in the wild, I conducted a scenario analysis to compare the baseline scenario ($D_d = 5$ years) with two extreme scenarios ($D_d = 2$ and $D_d = 9$ years for both models. I also evaluated the effect of additional harvest (hl) at 2%, 5%, and 10% along with the 1% annual baseline (h_b) harvest (so that the total harvest $h = h_b + hl$) through two scenarios for each model. In the first scenario, population recruitment was fully compensated to include baseline and additional harvest to maintain a stable population in absence of infection, so that $\Lambda = N(d+h)$ in model 1 and $\Lambda_2 = N(d_j+h_j+\Omega)(d_a+h_a)/(d_a+h_a+\Omega)$ in model 2 (Table 6). In the second scenario, additional harvest and infection were introduced simultaneously into the host population, but additional harvest was uncompensated by recruitment and both additional harvest and infection-induced mortality caused the population to decline so that $\Lambda_u = N(d+h_b)$ in model 1 and $\Lambda_{2u} = N(d_j+h_{bj}+\Omega)(d_a+h_{ba})/(d_a+h_{ba}+\Omega)$ in model 2 , where $h_{bj}=0.4h_b$ and $h_{ba}=0.6h_b$. These two scenarios provided a means to evaluate the interaction between harvest and disease under two extreme host reproductive responses to additional harvest

(i.e., compensated additional harvest by increased natality in scenario 1 and uncompensated additional harvest because of a stable natality in scenario 2).

Sensitivity analysis

I examined the sensitivity of the predicted disease-related population decline and R_0 to parameters' uncertainties (Table 6). Parameter distributions were selected supported by literature; population size was Log-normally distributed (Limpert et al. 2001), values for D_α, D_δ, and D_γ were exponentially distributed (Anderson & May 1991), and the remaining parameters with insufficient support were uniformly distributed (Table 6). I performed a sensitivity analysis by simulating 10,000 iterations of the (1) R_0 expressions (Eq. C1 and C2) and (2) ODE models (Eq. 1–5 and 6–15) run up to 10,000 days. Parameters were varied simultaneously using the Monte Carlo method and Latin Hypercube sampling that randomly-selected parameter values from their respective distributions (Helton & Davis 2003). With this number of iterations, R_0 was estimated with a precision of +/- 0.08.

Spearman's correlation coefficient (r_s) was used to calculate and test correlation between each uncertain parameter and R_0 (Table 6). I used $\alpha = 0.05$ as the statistical significance, which was adjusted for multiple testing by implementing the Bonferroni correction. The corrected significance level was $\alpha = 0.0045$ for model 1 and $\alpha = 0.0028$ for model 2. To explore how parameters interacted to create conditions of disease-free ($R_0 < 1$) or endemic ($R_0 \geq 1$) states, I used the parameter values and the associated R_0 estimates from 10,000 iterations per scenario to construct classification trees—binary decision trees that identify the most influential parameters in predicting disease-free or endemic conditions for the homogeneous and age-structured populations (Ivanek et al. 2009). The classification trees were build using the rpart package (Therneau et al. 2014). The gini index was used as a measure of node impurity along with a 10-fold cross-validation to select the tree with the smallest misclassification error (Vayssières et al. 2000). In the classification-tree analysis, results from all of the scenario analyses on life expectancy (D_d) and additional harvest ($h1$) were combined for a total of 120,000 data

points (iterations) to determine whether these two, and other, model parameters were important predictors of disease-free or endemic states.

In a separate analysis, I compared differences in R_0 estimates produced by models 1 and 2, by starting with equal parameters so that each model produced the same R_0 (i.e., age-structured parameters were set to be equal and to match those in model 1). I then varied the age-structured parameters (e.g., $c\beta_A$, c_m, p_{1j}, and p_{1a}) one at a time to evaluate their individual influence on R_0. This provided a method to compare results between the two models and to identify which parameters made the biggest difference in R_0 estimates.

Results

Dynamics of ND transmission, R_0, and harvest

The baseline R_0 estimates without additional harvest were 3.63 and 2.66 for models 1 and 2, respectively (Table 7). These baseline values were similar to mean R_0 estimates obtained from 10,000 simulations. The distribution range of the R_0 estimates (represented by the 5th and 95th percentiles) were slightly wider in model 1 compared to model 2 (Table 7). With just baseline harvest (i.e., no additional harvest), 21 and 28% of R_0 simulated values were < 1 for models 1 and 2, respectively, meaning that ND failed to become established in the host population (Table 7). The majority of simulated R_0 estimates were < 5 for both models (77% and 87%, respectively). The baseline outbreak dynamics peaked at approximately 120 days for the homogeneous population of white-winged parakeets (Fig. 5A), and closer to 150 days with less infected individuals and longer duration in the age-structured population (Fig. 5B). Short-term ND dynamics oscillated in both models, but the second infection cycle was slightly delayed in model 2 compared to model 1(Fig. 5; See Appendix E for separate juvenile and adult trajectories).

Table 7. Scenario analysis of the effect of uncompensated additional harvest ($h1$) on the basic reproduction number (R_0) and population size following introduction of Newcastle disease into a homogeneous (model 1) and age-structured (model 2) populations of white-winged parakeets.[a]

Additional harvest, $h1$ (%)	Baseline R_0	Mean R_0 (5th, 95th percentiles)	Proportion of simulations where $R_0 < 1$ (%)	$N(730)$[b] (5th, 95th percentiles)
model 1				
0[c]	3.63	3.65 (0.35, 11.30)	21	154.8 (84.9, 254.5)
2	3.31	3.32 (0.31, 10.29)	24	149.3 (81.9, 245.0)
5	2.92	2.93 (0.28, 9.05)	27	141.4 (77.6, 231.6)
10	2.44	2.44 (0.23, 7.52)	33	129.1 (71.1, 211.2)
model 2				
0[c]	2.66	2.62 (0.28, 7.53)	28	168.6 (94.9, 272.2)
2	2.54	2.50 (0.27, 7.18)	29	165.0 (92.9, 266.3)
5	2.39	2.34 (0.26, 6.71)	31	159.7 (89.9, 257.6)
10	2.17	2.12 (0.23, 6.07)	34	151.2 (85.2, 243.9)

[a] For each scenario, results were based on 10,000 simulations.
[b] Population size at day 730 post infection introduction was chosen to capture the short-term effect of harvest on the population size (the initial population size was Log-normally distributed with mean of 200 and the 5th and 95th percentiles were 109 and 329, respectively).
[c] In all scenarios, the uncompensated additional harvest ($h1$) was added to the 1% baseline harvest (h_b).

As shown in both panels in Fig. 6, population size was relatively stable for approximately the first 20 days, after which abundance decreased sharply and similarly for all tested harvest rates until approximately 180 days in model 1 and 200 days in model 2. This sharp decline, related to the disease outbreak and disease-induced mortality shown in Fig. 5, was followed by further, but slower, decline in population size. By two years (t = 730 days) post ND introduction with baseline compensated harvest, ND caused the initial population of 200 individuals to decrease by 33% in the homogeneous population ($N(730)$ = 135; Fig. 6A, blue line), but only by 24% ($N(730)$ = 153) when age structure was considered (Fig. 6B, blue line).
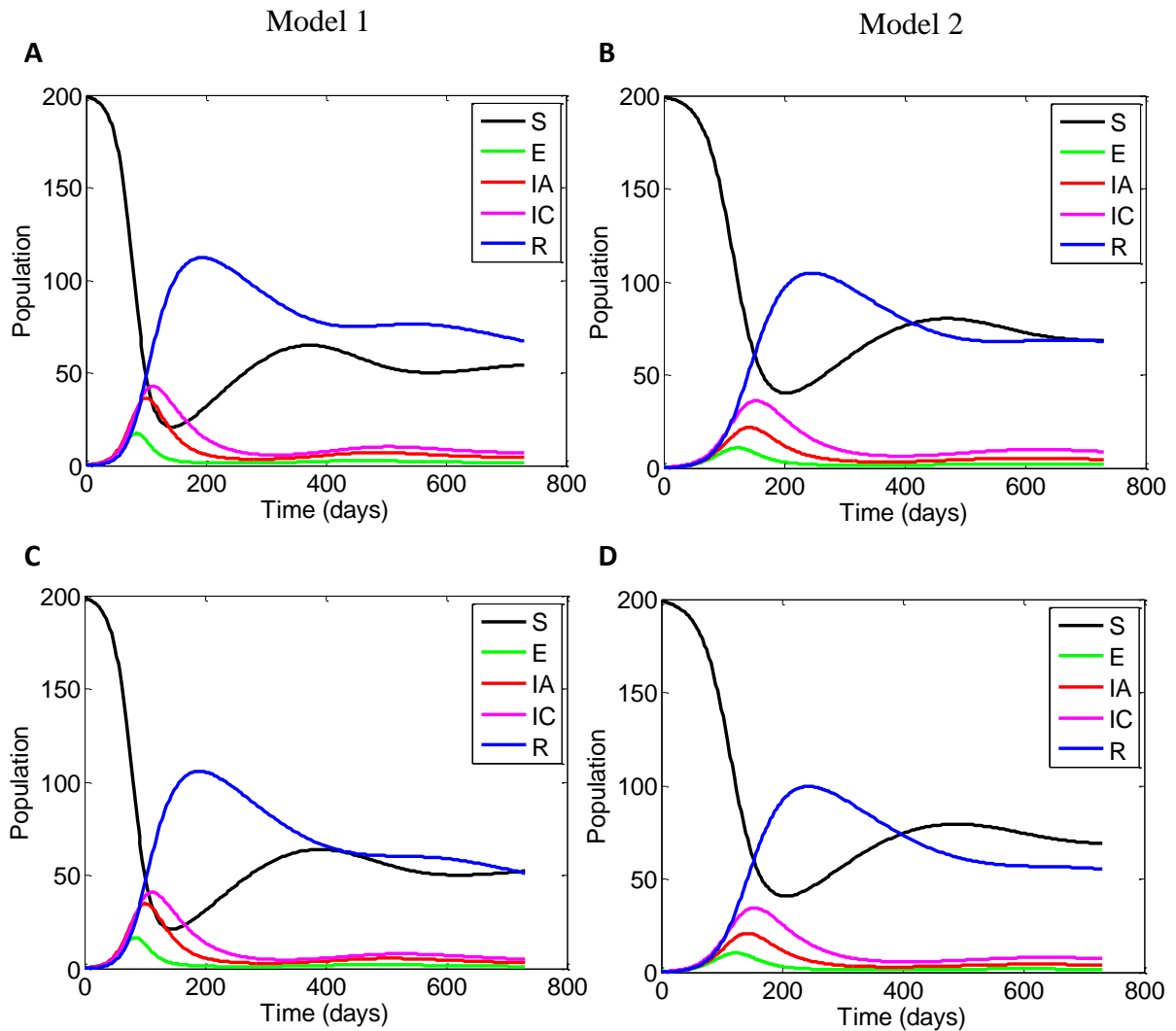
Figure 5. Deterministic two-year time trajectories for Newcastle disease transmission. Simulated outbreak dynamics from homogeneous (model 1) and age-structured (model 2) populations of white-winged parakeets with (A-B) no additional harvest ($hl = 0\%$) and (C-D) 10% additional (uncompensated) harvest ($hl = 10\%$). Depicted states of infection are: susceptible (*S*), exposed (*E*), acutely-infected (*IA*), chronically-infected (*IA*) and recovered (*R*). Age-structured panels (B, D) show summed juvenile and adult parakeets for each infection state. See Appendix E for separate juvenile and adult trajectories for model 2.

By 20 years post ND introduction, homogeneous and age-structured populations deceased more than 50% before stabilizing in an endemic state with no additional harvest (Fig. 7, blue lines). The distribution of the estimated number of parakeets from 10,000 ODE simulations was slightly wider for model 2 than model 1, which likely reflects additional uncertain parameters in model 2 (Table 7). When I fixed the initial population size to the baseline value ($N = 200$) so that I could evaluate the effects of harvest and disease-related mortality on population decline without the influence of the uncertain initial population size, the width of the 5th and 95th percentiles decreased by over half for both models (45–60%, results not shown).
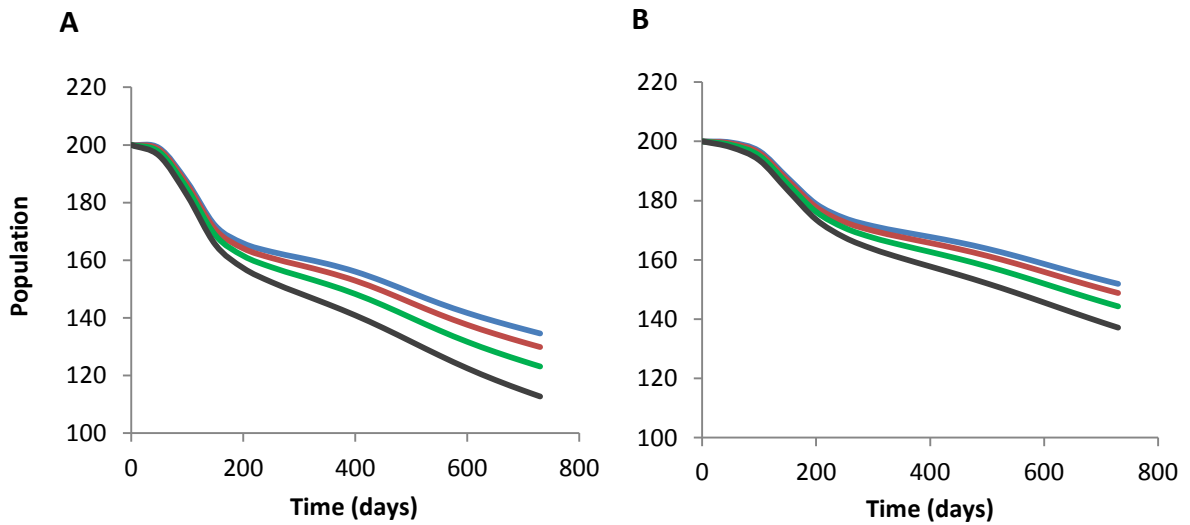
Figure 6. Population decline during two years post Newcastle disease introduction in (A) homogeneous (model 1) and (B) age-structured (model 2) populations of white-winged parakeets with no additional harvest and three additional, uncompensated harvest rates (*h1*; 0-blue, 2%-red, 5%-green, and 10%-black).

Scenario analyses

Varying life expectancy where $D_d = 2$ or 9 years produced minimal effect in ND transmission represented by mean R_0 estimates and host population size for either homogeneous or age-structured populations of white-winged parakeets (Appendix D). Uncompensated additional harvest dampened R_0 in both homogeneous and age-structured populations (Table 7). Increasing the additional harvest rate from 2 to 10% increased the probability of an infection fade out (measured by the proportion of $R_0 < 1$), by 9% in model 1, but by only 5% in model 2 (Table 7). Compensating for additional harvest, where natality (lambda) increased in response to higher harvest, caused R_0 to remain stable with increasing additional harvest in both models (Fig. 8); however, the confidence intervals for R_0 estimates with compensated and uncompensated harvest largely overlapped. Overall, disease dynamics were minimally affected by higher harvest (Fig. 5). The recovered class, which was the longest stage in the compartmental models, was the most affected by higher harvest rates in both models as noted by the lower number of individuals with 10% additional harvest versus baseline harvest (Fig. 5, panels C–D versus panels A–B, respectively).

Higher uncompensated harvest decreased the size of both homogeneous and age-structured populations of white-winged parakeets, although the decrease was more notable in model 1 versus model 2 and the decline was steeper with higher harvest rates (Fig. 6). At two years post ND introduction, 10% additional harvest decreased the homogeneous population of 200 individuals by 35%, but only by 24% in model 2 for the age-structured population (Table 7). The combination of ND and 10% uncompensated additional harvest (without density-dependent population regulation) caused the population to steadily decline, approaching zero within 35 and 60 years for models 1 and 2, respectively (Fig. 7).
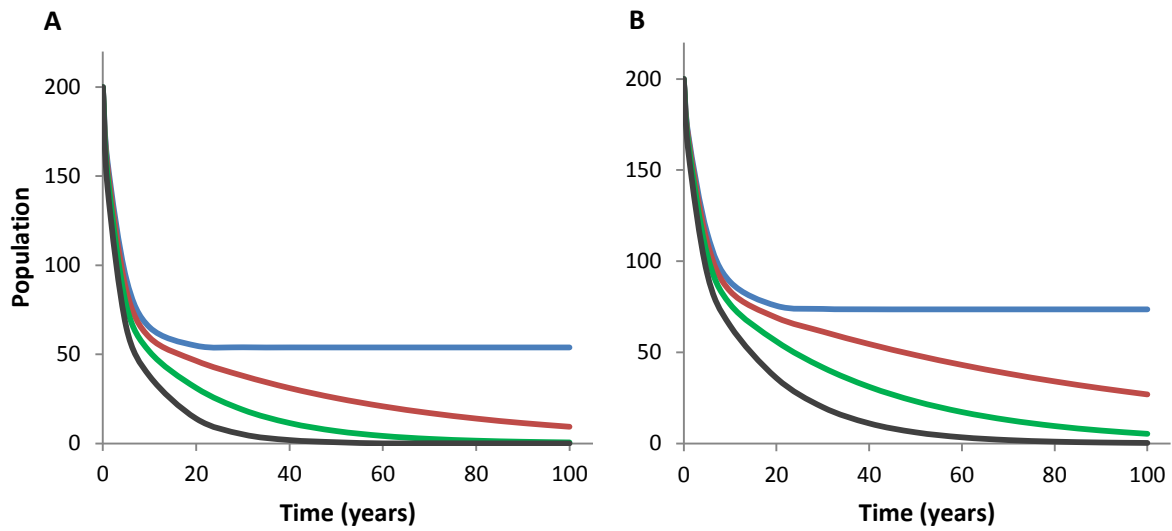
Figure 7. Population decline during 100 years post Newcastle disease introduction in (A) homogeneous (model 1) and (B) age-structured (model 2) populations of white-winged parakeets with no additional harvest rate and three additional uncompensated harvest rates ($h1$; 0-blue, 2%-red, 5%-green, and 10%-black).
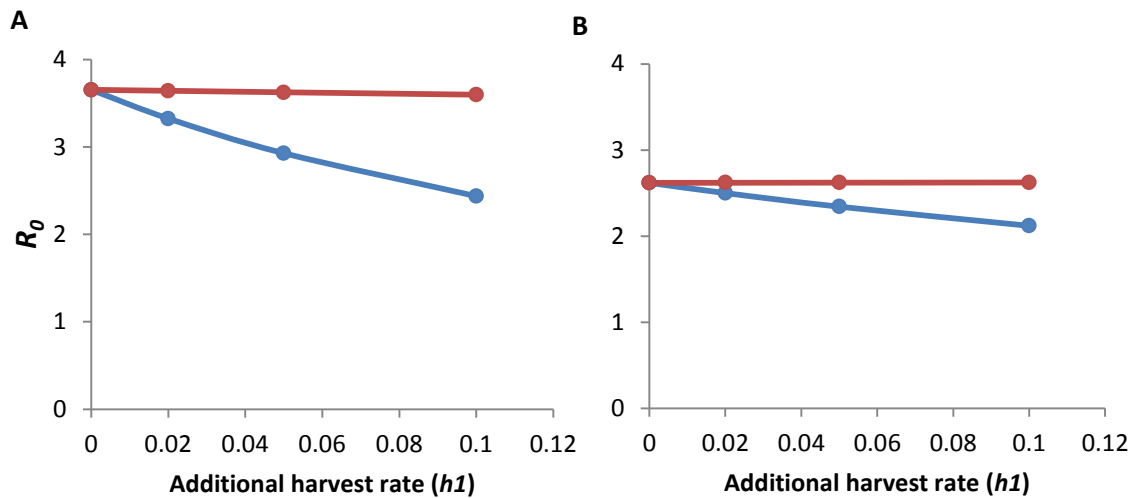
Figure 8. Comparison of mean estimates of the basic reproduction number (R_0) under assumptions of compensated (red) and uncompensated (blue) additional harvest rates (hl) for (A) homogeneous and (B) age-structured populations of white-winged parakeets following introduction of Newcastle disease.

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Sensitivity analysis

The duration of the acute-infectious stage (D_δ) was the most influential (positively correlated) parameter in determining R_0 for both homogeneous and age-structured populations of white-winged parakeets (Fig. 9). Initial population size and the transmission rate for acutely-infected individuals were also positively correlated with R_0. The probability of acute disease-related death (pd_A) was negatively correlated with R_0 in both models, but had a much stronger influence in model 2 (Fig. 9B). Along with pd_A, disease-related mortalities for acutely-infected juvenile (μ_{Aj}) and adult (μ_{Aa}) parakeets, both of which were partially derived from pd_A (Table 6), were highly negatively correlated with R_0 in model 2. The probability of chronic disease-related death (pd_c) was likewise negatively correlated with R_0, but only significant in model 2.
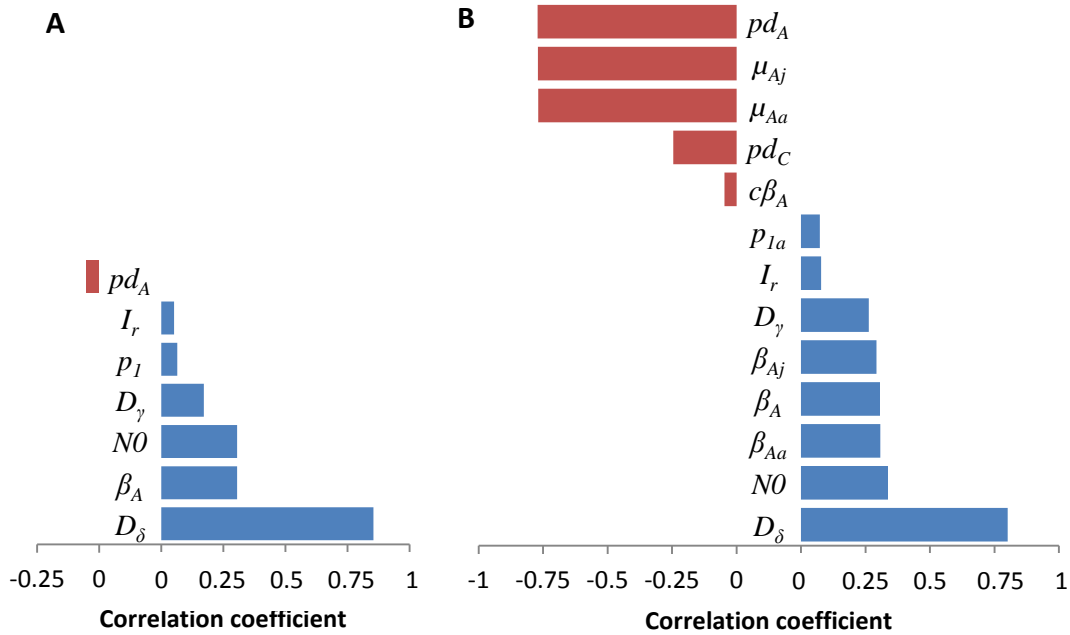
Figure 9. Spearman's coefficients indicating the strength of the relationship between parameters of the (A) homogeneous (model 1) and (B) age-structured (model 2) models and the basic reproduction number (R_0) with 10% additional harvest from 10,000 simulations. Only parameters with statistically significant coefficients are shown. See Table 6 for parameter descriptions.

In the correlation analysis, parameters were evaluated individually; in the multivariable classification trees analyses all uncertain parameters as well as life expectancy (D_d) and additional harvest ($h1$) were evaluated simultaneously. Parameters D_d and $h1$ were not identified as influential in predicting disease-free or endemic conditions. As with correlation analyses, the most optimal classification trees identified the duration of the acute-infectious stage (D_δ) as the most important factor determining whether the infection would persist or undergo fade-out, indicated by its position closest to the root of the tree (Fig. 10). By following the rule for branches to the right, endemic conditions ($R_0 \geq 1$) were predicted to occur under two scenarios in model 1: (1) $D_\delta \geq 11$ days, and (2) $D_\delta < 11$ days, but with a duration of chronic-infectious stage $D_\gamma \geq 48$ days, and a transmission rate for chronically-infected parakeets $\beta_c \geq 0.0001071$ (Fig. 10A). In model 2, the most optimal classification tree indicated that an endemic state was predicted by four parameters following three different pathways (Fig. 10B). As with model 1, D_δ, D_γ, and β_c were influential parameters in predicting endemic ND, along with the initial population size, $N(0)$. Cross-validation indicated that the predictive error rates were relatively low and similar for models 1 and 2 (12.5% and 12.7%, respectively).

By directly comparing models 1 and 2 and the age-related parameters that differed between the two, I determined that the age-dependent acute transmission factor ($c\beta_A$), which increased or decreased the transmission rate by 25% for acutely-infected juveniles and adults, respectively, made the biggest difference in R_0 between the two models. Specifically, lowering the transmission rate for acutely-infected adult parakeets (β_{Aa}) decreased R_0 by 21% from 3.63 in model 1 to 2.88 in model 2. Lowering the probability of acute adult infection (p_{1a}) in model 2 compared to the homogenous value (p_1) in model 1 decreased R_0 by 15%. The acute mortality factor (c_m), which lowered the disease-related mortality rate for acutely-infected adult parakeets (μ_{Aa}), resulted in increasing R_0 slightly by 4% compared to homogenous acute mortality. The corresponding increase in juvenile parameter values associated with $c\beta_A$, p_{1j} and c_m, in model 2 minimally influenced R_0 compared to model 1.
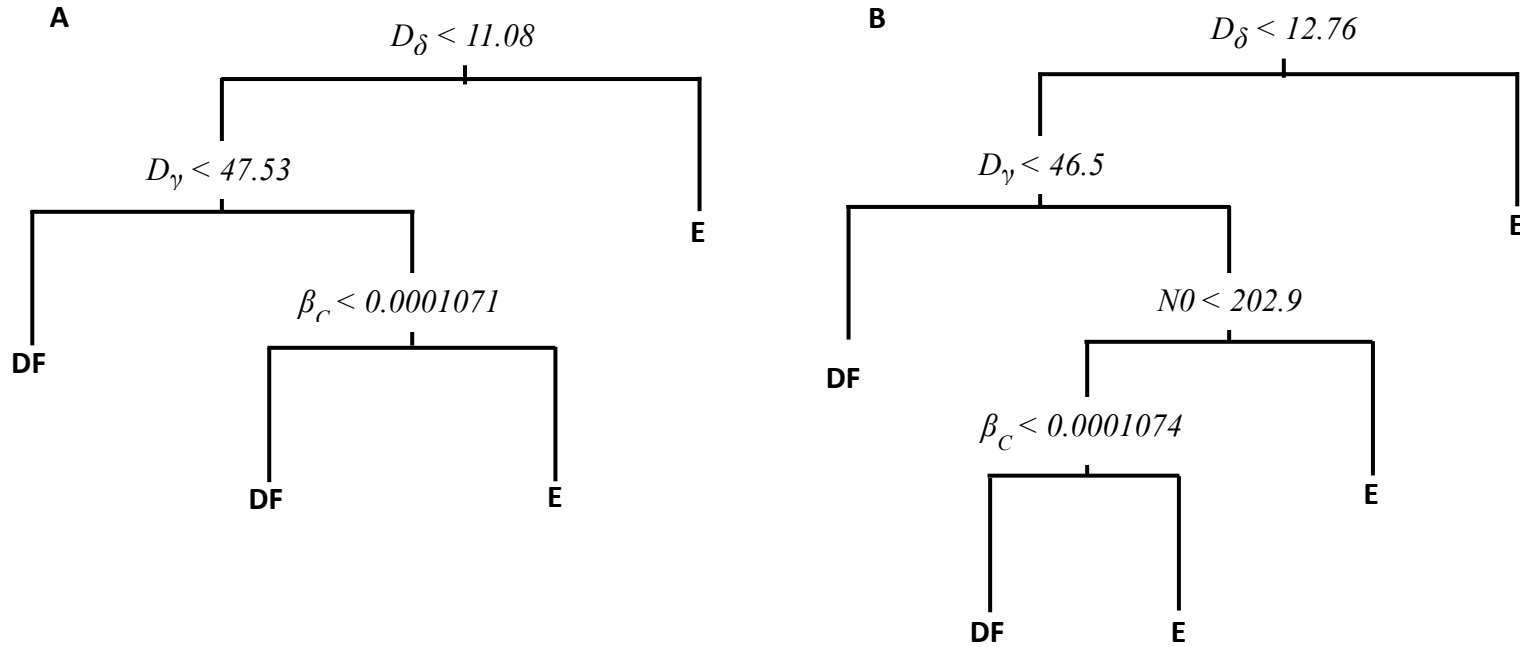
Figure 10. Classification tree for disease-free (basic reproduction number, $R_0 < 1$) or endemic ($R_0 \geq 1$) conditions of Newcastle disease (ND) in (A) homogeneous and (B) age-structured populations of white-winged parakeets. The rule for data partitioning is on top of each node. For example, in panel (A), the root node rule is the duration of the acute infectious stage (D_δ) less than 11.08 days; the subset of simulations satisfying this rule partitioned to the left daughter node and consecutively down the nodes. The terminal nodes represent disease-free (DF) or endemic (E) conditions for ND. See Table 6 for parameter descriptions.

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Discussion

My study shows that illegal harvest would play an important role in virus transmission during a ND outbreak. I developed two mathematical models to compare the influence of harvest on ND dynamics in a homogeneous and an arguably more realistic age-structured population of white-winged parakeets. I determined that introduction of ND would likely provoke considerable disease-related mortality, but the magnitude of the outbreak would be dampened by high harvest rates. Incorporating age structure into the model produced moderate differences in both R_0 and disease dynamics, primarily due to lower adult disease transmission, compared to the homogeneous population model. Most importantly, it demonstrated that the homogenous model likely overestimated the severity of an ND outbreak and highlighted the importance of incorporating even simplistic age structure in disease modeling despite increased complexity and reduced tractability.

R_0 and ND outbreak

The deterministic compartmental models demonstrated that introducing just one ND-infected individual would provoke an outbreak ($R_0 \geq 1$) in susceptible populations of white-winged parakeets with roughly 75% probability (Table 7). In the short term, without population compensation through density-dependent recruitment, population size decreased by 24–44% depending on the harvest rate and host population structure (Fig. 6). Even the low end of this range, observed in the age-structured population (model 2) with baseline harvest, is a conservation concern (Fig. 6B, blue line). The fact that some psittacine species can chronically shed the ND virus for extended periods (Erickson et al. 1977), implies this disease has the potential to become endemic and remain in the population causing low-level disease-related mortalities (Fig. 7). In a case of another infectious disease affecting wild avian populations, Hochachka & Dhondt (2000) found that epizootic *Mycoplasma* sp. conjunctivitis caused significant population decline in house finches along the eastern United States.

My results indicate that, in the long term, ND alone would not cause population extinction; however, the combination of ND and consistently high annual harvest (10%) would provoke > 75% population decline in 20 years without a density-dependent response in reproduction (Fig. 7). While I did not investigate the interaction between density-dependent effects and illegal harvest on the host population, it would be reasonable to expect that density-dependent regulation would help replenish the population by increasing reproduction (Ricklefs 2000). Higher recruitment could potentially increase the supply of ND susceptible parakeets, and thereby exacerbate and/or prolong the outbreak (Woodroffe et al. 2004; Choisy & Rohani 2006). The combination of illegal harvest and ND-related mortality could have potential devastating population-level effects, but without better demographic data for the white-winged parakeet, it is unclear from what level of decline the population could recover, or at least stabilize at a new carrying capacity (Hochachka & Dhondt 2000; Beissinger 2001).

Age structure

The importance of including realistic population demographic factors in disease modeling is well established (Hudson et al. 2002). In the case of ND, age structure is an important factor to consider because the disease disproportionately affects juveniles. The modeling results demonstrated that without including age structure (model 1), the severity of a potential ND outbreak was up to 28% higher based on mean R_0 estimates (Table 7) and disease-related population decline was 9–13% higher, depending on the harvest rate, in model 1 versus model 2 at two years post ND introduction (Fig. 6). To put this in perspective, a higher R_0 observed in model 1 compared to model 2 suggests that higher effort is needed to control the infection based on the herd immunity threshold (HIT), which denotes the minimum proportion of population to be vaccinated to control the infection (HIT = 1-1/ R_0). Although currently not feasible for psittacines in the wild, a higher proportion of population would need to be vaccinated in model 1 (74%) compared to model 2 (62%) (John & Samuel 2000; van Boven et al. 2008).

The dynamics of an ND outbreak were similar in homogeneous and age-structured populations of white-winged parakeets (Fig. 5); however, the mildly

prolonged infectious periods (I_A, I_C) in model 2 (Fig. 5B,D) would likely provide more opportunities for contact and cross-species exposure. Psittacine species, especially species of similar size, often interact at fruiting trees or clay licks (Galetti 1997; Burger & Gochfeld 2003). Up to 17 species and hundreds of individuals have been identified at clay licks in Peru (Powell et al. 2009), which would provide favorable conditions for ND transmission and spread among species (Butron & Brightsmith 2010). Expanding the age-structured model to include spatial connectivity for meta-population and interspecies interactions would provide valuable insight regarding ND dynamics on a larger scale (Hess 1996; Lande et al. 2001) and should be a focus of future research.

Comparison of models 1 and 2 demonstrated that the lower R_0 estimates predicted from model 2 primarily reflect disease dynamics in adult parakeets, specifically a lower transmission rate for acutely-infected adults (determined by $c\beta_A$) and, to a lesser degree, a lower probability of acute adult infection. Juvenile parakeets, despite being more infectious than adults, made little impact on R_0 estimates. This was due, in part, to the fact that 40% of juveniles were removed by natural mortality from the population by day 135, and the remaining would then "mature" to adults (Table 6). Adult parakeets, which comprised a much larger proportion of the population than juveniles (Table 6), naturally survived longer and had more time to influence ND transmission and R_0. As such, lower acute adult morality in model 2 (determined by c_m) slightly increased R_0 compared to model 1. This suggested that maintaining infected adults for longer time in the population (i.e., not dying from the disease), would exacerbate an ND outbreak even though adults were less infectious compared to juveniles.

I should emphasize that the parameters responsible for the differences in R_0 predictions between models 1 and 2 ($c\beta_A$, c_m, and p_{1a}) were uncertain and should be prioritized for future investigation, especially the transmission rate and probability for acutely-infected adult parakeets. However, because model 2 more closely reflected the biological system, it is reasonable to assume that it also more accurately predicted ND dynamics. By extension, it is reasonable to conclude that model 1 overestimated disease

transmission and the magnitude of the ND outbreak. In a similar situation, Brooks-Pollock et al. (2010) found that more realistic age-specific mortality versus constant mortality rates in mathematical models of human tuberculosis decreased R_0 estimates and the effort required for disease control.

Role of harvest

Through scenario analysis, I determined that increasing uncompensated harvest rates (i.e., those not compensated for by natality), had a modest dampening influence on R_0, meaning that higher uncompensated harvest increased the probability of ND fadeout ($R_0 < 1$; Table 7). Although the increase in the proportions of fadeout was less dramatic in model 2 versus model 1 (6% compared to 12%; Table 7), this must be considered along with the already lower R_0 estimates in model 2. Compensating additional harvest ($h1$) caused R_0 to remain high in both models (> 2.5), indicating that an influx of susceptible individuals (i.e., offspring), may help sustain higher potential for an ND outbreak (Fig. 8); however, because the confidence intervals for R_0 estimates with compensated and uncompensated harvest largely overlapped (results not shown), the influence of host population density-dependent response on R_0 should be interpreted cautiously.

Higher harvest rates produced slower population decline in the age-structured population compared to the homogeneous population (Fig. 6). This dampened effect in model 2 reflected, in part, the 40% removal of juveniles through natural mortality (Table 6). High juvenile mortality is often exploited in harvested populations because their lower survival rates and lower reproductive value increase the probability of compensation (Beissinger 2001). For this reason, Choisy & Rohani (2006) predicted that shifting harvest to younger age classes would decrease the risk of disease-related mortality in hypothetical scenarios, which is supported by my results.

Overall, higher harvest rates had minimal effect on ND dynamics (Fig. 5) and population size (Fig. 6). This is partly due to the way the annual harvest rate was prorated for the one-day time step in the model simulations, which diluted the effect of harvest, particularly over short time periods such as the 135-day juvenile period. In

addition, because the actual harvest rate is unknown, I set the baseline harvest (h_b) conservatively low and even compensated for it with natality (Table 6). It is likely that even the upper limit of 10% additional annual harvest ($h1$) was conservative. In model 2, I fixed the proportion of juvenile (40%) and adult (60%) harvest as the average of what was recorded in market surveys throughout the year (P. Mendoza, WCS, unpublished data). In reality, it is recognized that seasonal harvest differences exist, which would likely influence ND dynamics as they do for other diseases (Hosseini et al. 2004; Altizer et al. 2006). For example, when I changed the fixed harvest proportions to reflect harvest rates during a nesting period (juveniles 90%; adults 10%), R_0 was 20% higher, but the population decline at two years post ND introduction was 12% less compared to the opposite proportions (juveniles 10%, adults 90%; results not shown).

Key parameters

The duration of the acute (D_δ) and chronic (D_γ) infectious stages were most influential in determining R_0, as identified in both the univariate correlation (Fig. 9) and multivariable classification-tree analyses (Fig. 10). The positive Spearman correlations indicated that longer duration of the infectious stages resulted in higher R_0 estimates. In poultry operations, decreasing the duration of infectious stages (i.e., the length of time of ND viral shedding), is one of the primary goals for improving vaccination programs (van Boven et al. 2008; Miller et al. 2009). With captive pet birds, preventive measures such as vaccination could help diminish clinical signs and the duration and amount of viral shedding. The efficacy of ND vaccination in white-winged parakeets is unknown, although Denadai et al. (2010) determined that Australian parakeets could be safely and effectively vaccinated against ND. The negative correlation between the probability of acute disease-related death (pd_A) and R_0 in both models (Fig. 9) reflects the importance of removing acutely-infected individuals from the population. During an outbreak, this could be achieved by quarantining or culling acutely-infected individuals (Wobeser 2002). During outbreaks of ND in commercial flocks, quickly culling all infected and potentially-infected individuals has been a critical component of management strategies to prevent expansion of the outbreak (United States Department of Agriculture 2014).

Neither vaccination nor quarantine, however, would be feasible to control ND in wild populations of white-winged parakeets.

The classification-tree analyses provided a broad perspective of the key parameters and their interactions to produce disease-free or endemic ND states (Fig. 10). In addition to the duration of the acute (D_δ) and chronic (D_γ) infectious stages, the most optimal classification trees identified the transmission rate for chronically-infected parakeets (β_c) as influencing R_0, rather than the transmission rate for acutely-infected parakeets (β_a) as in the correlation analysis. When the interaction of transmission rates was evaluated along with other parameters, it became clear that the rate of virus transmission from chronically-infected birds (β_c) to susceptible individuals would become critical in determining whether ND would die out or persist, specifically when the chronic infection period (D_γ) lasted longer than approximately 47 days (Fig. 10). Such insight was impossible evaluating correlation alone, and demonstrates the value of multivariable analyses. Even though the most optimal classification trees retained only three or four parameters, the predictive error rates were relatively low for both models, indicating that the identified optimal classification trees correctly predicted infection fade out or an endemic state in almost 90% of independent simulations.

Limitations

My findings are dependent on several modeling assumptions. For instance, I assumed that ND transmission was density dependent in white-winged parakeets. Density-dependent transmission is commonly assumed for wildlife diseases (McCallum et al. 2001; Lloyd-Smith et al. 2005). In most cases of wildlife diseases, empirical data are difficult to obtain to confirm transmission, but Hochachka & Dhondt (2000) used pre- and post-enzootic data to conclude that mycoplasma conjunctivitis transmission in house finches was density dependent. In some situations, the mode of pathogen transmission may not be constant throughout the year as demographic seasonal traits affect social behavior and spatial structure of the host population (Oraby et al. 2014). For example, Hosseini et al. (2004) combined frequency- and density-dependent

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transmission for *Mycoplasma gallisepticum* to represent seasonal variation in social structure of house finches.

A similar situation could occur with ND transmission in white-winged parakeets as flock size fluctuates throughout the year (Shroads 1974). During the roughly 4-month breeding season, when pairs separate for nesting and flock size decreases, transmission may be more consistent with frequency dependence. During the post-breeding period, when adults along with their fledglings rejoin the flock, transmission may be density dependent. Addressing the role of chance in pathogen transmission could be evaluated by incorporating demographic stochasticity into the model. A stochastic approach could also assess the influence of changing the initial conditions, e.g., number of ND-infectious individuals released into the population. For instance, I assumed that just one infectious individual would be introduced into a susceptible population of white-winged parakeets. In reality, it is common for authorities to release dozens to hundreds of potentially exposed individuals confiscated from markets (E. Daut, Chapter 2). While this was beyond the scope of the present work, including demographic stochasticity and density-dependent population natality and mortality processes in a seasonal age-structured model would provide a method to more thoroughly investigate the influence of harvest on ND dynamics (Lande et al. 2001).

Recommendations

Few realistic options exist to control an ND outbreak in wild white-winged parakeets or other parrots. Assuring that *criollo* chickens and fighting cocks in the Amazonian region are vaccinated against ND would reduce the probability of cross infection to psittacine species in animal markets. In the models, I used a non-threatened psittacine species; however, many parrots are threatened in Peru—often by illegal trade—and could be seriously affected by an introduced infectious disease (BirdLife International 2014a). The most effective preventive measure would be to avoid releasing confiscated parakeets without prior health screening and, ideally, preventing illegal harvest in the first place. Authorities should coordinate more effectively with non-

governmental organizations in Peru working to decrease illegal wildlife trade (Daut et al. 2015), including wildlife rescue centers and zoological parks to assist with quarantine and rehabilitation of confiscated individuals. Similarly, authorities could increase collaboration with veterinary colleges to assist with physical exams and diagnostic testing of confiscated animals. Finally, combined efforts to increase enforcement of Peru's wildlife legislation and to decrease demand for wild-caught native birds for the domestic pet market would help mitigate the risk of introducing infectious diseases (Chapter 2).

In conclusion, this study improves understanding of ND dynamics in a wild population of harvested psittacines. I demonstrate that the hypothetical release of a confiscated individual infected with ND would provoke considerable population decline in a wild population of white-winged parakeets. To my knowledge, this is the first study to use infectious disease modeling to link illegal wildlife trade and disease introduction in a native wildlife population. The differences I observed in both R_0 and disease dynamics between the homogeneous and age-structured populations highlight the importance of incorporating even simplistic age structure in disease modeling. While I recognize that further enhancements, such as including density-dependent regulation and demographic stochastic properties, could contribute to the understanding of ND dynamics, my initial models provide a baseline for future evaluation. I encourage the conservation community to examine other disease risks associated with illegal wildlife trade, particularly in endangered species where disease may contribute to species extinctions.

CHAPTER IV

THE IMPORTANCE OF EPIDEMIOLOGY AND R_0 IN WILDLIFE

REHABILITATION[*]

Synopsis

Wildlife rehabilitators are at the intersection between individual and population–level wildlife health. Epidemiology is the study of diseases at population levels and mounting evidence suggests that disease outbreaks can impact wildlife populations. The basic reproduction number (R_0) is used as a threshold value to predict whether a disease will result in an outbreak or die out. It is defined as the expected number of secondary cases caused by one infectious individual (the index or primary case) during this individual's entire infectious period in a fully susceptible population. Rehabilitators should be familiar with the concept of R_0 and the important effect on and the role they have with wildlife disease epidemiology.

Introduction

Historically, wildlife biologists have speculated that parasites and disease have little impact on wildlife populations, believing that most infections are relatively benign (Hudson et al. 2002). Disease outbreaks may cause high mortality within a population, but typically these outbreaks were considered unusual exceptions resulting from environmental factors interrupting the delicate natural balance. However, evidence is mounting that disease, particularly wildlife epidemics, is a serious concern for the long–

term health of wildlife populations (Daszak et al. 2000) and is even capable of causing species extinction (Smith et al. 2006).

Disease can be unpredictable in wildlife populations. Why do some diseases suddenly emerge, sweep through a population, and then suddenly disappear without infecting all individuals? Why do other diseases remain endemic in many populations, causing high mortality each year? Investigating the answers to these questions is the labor of wildlife disease epidemiologists, with the goal of helping to manage and protect wildlife populations.

Epidemiology is the study of diseases (in this case infectious) and how often and why they occur in different groups of animals. The key term is *groups of animals*. Epidemiologists work at the level of populations. Individual animals are not a concern until they are included into categories such as "susceptible," "infected," "dead," or "recovered" (either temporarily or permanently immune) individuals. Wildlife rehabilitators, on the other hand, are primarily concerned with the health and well-being of individual animals and may find the population approach somewhat coldhearted. Nevertheless, individual wild animals unite epidemiologists and rehabilitators in many critical ways, the most fundamental being R_0, the basic reproduction number.

Basic reproduction number

How an infection behaves when it first appears in a population of susceptible individuals is critical to the health of the population. Being able to predict how an infection will act is important for management of the disease and the animal population. In most cases, the infection will follow one of three paths: (1) it will start an outbreak (epidemic), (2) it will burnout, meaning that after a few cases of infection it will disappear, (3) or it will become endemic, meaning it will become stable within the population. Which path the infection follows can be predicted by the basic reproduction number (symbolized as R_0). The definition for the basic reproduction number is the expected number of secondary cases caused by *one infectious individual* during this

individual's entire infectious period in a fully susceptible population (Heesterbeek 2002).

The concept of R_0 can be illustrated best by evaluating a practical example, such as the fictitious introduction of canine distemper virus into the raccoon population on Galveston Island, TX by a single infected raccoon. Assuming that the local raccoons have had no previous exposure to the distemper virus and therefore have no immunity to protect them from the virus, they all are susceptible to infection. Distemper virus is highly contagious, often fatal, and easily spread by direct contact (usually by inhalation) with infected bodily fluids. Raccoons that survive the infection are immune to future infections. The single infected raccoon (the index or primary case) will be infectious for three weeks after arriving on the island. The question to consider is: How many local raccoons will the infected raccoon contact—in close enough proximity to transmit the virus—during the 21 day infectious period? Although many factors could influence this scenario, one of the most important is the number of contacts that occur between infected and susceptible raccoons. Imagine, for instance, if the infected raccoon was released following the breeding season when many curious young juveniles were in the population versus being released during the coldest part of the year (as cold as it can get in Texas) when activity and potential contacts would be relatively low.

In reality, calculating R_0 according to the strict definition is almost impossible in wildlife populations that are experiencing an infectious disease outbreak. Epidemics are rarely identified at the moment an infected individual enters a susceptible population and the number of contacts between susceptible and infectious individuals is difficult, if not impossible, to estimate for most infections in the field. Yet, despite the challenges with calculating the actual value of R_0, it is still an essential concept in epidemiology and infectious diseases and arguably "one of the foremost and most valuable ideas that mathematical thinking has brought to epidemic theory" (Heesterbeek & Dietz 1996).

The significance of R_0 is not in the actual number, but in what it represents—a theoretical threshold. In simplified disease scenarios, R_0 is a cutoff point that predicts whether an infection will spread, which is what we really are interested in knowing. Is

the disease likely to result in an epidemic, a sudden outbreak of the disease? Or will the disease die out? Under more complicated scenarios, R_0 helps predict whether a disease will become endemic, indicating that it will persist in the population, often at some low level. In order for an infection to spread and result in an outbreak, R_0 must be greater than one. This means that every infected individual, on average, infects more than one new individual, resulting in a chain reaction of new cases (Fig. 11).

Index Case
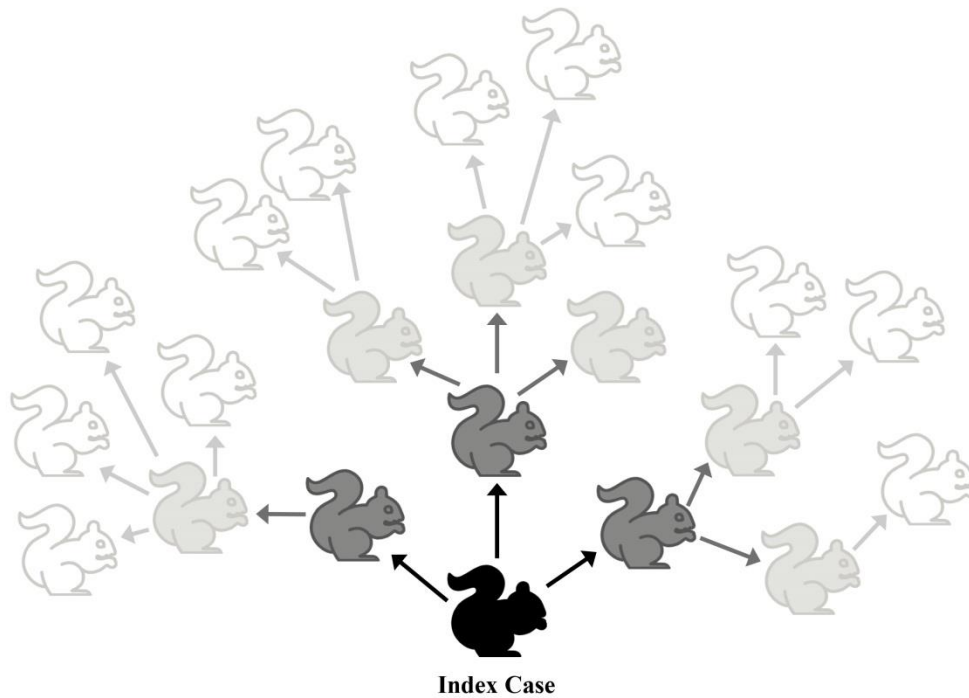
Figure 11. Graphical representation of new cases of infection during an outbreak. In this case, each infected squirrel spreads the infection to 0–4 susceptible squirrels. The average number of new cases is 2.1.

If R_0 is less than one, each infected individual produces, on average, less than one new infected individual, indicating that the infectious disease eventually will die out in the population. When R_0 equals one, the disease is likely to remain in the population

with roughly the same number of individuals infected all the time (Kermack & McKendrick 1927), so that:

$R_0 < 1$ – disease will eventually disappear
$R_0 = 1$ – disease will become endemic
$R_0 > 1$ – disease will result in an epidemic.

Threshold levels are familiar concepts in wildlife ecology. You may be familiar with the analogous threshold property of λ, the Greek letter lambda (also written as just R), which represents the fundamental net reproductive rate of a population under simplified conditions. Lambda combines the birth of new individuals with the survival of existing individuals. The value of the concept lies in its threshold property similar to R_0. If λ is greater than one the population will grow; if λ is less than one the population will decline (Dublin & Lotka 1925) .

R_0 has other important uses for wildlife diseases in addition to its threshold property. The magnitude of R_0 can be used to gauge the risk and severity of an epidemic of an emerging infectious disease (Heesterbeek 2002) and the final size of the epidemic—specifically the number of susceptible individuals remaining at the end of the epidemic (Andreasen 2011). If a disease is endemic, R_0 helps evaluate control strategies such as vaccination campaigns. Different control efforts can be incorporated into mathematical disease models to test which strategy and how much effort (cost) it would require to reduce R_0 below one, and theoretically eliminate the infection from the population (Li et al. 2011). For example, R_0 estimates were used to illustrate that mosquito control would probably be much more effective in controlling an outbreak of West Nile virus (WNV) than would be attempting to control bird populations (Wonham et al. 2004). In fact, it was shown that reducing American crow (*Corvus brachyrhynchos*) densities—the bird species that has suffered some of the greatest mortality in the United States due to WNV—might actually increase the chance of disease transmission and provoke an outbreak.

Calculating R_0

        Because it is virtually impossible to calculate R_0 using actual outbreak data, there are numerous methods to estimate R_0–like thresholds for a specific disease and population. Some methods are very basic and incorporate the bare minimum information necessary. Other methods use complicated models to incorporate more sophisticated data about the population under study, such as different age and social groups, physical distribution in the environment, and status of immunity. An important point to consider is that there is no universal R_0 value for a disease (Li et al. 2011). For example, R_0 for squirrel pox virus will not always be 2.05 because it depends on the situation where and when this value was calculated. The R_0 for another outbreak of squirrel pox may be 2.12, but it should never reach a hugely different value such as 19.0, assuming the same method was used for calculation because such a large value would be inconsistent with the disease's behavior. What this means is that R_0 must be interpreted within the context of the disease and population at the time it is investigated and, most importantly, the method used to calculate R_0.

        Most methods to calculate R_0 include aspects of the three main factors of infectious disease epidemiology: (1) the natural history or progression of the infection in an individual host, (2) how the infection spreads from infected to susceptible individuals, and (3) the environment and behavioral characteristics of the specific host population (Ward et al. 2009). Calculating an R_0–like threshold value for a hypothetical outbreak of distemper virus on Galveston Island can be done relatively easily by using basic disease parameters published in the scientific literature regarding distemper epidemiology (Deem et al. 2000) and previously studied outbreaks in raccoons (Roscoe 1993). Important values to estimate are the transmission probability (how likely is it that the disease will be passed from an infectious to susceptible individual), the contact rate (how many individuals, on average, will the infected raccoon contact on a daily basis), and how long the infected raccoon will remain infectious. Estimates for these values, along with several simplifying assumptions, can be used to calculate R_0 for a susceptible raccoon population of 1,000 individuals on the island. By using the Jacobian method

(Roberts 2007), R_0 would be approximately 8.45. Since this threshold value is greater than one, it strongly suggests that there would be an epidemic of distemper in the raccoon population on the island.

Conclusion

Wildlife rehabilitators are at the intersection between individual and population–level wildlife health. From an individual perspective, rehabilitators deliver a valuable service providing care and assisting wild animal welfare. From a population perspective, rehabilitators collectively observe and handle a large sample of wild animal populations from across the United States. These observations have been critical for surveillance programs such as West Nile virus (Nemeth et al. 2006), but overall have been sorely under–utilized. Recent efforts are encouraging rehabilitators to use standardized on–line patient record systems to maximize the collection and distribution of wildlife health information generated by rehabilitators across the country; WILD–ONe, which stands for Wildlife Incident Log/Database and Online Network, recently launched by the Wildlife Center of Virginia is one example. Collating records across geographic regions and standardizing data entry will make the data more accessible and useful for disease surveillance.

Lastly, rehabilitators interact with wildlife populations every time a rehabilitated animal is released back to the wild. By definition, the basic reproduction number, R_0, is an individual–based metric that sheds valuable light on potential impacts of disease on wildlife populations. By definition, a single infected individual can cause an epidemic, which should be enough to cause all of us to pause the next time an animal is released back to the wild.

CHAPTER V

ROLE OF NON-GOVERNMENTAL ORGANIZATIONS IN COMBATING

ILLEGAL WILDLIFE-PET TRADE IN PERU

Synopsis

Illegal trade in wild animals for pets is a global conservation and animal-welfare concern. Non-governmental organizations (NGOs) with different philosophical perspectives toward wildlife work to decrease illegal trade at international and national levels. My objective was to examine the efforts of conservation and animal-welfare NGOs working to decrease illegal wildlife-pet trade for domestic markets in Peru. I identified 28 NGOs potentially engaged in reducing the trade, and conducted semi-structured interviews with $\geq$ 1 representative from each (n = 33 interviews). Only five NGOs, each with a strong dual-perspective toward wildlife that prioritized both wildlife populations and individual wild animals, demonstrated high effort to decrease illegal wildlife-pet trade. These dual-perspective NGOs incorporated anti-trade efforts in all four work categories I identified (i.e., outreach, advocacy, development, and husbandry). Using thematic analysis of interview transcripts, I determined that dual-perspective interviewees were motivated to combat the trade by concern for individual animals and populations—in essence, their moral pluralism. Overall, interviewees considered the government lax with enforcement of wildlife legislation. Interview data suggest that the dual-perspective NGOs' persistent efforts have decreased illegal wildlife-pet trade in two regions of Peru. I recommend that stakeholders and governments searching for

collaborators to help curb illegal trade consider approaching NGOs with programs that address both conservation of wildlife populations and individual wild animal welfare. I urge the scientific community to evaluate the effectiveness of strategies under different ecological and socio-economic conditions to assist on-the-ground efforts to decrease illegal wildlife-pet trade.

Introduction

Illegal wildlife trade is a global conservation and animal-welfare concern. Illegal harvest and trade of wild animals undermine natural resource management (Broad et al. 2003), threaten biodiversity (Nekaris et al. 2010; Sung et al. 2013), foster corruption and violence (Warchol 2004), permit spread of infectious diseases (Karesh et al. 2012) and invasive species (Carrete & Tella 2008), and result in considerable animal suffering and mortality (Cantú et al. 2007; Sollund 2013). Controlling illegal wildlife trade is a global challenge (Wilson-Wilde 2010; House of Commons 2012; Schneider 2012; Wyatt 2013b). Several types of groups work to decrease illegal wildlife trade, including intergovernmental organizations such as Interpol, government agencies, and, increasingly, non-governmental organizations (NGOs). In recent decades, the role of NGOs has expanded to include assisting governments with wildlife management and development of conservation and animal-welfare policy (Lapham & Livermore 2003; Wilkins 2005; Rodríguez et al. 2007). Many NGOs also support a spectrum of efforts to decrease illegal wildlife trade ranging from raising public and government awareness (World Wildlife Fund / Dalberg 2012; African Wildlife Foundation 2013; Conservation International 2013b; Humane Society International 2013) to directly increasing enforcement of laws designed to protect wildlife or manage sustainable harvest (Freeland Foundation 2013; International Fund for Animal Welfare 2013; The Last Great Ape Organization 2013; Wildlife Conservation Society 2013).

Many factors influence NGOs' decisions to engage in the work they do (Powell & Steinberg 2006; Lewis & Kanji 2009). Choosing to combat illegal wildlife trade may stem, in part, from perceived need, available funding, and compatibility with the NGO's

mission (Gauri & Fruttero 2003; Townsend & Townsend 2004; Delfin & Tang 2008; Brockington & Scholfield 2010a). On an international level, prominent NGOs that raise awareness and promote their efforts to combat illegal wildlife trade can be broadly divided into two categories differing in their philosophical perspectives toward wildlife. Conservation NGOs, based on principles synthesized by Soulé (1985), typically focus on managing sustainability of species, populations, and ecological processes. In *Conservation Biology*, Soulé (1986: pg. 10) argued that: "Conservation biology is the biology of scarcity. The conservation biologist is called in when an ecosystem, habitat, species or population is subject to some kind of artificial limitation—usually a reduction of space and numbers." Conversely, animal-welfare NGOs, whose contemporary ideology was formalized by Singer (1975), prioritize individual, sentient animals and defend their well-being. This differs from the "animal-rights" movement that focuses on deeper political and philosophical claims about legal status of animals (Regan 1983). Reducing individual pain and suffering is a key concept for animal welfarists as Singer (1975: pg. 17) wrote in *Animal Liberation*: "There can be no moral justification for regarding the pain (or pleasure) that animals feel as less important than the same amount of pain (or pleasure) felt by humans."

These philosophical differences have led to clashes between conservationists and animal-welfarists over certain wildlife management practices that forsake non-human organisms in order to protect native biodiversity (Hutchins & Wemmer 1987; Rawles 1997; Hutchins 2007; Perry & Perry 2008). Many animal welfarists, for example, protest hunting or culling of individuals to prevent habitat degradation due to over-abundance of certain species, such as ungulates (Rawles 1997), or threats to native wildlife caused by introduced species (Perry & Perry 2008). With respect to illegal wildlife trade, conservation and animal-welfare NGOs' philosophical differences are often reflected in the priorities and activities they perform, which can be complementary (Fraser 2010; Paquet & Dairmont 2010; Dubois & Fraser 2013). In a case study of three NGOs combating illegal wildlife trade in Cambodia, Wyatt (2013a) described how all three aided law enforcement, but in different parts of the country. Conservation NGOs usually

prioritize combating illegal trade of endangered and/or keystone species, such as tigers, elephants, and rhinos (Sitas et al. 2009; Conservation International 2013a; World Wildlife Fund 2014). Animal-welfare NGOs, likewise strive to save these charismatic creatures, but also prioritize individuals of common species regardless of their conservation status, often through rescue centers (Humane Society International 2011).

In many nations, illegal trade in wild animals for the domestic pet market exceeds smuggling of wild animals for international markets (Shepherd 2006; Alves et al. 2012; Pires 2012). Although not as well studied or publicized as international wildlife trade of charismatic species, recent publications are raising awareness of the magnitude of domestic wildlife-pet trade (Ceballos-Mago et al. 2010; White et al. 2012; Sung et al. 2013), and the species involved such as turtles (Ceballos & Fitzgerald 2004) and songbirds (Godoy & Matushima 2010). These types of wild animals, among others such as parrots, snakes, and primates, are popular pets in many Neotropical countries (Drews 2001; Duarte-Quiroga & Estrada 2003; Moreno & Plese 2006; Cantú et al. 2007; Herrera & Hennessey 2007; Ceballos-Mago & Chivers 2010; Alves et al. 2012).

Peru is an archetypal example of a megadiverse Neotropical country with a thriving illegal wildlife-pet trade designed to fulfil demand from domestic consumers, particularly in urban areas (Ríos et al. 2008; Gastañaga et al. 2010; Shanee 2012). Much of Peru's domestic trade was established during the 1960s and 1970s when Peru was one of the largest wildlife exporters in Latin America (Dourojeanni 1972; Thomsen & Brautigam 1991). Excess animals, or those not selected for export, were then sold in local markets. Today, although significant global demand still exists for exotic animal pets (Bush et al. 2014), Peru is not a major international supplier (MINAG 2011). Limited commercial harvest for export is allowed for certain wildlife species (mostly songbirds), permitted under an annual quota system (see Methods in Chapter 2 for legislative details). While the quota system theoretically could provide a legal path for domestic consumers to own a wild-caught animal as a pet, Peruvian authorities regard essentially all domestic wildlife trade as illegal because it is conducted without

appropriate permits and licenses (C. Abramonte, *Administración Técnica Forestal y de Fauna Silvestre*, personal communication).

With a strong domestic demand in Peru, individuals from common to globally endangered species are captured from the wild and offered for sale in animal markets throughout the country (Ríos et al. 2008). Peruvian governmental records demonstrate that 1,125 juvenile yellow-footed tortoises *Chelonoidis denticulata*, a threatened species, were confiscated between 2000 and 2012 (IUCN 2013a; E.F.Daut, unpublished data). This is a concern because confiscated individuals typically represent approximately 3% of the trade (Cantú et al. 2007; Nguyen 2008), and adult *C. denticulata* are heavily hunted for bush meat (Pilco 2012). In a recent survey of Peruvian animal markets, Gastañaga et al. (2010) estimated that 80,000–90,000 wild-caught parrots were sold illegally in the domestic market annually. Because conservation and animal-welfare organizations are active in Peru, it is reasonable to assume that both types of NGOs work to decrease the domestic illegal wildlife-pet trade.

To my knowledge, no study has examined NGOs working to decrease domestic illegal wildlife-pet trade in Latin America. Evaluating NGOs and the strategies they use to curb illegal trade should assist stakeholders and governments attempting to direct funding and encourage efforts to decrease the trade. Peru is an ideal country to conduct such a study because it has considerable illegal wildlife-pet trade, numerous conservation and animal-welfare NGOs are active there, and it is probably representative of regional trade issues within tropical biodiversity hotspots (Myers et al. 2000). The aim of my study was to identify NGOs working to decrease illegal wildlife-pet trade in Peru and characterize key NGO actors' perceptions of the trade. Specifically, I addressed two questions with respect to differing philosophical perspectives toward wildlife: (1) what differences exist in NGOs' efforts to decrease the trade and activities used? and (2) what drives NGO actors to combat illegal wildlife-pet trade? Although this study was not designed to quantify effectiveness of their anti-trade activities, I provide examples where NGOs' efforts appear to have successfully decreased the trade. Finally, I draw

conclusions for those interested in supporting or replicating Peru's NGOs' anti-trade efforts.

Methods

I used a symbolic interactionist framework to guide my qualitative research and content analysis (Mead 1934; Čapek 2006). Symbolic interactionism is a theoretical perspective that attempts to make meaning out of social life and views humans as the active constructors of social life. It is an appropriate approach to use for studying how NGO participants bestow meaning on wildlife and illegal wildlife-pet trade and for trying to understand their motivations for combating trade. Traditionally, interactionism is based on acting people—humans that receive social stimuli (objects)—which they then evaluate in terms of their self, previous experiences, and on-going judgment. Blumer (1986: pg. 81) explained this process as self-indication; a "moving communicative process in which the individual notes things, assesses them, gives them a meaning, and decides to act on the basis of the meaning."

Selection of NGOs

During fieldwork in Peru (October 2012–May 2013), I searched for NGOs working with wildlife and potentially combating illegal trade in wildlife for use as pets. I did not consider illegal bush meat trade or non-commercial wildlife harvest by native communities as part of the search rubric. I searched among traditional conservation NGOs, zoological parks, wildlife rescue centers, and animal-welfare organizations that typically focus on domesticated pets regardless of their funding level, size, duration of work, or geographic focus (international, national or regional within Peru). To identify potential NGOs and the type of work they engage in, I examined (1) websites, blogs, and Facebook pages found by using the Google search engine, (2) published materials such as conference proceedings and technical reports, and (3) information provided by governmental development agencies (Brockington & Scholfield 2010b). Several NGOs were identified during initial informal interviews conducted by E. Daut through the

snowball method, where one interviewee recommends other potential subjects (Wright & Stein 2005). Snowball sampling facilitates identification of potential participants in a select, less accessible, population (Wright et al. 1992). I also received suggestions from two NGO members working with wildlife who reviewed my draft list. My search generated 131 NGOs that broadly fit my criteria including, 49 conservation NGOs, 18 animal-welfare organizations, and 64 zoos or wildlife centers. I expect that my database includes most, if not all, NGOs combating illegal wildlife-pet trade in Peru during my study.

I divided the NGOs into three categories according to their philosophical perspective toward wildlife: whether they primarily focused on (1) wildlife populations, (2) individual wild animals, or (3) both. For simplicity, I labelled these NGOs as conservation, animal-welfare, and dual-perspective, respectively. After reviewing the NGOs' on-line and/or published materials, I identified 31 NGOs likely to be working to decrease illegal wildlife-pet trade, and of these, interviewed representatives of 28 (14 conservation, nine animal-welfare, and five dual-perspective, Table 8). I was unable to interview representatives from three NGOs due to logistical constraints. All 28 NGOs had been working in Peru for ≥ 5 years. They were located in eight political departments across Peru, and included (1) all NGOs I confirmed as working to decrease illegal wildlife-pet trade in Peru, (2) national NGOs with a strong potential to work in this arena, and (3) transnational conservation NGOs with known wildlife-trade efforts in other countries.

Table 8. Non-governmental organizations evaluated in Peru, their perspective toward wildlife (conservation, animal-welfare & dual-perspective), and level of effort based on the number of work categories (n = 4) and work activities (n = 12) in which they participated.

No.	NGO	Perspective	Category[a] effort	Activity[b] effort
1.	Amazon Shelter (For Animal and Environmental Protection)	Dual-perspective	4	9
2.	Centro de Rescate Taricaya	Dual-perspective	4	8
3.	Ikamaperu	Dual-perspective	4	7
4.	Neotropical Primate Conservation (NPC)	Dual-perspective	4	9
5.	Pilpintuwasi	Dual-perspective	4	7
6.	Unidos por los Animales (UPA)	Animal-welfare	3	5
7.	Wildlife Conservation Society (WCS)	Conservation	3	3
8.	Asociación Crax Perú	Animal-welfare	2	2
9.	Centro de Rescate de Osos Andinos	Animal-welfare	2	2
10.	Conservation International	Conservation	2	2
11.	Esperanza Verde	Animal-welfare	2	2
12.	La Granja Villa - Norte y Sur	Animal-welfare	2	3
13.	Organización Científica para Conservación de Animales Acuáticos (ORCA)	Animal-welfare	2	3
14.	Parque de las Leyendas	Animal-welfare	2	3
15.	Pronaturaleza (Fundación Peruana para la Conservación de la Naturaleza)	Conservation	2	2
16.	Sociedad Zoológica de Frankfurt	Conservation	2	3
17.	Amazon CARES (Amazon Community Animal Rescue, Education and Safety)	Animal-welfare	1	2
18.	Brigada Fauna Silvestre	Animal-welfare	1	2
19.	Fauna Forever	Conservation	1	1
20.	Naturaleza y Cultura Internacional	Conservation	1	1
21.	World Wildlife Fund (WWF)	Conservation	1	1
22.	Yunkawasi	Conservation	1	1
23.	Asociación para la Conservación de la Cuenca Amazónica (ACCA)	Conservation	0	0
24.	Center for International Forestry Research (CIFOR)	Conservation	0	0
25.	Centro de Conservación, Investigación y Manejo de Áreas Naturales (CIMA)	Conservation	0	0
26.	Centro de Ornitología y Biodiversidad (CORBIDI)	Conservation	0	0
27.	ProPurús	Conservation	0	0
28.	The Nature Conservancy (TNC)	Conservation	0	0

[a] Categories: outreach, advocacy, development, and husbandry.

[b] Activities: direct public education, indirect public education, television/radio spots, public protests, directly assisting authorities, policy/legislation advancement, development and management of conservation or protected areas, community development, natural resource management, research, ecotourism, wildlife rehabilitation/husbandry of individual wild animals.

Work activities

To characterize the work that each NGO undertook, I evaluated 12 typical activities discussed in literature in which conservation and/or animal-welfare NGOs participate (Castro & Locker 2000; Salem & Rowan 2007). I used data gathered from published materials and my semi-structured interviews (see next section) to assess each NGO's participation in the 12 activities during a 10-year period (2002–2012), or for however long the NGO had been working in Peru if < 10 years. I then assigned a binomial value (0 = no; 1 = yes) for each activity the NGO participated in with respect to decreasing illegal wildlife-pet trade. Data were not available to quantify the time spent or effort made within each activity, so all activities were weighted equally. For simplicity, and to avoid overlap among similar activities, I grouped the 12 activities into four general work categories: (1) Outreach (direct public education, indirect public education, television/radio spots), (2) Advocacy (public protests, directly assisting authorities (including community-level authorities), policy/legislation advancement), (3) Development (conservation/protected areas, community development, natural resource management, research, ecotourism), and (4) Husbandry (wildlife rehabilitation/husbandry of individual wild animals).

The 28 NGOs were assigned a level of effort in decreasing illegal wildlife-pet trade depending on their participation in the four general work categories: none (no work categories), low (one or two categories), medium (three categories), or high (all four categories). To confirm that there were no specialized NGO that worked within one category, but with many activities, I conducted a parallel analysis of level of effort by summing the number of the 12 activities in which each NGO participated (possible values: 0-12). The results were essentially identical to the category-level analysis; therefore, for brevity and clarity, I report only the category-level analysis (Table 8). In this study, "level of effort" is an indirect measure of NGOs' work to decrease illegal wildlife-pet trade based on the number and diversity of categories in which the NGOs participate. I assumed that highly dedicated NGOs are driven to combat the trade and use different tactics because (1) the perceived complexity and magnitude of the trade

mandates a multifaceted approach, and (2) there is a lack of dedicated single-activity NGOs in Peru specialized to combat one or two aspects of the trade.

Semi-structured interviews

I conducted semi-structured individual interviews (Peterson et al. 1994) with ≥ 1 member of the 28 NGOs (n = 33 interviews). An interview guide (Table 9) was used to provide a framework for exploring themes related to illegal wildlife-pet trade. The interview objectives were to (1) identify activities, if any, performed by the NGOs to help decrease illegal domestic wildlife-pet trade, and (2) explore the interviewees' knowledge and opinion of the trade and possible motivations to combat the illegal domestic trade in Peru. Prospective interviewees were contacted either through email or by visiting the NGO's office. I selected interviewees purposively by their level of knowledge regarding the NGO's activities and/or their role with wildlife-related projects. All interviewees had extensive experience (≥ 10 years) working with NGOs in Peru and/or Ecuador. Interviewees were told that the purpose of the research was to better understand domestic wildlife (especially parrot) trade in Peru and the roles of different actors in the trade. Interviews were conducted in either Spanish or English depending on the interviewee's preference, lasted 30–90 minutes, and 29 were conducted in-person and four via Skype. Interviews were digitally recorded if permission was granted by the interviewee (29 of 33 interviews). Hand written notes were taken during and immediately following interviews. All interviews were conducted by E. Daut during part of her yearlong field season in Peru (August 2012-July 2013).

Table 9. Guiding questions for semi-structured interviews regarding NGOs' (conservation, animal-welfare & dual-perspective) role in decreasing illegal wildlife-pet trade in Peru.

1. What is your role with the NGO?	1. ¿Cuál es su papel en la organización?
2. How long have your worked with the NGO?	2. ¿Cuánto tiempo ha trabajado con la ONG?
3. What are the general goals of the NGO?	3. ¿Cuáles son los objetivos generales de la ONG?
4. What type of work does the NGO do with wildlife?	4. ¿Qué tipo de trabajo hace la ONG con la fauna silvestre?
5. What activities does the NGO participate in to decrease illegal wildlife-pet trade? (if any)	5. ¿Qué actividades realiza la ONG para reducir el comercio ilegal de fauna silvestre como mascotas? (si existen)
6. What is your opinion of illegal wildlife-pet trade?	6. ¿Cuál es su opinión sobre el comercio ilegal de fauna silvestre como mascotas?
7. What is the government doing to monitor or control the trade?	7. ¿Qué está haciendo el gobierno para monitorizar o controlar el comercio?
8. Have you observed illegal trade in the field or in the markets?	8. ¿Ha observado el comercio ilegal en el campo o en los mercados?
9. Can you describe an example of a positive impact of the activities the NGO has implemented to decrease the trade?	9. ¿Puede describir un ejemplo de un impacto positivo de las actividades que la ONG ha realizado para reducir el comercio?
10. Do you know of any other NGO that is working to decrease illegal wildlife trade in Peru?	10. ¿Sabe usted de cualquier otra ONG que trabaja para reducir el comercio ilegal de fauna silvestre en el Perú?

Illegal wildlife trade themes

I analyzed the thematic content of language used in the 29 recorded interviews to evaluate interviewees' perceptions and knowledge regarding illegal wildlife-pet trade and their motivations to combat the trade. These interviewees represented 24 of the 28 NGOs, and included 15 conservation, eight animal-welfare, and six dual-perspective interviewees. Recorded interviews were transcribed and statements pertaining to wildlife trade in Peru coded using Atlas.ti7 Scientific Software Development GmbH (Berlin, Germany).

Four broad code categories, grounded on interview data, were used: *level of knowledge, trend of illegal wildlife trade (IWT), aware of IWT work*, and *wildlife-work priorities*. The *level of knowledge* code was used for any statement that reflected the interviewees' knowledge (or lack thereof) and opinion regarding illegal wildlife-pet trade. Opinions concerning the historic trend of the trade in Peru were coded as *trend of IWT*. Statements regarding interviewees' knowledge of specific NGOs (other than their own) working to decrease the trade were coded as *aware of IWT work*. Comments indicating the interviewees' perspective toward wildlife and priority to protect individual wild animals or conserve wildlife species/populations and their habitat were coded as *wildlife-work priorities*.

Interviewees' knowledge regarding illegal wildlife-pet trade was further classified and coded as *considerable IWT knowledge* or *fair IWT knowledge*. I based this classification on the degree of detail regarding the trade, including any indication of personal experiences with, or observation of, illegal trade activities. "Every time we go to work in the communities we find all types of wild animals as pets… particularly monkeys" is representative of statements coded as *considerable IWT knowledge*. Whereas, "… in Iquitos, I have heard that primates are caught for medical studies… I don't know how many they take from the forests" represents statements coded as *fair IWT knowledge*.

The code *awareness of IWT work* was sub-coded as *authority work* to evaluate statements regarding the government's efforts, and specifically ineffectiveness, to

decrease illegal wildlife-pet trade. Statements were categorized using the following three codes: c*orruption, decentralization*, and *not a priority*. While the first and third code are self-explanatory, *decentralization* refers to the government's policy that transferred oversight and control of Peru's natural resources to regional governments (MINAG 2007a). Codes were then sorted with respect to the three NGO categories (conservation, animal-welfare, and dual-perspective) for descriptive statistics.

Comments coded as *wildlife-work priorities* were sub-coded as *individual* and *population* to reflect interviewees' concerns for one or the other, and to evaluate what may drive their work priorities. Statements coded as *individual* indicated concern for individual wild-animal welfare, such as, "There was the feeling of total disgust you get, to see so many animals in poor condition, dirty, in small cages… monkeys with cats, turtles with rabbits, all types of parrots." Statements that reflected interest in wildlife species and populations, including their habitat, were coded as *population* and are represented by, "The work we do with wildlife is to generate some norms for use— hunting and fishing—to restrict the hunting of vulnerable species," and " The threats to wildlife that I see right now are primarily from habitat destruction."

Results

I present the results in two parts, starting with a mixture of quantitative and qualitative findings to highlight differences among NGOs' effort and activities used to tackle Peru's illegal wildlife-pet trade. I follow with a qualitative presentation of interviewees' perspective of wildlife and how concern for individual wild animals, wildlife populations, or both may influence their motivation to combat illegal trade.

Overall, 79% of the 28 NGOs made some effort to decrease illegal wildlife-pet trade in Peru (Table 10). The only NGOs that made no effort to decrease the trade, according to their work activities, were six conservation NGOs. More than half of the 28 NGOs (54%) scored low for their effort to decrease the trade, while 7% made a medium effort. The five dual-perspective NGOs (18%) were the only ones that demonstrated high effort to decrease illegal wildlife-pet trade.

Table 10. Percentage of conservation, animal-welfare, or dual-perspective non-governmental organizations' (n) effort and participation in work categories designed to decrease illegal wildlife-pet trade in Peru, 2002–2012.

Perspective toward wildlife	Effort			Categories							
				Outreach[a]		Advocacy[b]		Development[c]		Husbandry[d]	
		n	%	n	%	n	%	n	%	n	%
Conservation (14)	none	6	43	0		0		0		0	
	low	7	50	7	50	0		2	14	0	
	medium	1	7	1	7	1	7	1	7	0	
	high	0									
Animal-welfare (9)	none	0									
	low	8	89	8	89	0		2	22	6	67
	medium	1	11	1	11	1	11	0		1	11
	high	0									
Dual-perspective (5)	none	0									
	low	0									
	medium	0									
	high	5	100	5	100	5	100	5	100	5	100

[a] Outreach activities: direct public education, indirect public education, and television/radio spots.
[b] Advocacy activities: public protests, directly assisting authorities, and policy/legislation advancement.
[c] Development activities: development and management of conservation or protected areas, community development, natural resource management, research, and ecotourism.
[d] Husbandry activities: wildlife rehabilitation/husbandry of individual wild animals.

Indirect public education, such as publishing posters or fliers, was the most common activity employed by NGOs (68%) to help decrease the trade. A typical conservation NGO in the study participated in one or two education campaigns concerning illegal wildlife-pet trade during the 10-year period evaluated. By comparison, animal-welfare NGOs more actively used direct and indirect public education to raise awareness about the trade through permanent informative billboards and/or weekly public presentations at their facilities.

The dual-perspective NGOs not only employed diverse public education strategies to raise awareness and decrease the trade, but also systematically incorporated anti-trade effort throughout all four work categories (Table 10). Their efforts ranged from typical animal-welfare tasks, such as caring for individual wild animals, to traditional conservation strategies including either creating conservation areas or supporting natural resource management projects designed, in part, to alleviate illegal wildlife-pet trade. Further, all five dual-perspective NGOs were involved with research, conservation, and/or rehabilitation and release of threatened primate species. Direct public education and advocacy activities comprised the backbone of their anti-trade efforts. Dual-perspective interviewee P133 explained their NGO's educational strategy targeting individual and population elements this way:

> You always have to focus on the education in schools and with very small children—so the message sticks—because, frequently they [the children] are the ones that ask for the animals, and the parents are going to fulfil their wish. So, on the one hand, there is the need to educate to reduce demand….But, it is also important to educate for respect of biodiversity. We are a megadiverse country and all of our biodiversity is passing through the markets.

The majority of the interviewees (79%), regardless of the NGO category they represented, possessed considerable knowledge regarding details of illegal wildlife-pet trade in Peru (Fig. 12A). Only one interviewee had no knowledge of the trade, whereas six interviewees demonstrated fair knowledge. Of the 12 interviewees who expressed opinions regarding the trend of illegal wildlife-pet trade, most (83%) maintained the

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trade was decreasing (Fig. 12B) particularly in comparison to the rampant trade in the 1980s–1990s. Conservation interviewee P97 stressed the importance of keeping the trade in historic perspective and shared his first-hand experience:

> In the past [early 1970s] there was much more trade. Hundreds of thousands of parrots were sent through Iquitos—a gigantic operation. There was impressive mortality. The legal exports were 20–30 thousand birds a year, but in reality they captured 100–150 thousand, but most died from poor care in Iquitos.

Two interviewees, both from dual-perspective NGOs, argued the trade was increasing where they worked due to vendors marketing more heavily to tourists in Amazonian regions. Dual-perspective interviewee P50 explained the situation this way:

> The illegal trade is getting worse because of all the tourists. They buy baby animals thinking they are saving them. I have been here for 30 years, and up until 15 years ago, there never were any baby ocelots, or sloths in the market, because the locals know that they are difficult to raise, and they are not pets. The tourists think they saved them, but they do not realize that they had to kill the mother to get the baby. Fifteen years ago, the locals used to hunt sloth and they would feel bad whenever they found a baby. But now, there are so many [wildlife] "rescue" centers around Iquitos that exhibit animals just for the tourists, the locals know that the centers or tourists will buy these animals.

(A) Level of knowledge

(B) Trend of trade

(C) Aware of wildlife trade work
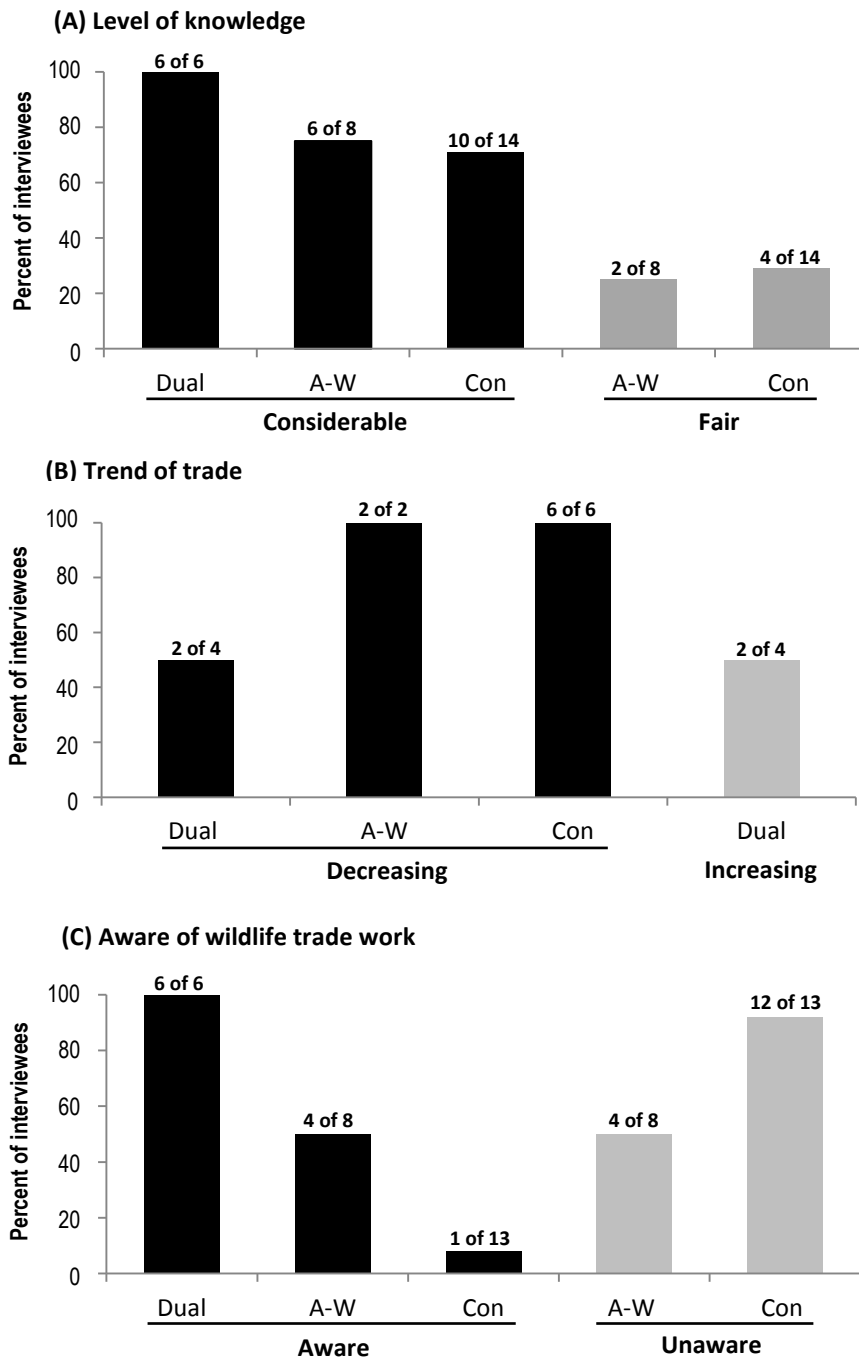
Figure 12. Percentage of interviewees' responses NGOs' philosophical perspective toward wildlife [dual-perspective (Dual), animal-welfare (A-W) and conservation (Con)] regarding illegal wildlife-pet trade in Peru (October 2012–May 2013) by (A) level of knowledge about the trade, (B) trend of wildlife trade, and (C) awareness of high-effort NGOs working to decrease illegal wildlife-pet trade. Proportion of interviewees responding per NGO is listed above columns.

Of the interviewees from conservation and animal-welfare NGOs, only 24% were aware of the high-effort NGOs working to decrease the trade (Fig. 12C), and notably, only one conservationist interviewed was aware of any of the dual-perspective NGOs' work.

Nineteen interviewees (58%) mentioned that the Peruvian government was not doing enough to decrease illegal wildlife-pet trade. Seventeen of these interviewees offered at least one of the three primary reasons for the government's laxity (Fig. 13). The most common reason mentioned was that the government did not prioritize wildlife as part of its effort to combat illegal commercialization of natural resources, because most officials regulating trade are forestry engineers and therefore focus on timber extraction. Animal-welfare interviewee P57 reflected on the irony of the governmental agency's name responsible for managing Peru's natural resources, the *Dirección General Forestal y de Fauna Silvestre* (General Direction of Forestry and Wildlife):

> In this case, it is the *Dirección General de Forestales,* because they are most concerned about timber harvest. Timber generates much, much more money, especially in comparison to wildlife…but, consequently they permit the destruction of habitat. So, on one side, they do not control the sale of [native] birds on the streets and in the markets, and on the other side, nor do they stop the tremendous illegal [timber] extraction.
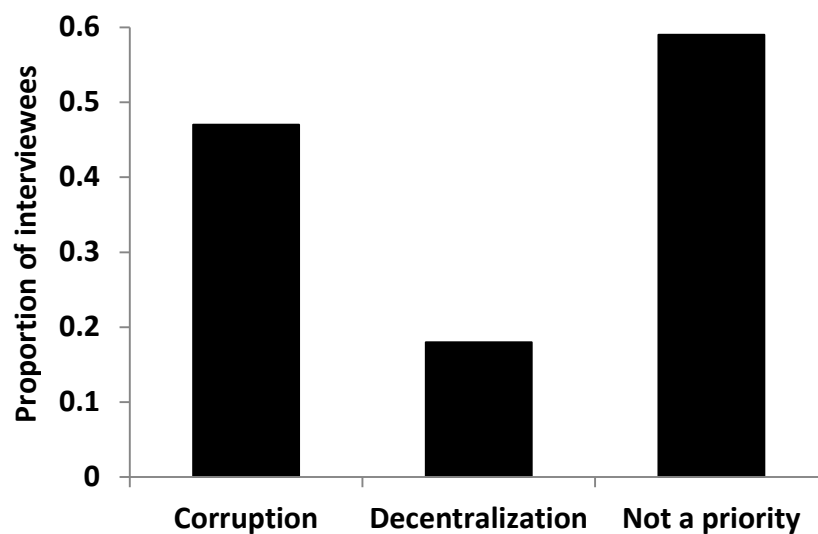
Figure 13. Percentage of non-governmental organizations interviewees' opinions (n = 17) regarding reasons why Peruvian government does little to tackle illegal wildlife trade (October 2012–May 2013): *corruption*, *decentralization* (transfer of wildlife regulation to regional control), and *not a priority*.

Corruption was the second most common explanation for the government's lack of enforcement of wildlife and natural resource conservation legislation. While discussing illegal wildlife trade in Peru, conservation interviewee P71 explained:

> The state has a department to monitor that it does not happen. The thing is that the government does not follow through with the sanctions—they are not fulfilled. I think the laws here are good, but not enforced. Part of the problem is that there is corruption—pay the judge or the police and *ya*, you are free.

Another conservation interviewee P140 jokingly expressed the government's corruption problem by punning the agency's name:

> The *Dirección General Forestal y de Fauna Silvestre* [DGFFS], you know the nickname don't you? It's the *Dirección General de Falcificación, Fraude y Soborno* (General Direction of Falsification, Fraud and Bribery). And, I mean it's true. It has to be the most corrupt place in Peru.

Three interviewees mentioned that corruption and overall ineptitude was facilitated by the government's policy to decentralize oversight and control of Peru's natural resources

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to regional governments. The legislative chaos that ensued was considered, in part, responsible for the government's laxity with confronting illegal wildlife-pet trade.

Although interviewees from all three types of NGOs expressed concern for individual animals, the level of passionate concern for individual wild animal welfare was most prominent and consistent from dual-perspective interviewees and considered a primary driver to combat illegal wildlife-pet trade. Dual-perspective interviewee P115 said succinctly: "The first thing I have to do when I see a captured monkey [for sale or as a pet] is that I have to rescue it." Dual-perspective interviewee P133 similarly expressed concern for wild animals for sale:

> When I go to the [animal] markets, I get this sensation, like it is a jail for the animals. The central market made renovations and now it is more clean and modern, but it is the same cruelty. It has to stop.

There appeared to be no exclusion criteria for the type of wild animal that dual-perspective NGOs would assist, such as taxa or abundance in the wild. According to dual-perspective interviewee P62, concern for the individual wild animal, regardless of its conservation status, motivated their NGO to action:

> The individual animals are very important to us. That is why we are more activists, because we want to protect individuals. It doesn't matter if the species is endangered or not. For example, the capuchin monkeys…they [conservationists] would never spend money to protect those common species. We do it because we have the passion.

While concern to help individual wild animals captured for the illegal pet trade was a major driver for dual-perspective interviewees, conservation of wild-animal populations was also frequently mentioned and considered a second important motivator to combat the trade. In reference to their wildlife rehabilitation efforts, interviewee P118 explained:

> In our type of work, it is always a big debate. Do you go for population and habitat protection, or do you protect the individual? I think you need to go in between. There are many factors involved without one simple solution. What do

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we want to protect? Ultimately, we want to protect the wild ones and we have to minimize any risk from animals that we introduce.

Dual-perspective interviewees were acutely aware of the debate between individual and population approaches to wildlife welfare and conservation. Despite possible criticism from conservationists, the dual-perspective interviewees embraced their "dualness". Unique among these interviewees was the affirmation of a strong connection between individual wild animals and wildlife populations and the importance to consider both. Interviewee P59 expressed their NGO's philosophy this way:

Specifically, we try to join the two things, populations and individuals. We deny a difference between the individual and the population, they are the same thing…, and when you worry about the welfare of the individual wild animal that permits you to better understand the species and stimulates more serious work with wild populations.

Dual-perspective interviewee P62 elaborated further on how their NGO's approach differs from a typical conservation (population) focus:

We go out to directly help the animal. You gain awareness when you see many cases of suffering animals. The conservationists think they are going to save the wildlife populations with their studies and publications. I think they don't understand the situation, because they don't know the individual. They are more focused on conserving the animals because they are part of nature. Meanwhile, we see the wild animals as living beings that deserve protection individually— and as part of their populations.

Dual-perspective interviewees were not the only interviewees to express concern for individual wild animals. Occasionally conservation interviewees expressed concern for individual animals caught for the illegal wildlife-pet trade; however, the dominating perspective was that trade was not a serious threat to populations, as conservation interviewee P91 said:

In the wild, I do not think the trade is affecting species. Despite the enormous numbers that are trafficked, they are still lower than what they were. It is not

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going to affect the wildlife populations—of those species—because they reproduce so quickly. What is worse than the damage to the populations, for me what is unjustified, is the mistreatment of the animals. For me, that is unacceptable.

Several animal-welfare interviewees also expressed concern for individuals, such as interviewee P28 who said:

The issue that angers me most, and in which I try to help when I can, is the trafficking of the wildlife….I have gone to the markets, but for me, I cannot go much, because it is too traumatizing to see all the animals.

However, this same interviewee explained the pragmatic reason why their NGO did not prioritize combating illegal wildlife-pet trade despite the impact it can have on animal welfare:

Well, you have to start with something. Here in Peru, the problem with stray dogs is very severe, so we started with the stray dogs on the street. But we give funding to help wildlife rescue centers and for animal transport.

The decision to prioritize work that addressed "severe" needs in Peru was echoed by many conservation interviewees. With respect to wildlife, conservation interviewees considered the greatest needs as habitat preservation and resource management to conserve wildlife species and populations. Most interviewees from conservation NGOs mentioned their efforts within and around protected areas to preserve forested areas and/or to improve community control of their natural resources, including forestry and hunting management. Illegal wildlife-pet trade was not considered a serious threat to populations and therefore not a work priority, as conservation interviewee P71 explained:

I do not think the wildlife trafficking is a serious problem. I do not know the volumes or the quantities of wildlife that are being commercialized. But, I do know that deforestation is a big threat, and also the big construction projects like the new highways and hydro-electric dams—without any environmental plans.

Most interviewees, regardless of their NGO type, acknowledged that Peru has many human-driven activities resulting in habitat loss and degradation that threaten wildlife populations and biodiversity. Conservation interviewees' concerns overwhelmingly prioritized these broad habitat and population-level threats and were considered a primary driver for their work. Interviewee P72 summarized many of the major threats mentioned by conservation interviewees:

> The threats to wildlife, that I see now, principally are the destruction of habitat—the deforestation from illegal timber harvest. But, much more damaging are land use changes, in general, for agriculture. They [farmers] burn all the forest to make their crops or put their cattle—that is the worst of all—even worse than the [legal] mining operations. The mining operations affect a huge area, but they are obligated to strengthen the conservation around the area. Instead, with the farmers, they go and burn, then move to the next plot and nobody forces them to be responsible for the land….The *illegal* [gold] mining, on the other hand, is impressively damaging in *Madre de Dios*. Those are the big threats for biodiversity.

Discussion

My results demonstrate that NGOs in Peru are working to decrease the illegal wildlife-pet trade, but suggest that effort expended is related to the NGO's philosophical perspective toward wildlife. Although both conservation and animal-welfare NGOs sometimes worked to decrease the trade, NGOs with a philosophical perspective that prioritized both wildlife population conservation and individual wild animal welfare were the most dedicated, directing most, if not all, of their work activities on the issue of illegal wildlife-pet trade. The dedication of these NGOs was surprising because the literature typically represents NGOs as either focusing on wildlife conservation or animal-welfare, not both (Irwin 2003; Brockington & Scholfield 2010b). However, a recent study demonstrated that it is not uncommon for animal welfare and conservation-oriented citizens to share concern for both the conservation of wildlife populations and

welfare of individual animals (Dubois & Fraser 2013). Dual-perspective NGOs appear to balance commitment for both individuals and populations by not distinguishing differences between the two—individuals make up populations and, therefore, both are threatened by illegal wildlife-pet trade.

It is reasonable to assume that firmly held wildlife-conservation and animal-welfare values synergistically drive dual-perspective NGOs to tackle the illegal wildlife-pet trade while many other NGOs do not. As Booth (2009) maintains, such moral pluralism can compound motivation. Further, all five dual-perspective NGOs are small and primarily volunteer-based. Previous research on motivations of volunteers suggest that multiple drivers exist for volunteers helping at wildlife-rehabilitation centers or with conservation projects (Kidd et al. 1996; Martinez & McMullin 2004). For example, direct hands-on and practical activities appeal to volunteers from both groups, such as working directly with individual animals, while long-term benefits for the environment and populations, such as those gained from habitat protection and public education, are important concerns for both conservation (Caissie & Halpenny 2003) and wildlife-rehabilitation volunteers (Siemer et al. 1994).

The comparatively low effort to decrease the illegal trade expended by both conservation and animal-welfare NGOs suggests that tackling this issue was not a priority for these organizations. Although most interviewees were well aware of the trade (Fig. 12A), and often expressed concern for the individual wild animals in the trade, other more severe needs appeared to motivate conservation and animal-welfare NGOs. Domestic animal welfare was the primary driver for the few "traditional" animal-welfare organizations included in the study, while zoo and wildlife rescue centers prioritized providing care for their captive animals—a costly commitment, particularly with a never ending supply of confiscated wild animals for which to care. It is also possible that the animal-welfare NGOs did not prioritize anti-trade work because they were aware of the efforts of the dual-perspective NGOs and did not feel obligated to duplicate such work (Fig. 12C).

Conservation interviewees clearly prioritized conservation of wildlife populations and mitigating serious threats caused by habitat degradation and resource misuse. Further, because the illegal wildlife trade in Peru is largely composed of common species (Ríos et al. 2008), and the general opinion that the trade had decreased over time (Fig. 12B), conservation NGOs were consistent with the mission formalized by Soulé (1986). It was surprising, however, that so little collaboration existed between conservation and dual-perspective NGOs, particularly with respect to the dual-perspective NGOs' conservation and rehabilitation efforts of threatened primates. Many large conservation NGOs are involved with wildlife rehabilitation projects in other countries (e.g., Conservation International 2012; Wildlife Alliance 2014). Dual-perspective interviewees claimed they were rebuffed by the large conservation NGOs following many proposals for collaborative projects. Because only one conservation interviewee acknowledged knowing of the anti-trade work conducted by the dual-perspective NGOs (Fig. 12C), it may be that the dual-perspective NGOs need to better promote their work.

Most interviewees strongly agreed that the Peruvian government should do more to combat illegal wildlife-pet trade (Fig. 13). In many cases, interviewees implied that control of the trade was the government's responsibility (despite the governments lack of interest and corruption) and beyond the scope of their NGO's work. Allegations of governmental corruption and ineptness are not novel. Previous studies have documented the Peruvian government's poor regulation and control of the country's natural resources (Sears & Pinedo-Vasquez 2011; Swenson et al. 2011; Urrunaga et al. 2012), including wildlife (Shanee 2012). The degree of official corruption, however, including accusations of local authorities as wildlife traffickers, was alarming, but unfortunately not unique to Peru (Christy 2010; Kakabadse 2011).

I equated NGOs' effort to decrease illegal wildlife-pet trade to the number and diversity of categories in which they work. In theory, an NGO could be highly dedicated to decreasing trade by focusing effort within one of the four work categories or even just one of the 12 activities I evaluated. However, I found no evidence of this from the 28

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NGOs in my study. It appears that the NGOs strongly interested in decreasing illegal wildlife-pet trade—the dual-perspective NGOs—deliberately used multifaceted approaches to pursue their goals. I suspect the reason may be a consequence of the interconnected elements of illegal trade and the NGOs dedication to tackle multiple aspects of the trade as part of an integrated program. For example, awareness of the challenges of caring for confiscated wildlife could lead to assisting authorities during market raids, followed by public education to decrease demand for wildlife pets and establishing protected areas to decrease illegal harvest.

Although, the five dual-perspective NGOs represent only 4% of the original 131 NGOs I identified, they appear to be having a positive impact. Two areas of Peru now have less illegal wildlife-pet trade largely due to their efforts. The first is Lima, Peru's capital, where the municipality recently closed the largest and most historic animal market in an effort to decrease illegal wildlife-pet trade, mistreatment of animals, and risks to public health (Anon. 2013). Municipality officials stated that years of pressure from *animalistas* (animal activists), and changing public sentiment, helped decrease the trade, and was what motivated them to close the market (A. Anicama, *Municipalidad de Lima*, personal communication). Wildlife authorities suspect that closing the market will decrease illegal trade further, because it will make it more difficult for illicit vendors to sell wildlife and it sends a clear message to society that the municipality is taking illegal trade more seriously (C. Abramonte, *Administración Técnica Forestal y de Fauna Silvestre*, personal communication). The second area includes the city of Tarapoto and rural communities along the eastern Andean slopes in northern Peru. Two dual-perspective NGOs have worked a combined 22 years educating the public about consequences of illegal wildlife-pet trade on individual animals and populations, and increasing government effort to tackle trafficking in this area (Shanee 2012).

It is unclear which strategies are most effective for decreasing illegal wildlife-pet trade in domestic markets. Although rarely discussed in the scientific literature, raising public awareness about the harm illegal wildlife trade has on individual animal welfare may be an effective tool to help reduce the wildlife trade (Baker et al. 2013). Raising

awareness, increasing enforcement, decreasing demand, offering market alternatives, and improving regulation of sustainable harvest are all commonly discussed strategies, and individually have been successfully implemented by NGOs. Targeted education campaigns by NGOs have decreased demand for parrots in Saint Lucia (Jenks et al. 2010), rhino horn in Yemen (Vigne & Martin 2013), and *shahtoosh* in India (Misra 2003). Strategies promoted by NGOs to increase enforcement of domestic wildlife statutes have helped conserve snakes in China (Jiang et al. 2013). Further research is needed, however, to evaluate the effectiveness of the array of strategies used to decrease illegal wildlife trade under various ecological and socio-economic conditions. I encourage the conservation and animal-welfare communities to engage in evidence-based research and systematic reviews to assist on-the-ground efforts to decrease all forms of illegal wildlife trade (Pullin & Knight 2001; Blumstein 2013).

Conclusion

Illegal wildlife trade is driven by complex socio-economic factors (Singh 2008; TRAFFIC 2008; Nekaris et al. 2010). Response by Peru's most dedicated NGOs combating the trade is equally complex, in part, because illegal wildlife-pet trade is at the intersection of wildlife conservation and animal welfare. Nowhere else are these two philosophical perspectives wedded so closely in terms of numbers of individuals traded and species threatened by the trade. My findings that dual-perspective NGOs make more effort than either conservation or animal-welfare NGOs to decrease the illegal wildlife-pet trade implies their willingness to tackle the complexity of the trade—a willingness driven by their motivation to prioritize both individual wild animals and wildlife populations. Because many NGOs combating illegal wildlife-pet trade are small and volunteer-based, I recommend that NGOs consider developing a dual focus for their anti-trade efforts that addresses both individual wild animals and wildlife populations to attract motivated volunteers to further their causes. Stakeholders, including governments as well as large international conservation and animal-welfare NGOs, searching for partners dedicated to decreasing illegal wildlife-pet trade should consider NGOs with integrated dual perspectives toward wildlife.

CHAPTER VI

CONCLUSION AND RECOMMENDATIONS

My dissertation adds to the limited knowledge regarding the scale, regulation and potential health consequences of legal and illegal wildlife, particularly avian, trade in Peru. The methodological approaches I used and many of my research findings could be applied to illegal wildlife trade systems in other countries. Specifically, I addressed (1) the magnitude and composition of the Peru's domestic pet-bird market and the influence of legal export quotas on the illegal native bird trade for domestic consumers, (2) the consequences of a hypothetical introduction of an infectious pathogen, Newcastle disease virus, into a susceptible population of wild white-winged parakeets and the utility of epidemic threshold values, and (3) the role of NGOs in combating illegal wildlife-pet trade in Peru and how different philosophical perspectives toward wildlife influence NGOs' effort. The following is a summary of the major findings of my dissertation research. I end with recommendations to decrease illegal wildlife trade in Peru and future research needs to fill knowledge gaps.

In Chapter II, through analysis of a five-year market study, I determined that Peru had an extensive illegal trade in wild-caught native birds, predominantly psittacines, for the domestic pet market. I found that Peru's current legal quota system, which started in 2001, had little influence on avian species abundance in domestic markets. While the current legal export trade did not facilitate illegal domestic trade, regression analyses demonstrated that high historic export trade increased avian species abundance in the markets. This indicates that banning export trade would likely not eliminate Peru's domestic trade and raises the importance of historic export trade. High export trade of native birds in the 1960s and 1970s helped create Peru's domestic market and is now essentially a proxy for the established tradition of trade in native birds to fulfill demand from domestic consumers. In Chapter III, using mathematical models, I demonstrated that illegal bird trade could theoretically expose a susceptible population

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of white-winged parakeets to ND provoking an outbreak with considerable disease-related mortality. High harvest rates would dampen the magnitude of the outbreak. Lower, more "realistic" estimates of the basic reproduction number (R_0) were generated when ND transmission was modeled including age-structure versus a homogenous parakeet population. My results should encourage conservation scientists to use age-structured infectious disease modeling as an informative tool to investigate potential synergistic effects of disease and illegal trade on wildlife populations.

In Chapter IV, I extended the discussion of the importance of epidemic threshold values (R_0) to the wildlife rehabilitation community and demonstrated that, as an example, a single infected raccoon released into a susceptible population could provoke an outbreak of distemper. Increased awareness of wildlife disease transmission and dynamics should motivate wildlife rehabilitators to ensure their patients are free of infectious pathogens prior to release. In Chapter V, I used a qualitative approach to demonstrate that many NGOs in Peru were working to decrease the illegal wildlife-pet trade, but the effort expended was related to the NGOs' philosophical perspective toward wildlife. The NGOs most dedicated to combating the illegal trade had a dual philosophical perspective that prioritized both wildlife population conservation and individual wild animal welfare. This indicates that stakeholders and governments searching for committed collaborators to help curb illegal wildlife trade should consider approaching NGOs with integrated conservation and animal-welfare perspectives toward wildlife.

Recommendations

The drivers, consequences, and mitigation of illegal wildlife trade are complicated, as indicated, for instance, by the non-linear relationship between legal and illegal trade. Given the complexity, each trade system should be evaluated independently to understand the unique elements involved and, as such, provides an ideal opportunity to develop interdisciplinary scientific collaboration. By working together, conservation and animal-welfare scientists along with criminologists, economists, and conservation

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psychologists offer complementary approaches to document impacts of illegal trade, improve understanding of drivers, and develop effective mitigation strategies including integrated programs to reduce supply and demand. With mounting evidence documenting illegal wildlife trade for domestic consumers, collaborative research efforts should increase focus on illegal trade within source countries and take advantage of local and regional NGOs with expertise combating domestic trade.

Increased globalization and demand for exotic animal pets has created worldwide movement of wild-caught and captive-bred animals, and with them, potential pathogens. While the risk of spreading infectious diseases from illegal wildlife trade on a national level is considerable, the risk and potential consequences are greater on an international level where infectious pathogens could be introduced across continents. Increased collaboration between wildlife ecologists and epidemiologists is needed to provide the knowledge and specific data on wildlife population demographics and disease dynamics. This information then needs to be linked with global trade figures, economic drivers and policy measures to help develop realistic risk assessments and simulation models to better understand the potential outcome of introduced infectious diseases via global wildlife trade.

In Peru, I am optimistic that coordinated mitigation and strong political will could swiftly decrease supply and demand for illegally-captured wildlife for the domestic pet market. I include the following recommendations, based on my research findings and experiences in Peru, to assist the government and relevant stakeholders decrease the illegal wildlife trade.

(1) Increase training of wildlife authorities and national and municipal police in wildlife species identification, confiscation records management and proper handling and basic husbandry. Several identification guides for commonly confiscated species already exist and should be made widely available in print and electronic form. Additional information regarding confiscation and husbandry protocols could be provided in short training videos with help from wildlife rescue centers, zoological parks and relevant NGOs.

(2) Increase enforcement of wildlife legislation in primary source regions, particularly ports and markets in the Amazonian cities Iquitos and Pucallpa, before the captured animals leave their native habitat and are transported long distances to Lima and other coastal cities. Sentencing guidelines should be established and widely distributed to local prosecutors, judges, and the media to increase the perception that illegal wildlife trade is a serious crime. Penalties should be extended to include owners of transport companies (shipping and trucking) from which wildlife are confiscated to increase accountability. Also, penalties should be increased for trafficking wild animals that have been "altered" in some form, such as cutting birds' wing feathers to prevent flight and dying feathers to change appearance. Such alterations greatly increase the time required in rehabilitation and diminish chances of release back to the wild.

(3) Improve transparency and promotion of enforcement of wildlife legislation by publicizing every wildlife confiscation and outcome through coordination with the media, and writing press releases and posts on departmental websites. Several NGOs have active websites that could serve as links to improve public relations, and combat the image of governmental corruption, especially within the conservation and animal-welfare communities.

(4) Coordinate more effectively with NGOs working to decrease the illegal wildlife trade, including wildlife rescue centers and zoological parks, to assist with confiscations, quarantine and rehabilitation of individuals. Increase collaboration with veterinary colleges to assist with physical exams and diagnostic testing of confiscated animals.

(5) Coordinate public-education campaigns with pet industry representatives (i.e., pet-supply companies, breeder associations, veterinary colleges and associations) to demonstrate the benefits of owning captive-bred pets and to increase stigma for purchasing a wild-caught native species, as native wildlife are a critical part of Peru's unique cultural and biodiversity heritage.

(6) Coordinate public-education campaigns with the Tourism Ministry (*Ministerio de Comercio Exterior y Turismo*) and international and national tourism companies to raise awareness of Peru's wildlife conservation legislation to decrease purchase of wildlife and their derivatives, and to cultivate respect and national pride to conserve Peru's distinguished role as a megabiodiverse country.

(7) Encourage collaboration among NGOs working to decrease illegal wildlife trade to maximize the outcome of their efforts. Large, well-funded, conservation NGOs should consider partnering with smaller, dual-perspective NGOs that have established community-based and social-media networks for public education programs.

Future research

My dissertation provides a foundation to investigate future research questions, for example:

(1) **How does supply and demand interact to drive Peru's domestic pet bird trade?** In case of the most abundant native bird illegally for sale in Peru's market, *Brotogeris versicolurus*, it appears that the market may be supply driven. For other species, such as larger psittacines that have good talking abilities, high consumer demand appears to drive the trade. Understanding the drivers of the trade would help design best practices to decrease the illegal trade, such as providing consumers options of captive-bred (native or exotic) birds.

(2) **How could Peru's nascent aviculture industry develop to fulfill demand for pet birds from domestic consumers?** Captive-bred exotic birds such as Australian parakeets and canaries made up 62% of the entire pet bird market during our study, indicating strong demand and potential for exotic birds to serve as conservation "green" substitutes for consumers. Many aviculturists expressed interest in expanding breeding operations to include more exotic species and native birds, but stringent governmental regulations limit opportunities. However, consumer preferences are unknown. For example, do

consumers prefer exotic or native birds as pets? Could consumers be persuaded to purchase captive-bred individuals to benefit conservation of Peruvian species?

(3) **How would ND transmission dynamics change when additional host species such as other parrots and poultry are involved?** Many parrot species are susceptible to ND, and while feeding together at fruiting trees or clay licks, individuals could be potentially exposed to ND. Furthermore, along with the growing human population in many Amazonian regions, so are the formal and informal poultry operations, which increase the potential risk for disease transmission between domestic and wild birds.

(4) **What are the most effective mitigating strategies to decrease Peru's illegal wildlife-pet trade?** Peru's NGOs use various tactics to decrease illegal trade, such as public education and policy development, but the outcomes and cost-effectiveness of their efforts are unclear. Improved understanding of the most effective mitigating strategies would assist efforts to combat illegal wildlife-pet trade throughout the region.

By most measures, native wildlife populations are doing poorly (Pimm & Raven 2000; Sitas et al. 2009; Butchart et al. 2010; Hoffmann et al. 2010). Illegal wildlife trade for the pet industry contributes to the decline of many populations of wildlife species, in addition to compromising individual animal-welfare, and being a source of potential disease transmission—grim consequences simply to fulfill demand for pets. Arguably, having a wild-caught animal as a pet is not a requirement to sustain life, and differs from other types of wildlife trade that have long-standing cultural traditions associated with perceived medicinal benefits and/or consumption for sustenance. Decreasing illegal wildlife trade will require coordinated efforts at local, national, regional and international scales, starting with increased knowledge and appreciation of nuanced features of specific trade systems. My dissertation provides an example of how natural and social science research approaches were used to improve understanding of Peru's

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illegal wildlife trade system. It is my hope that my findings will encourage the scientific community to similarly investigate other trade systems.

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APPENDIX A

DETAILED EXPLANATION OF INDEPENDENT VARIABLES

Detailed explanation for 16 independent variables used in my analysis of export quotas and avian abundance in Peruvian animal markets and in governmental seizure records (2007–2011).

Biological factors:

Region: one of the four major biogeographical regions where species were most predominantly distributed in Peru: Amazon basin, dry forest, coastal plains, and Andean mountains (Schulenberg et al. 2007). For the parrots-only subset model, this variable was condensed into two regions, Amazon and non-Amazon.

Range (km^2): estimates of the size of wild geographical ranges of native species in Peru based on shapefiles used for distribution maps in Birds of Peru guide (Schulenberg et al. 2007). Values were calculated using ArcGIS software V.10 (Esri, Redlands, CA) directly from the polygon data.

Abundance: a 3-point scale of wild-range abundance based on Birds of Peru guide (Schulenberg et al. 2007): 1 = vagrant to uncommon, 2 = uncommon-fairly common to fairly common-common, and 3 = common to abundant. For species that had ≥ 2 distinct geographical areas with different abundances, I used the higher abundance. For the parrots-only subset model, abundance was condensed into a 2-point scale: 1 = vagrant to uncommon-fairly common and 2 = fairly common to abundant. An abundance score was unavailable for one species, *Phoenicopterus chilensis*.

Conservation rank: a binomial scale for the conservation status of native birds included in the study based on the IUCN Red List of Threatened Species (2013b) and on Peru's 2004 list of threatened species (MINAG 2004): 1 = least concern, 2 = near threatened, vulnerable, or endangered. I used the more threatened status for those species that were included on both IUCN and Peru lists.

Capture: a 3-point ease-of-capture scale of how easily individuals of avian species recorded in the study can be captured from the wild, for example by removing chicks from nests, using mist nets or other types of traps such as bal-chatri traps or a combination of methods: 1 = easy, 2 = moderate, and 3 = difficult.

Body mass (gm; log-transformed): a measure of avian body size (Dunning Jr. 2008) was available for 146 of the 150 species included in the study. A sympatric substitute with similar body dimensions was used for three species. I was unable to obtain a published weight or suitable substitute for one species, *Piezorhina cinerea*. When male and female values were available, I used an average. For the parrots-only subset model, body mass and price were highly correlated (VIF > 5); I retained the price variable as it contributed more to the model.

Color (square-root transformed): a composite, unit-less, value based on the number of contrasting colors of male plumage, (if sexually dimorphic), per species x the % of body coverage of those contrasting colors, based on color plates in Birds of Peru bird guide (Schulenberg et al. 2007). I defined contrasting colors as primary colors not typically found in background (terrestrial) nature and include: red, orange, yellow, blue, indigo, violet, and white. Only obviously contrasting shades of the same primary color were counted as separate colors, such as dark aquamarine blue and powder blue. Only colors easily observable on a bird in a perched or standing position were considered and included contour, tail and wing feathers (top sides) and colors around the eye and face patch. I did not include color of the beak, iris, legs or feet.

Voice: a 3-point scale of the species' ability to mimic sounds ("talk" in the case of parrots) or to sing in complex and/or pleasing sounds. I used on-line resources (http://www.all-pet-birds.com/parrot-characteristics.html) and expert opinion to gauge parrots' talking ability and the "Xeno-Canto" website (http://www.xeno-canto.org/) to listen to birds' songs and to subjectively rank them on the pleasantness of their song: 1 = poor talking ability or simple/harsh vocalizations, 2 = medium talking ability or semi-pleasing vocalizations, and 3 = excellent talking ability or pleasing/complex singing vocalizations.

Trade factors:

Current quota[a] (square-root transformed): summed national commercial harvest (export) quotas for native avian species (2007-2011) recorded in the market survey and/or seizure records during the study (MINAG 2007b, 2008, 2009, 2011).

Past quota[a] (square-root transformed): summed national commercial harvest (export) quotas for native avian species (2001-2006) recorded in the market survey or seizure records during the study (e.g., MINAG 2001b).

Total quota[a] (square-root transformed): summed national commercial harvest (export) quotas for native avian species (2001-2011) recorded in the market survey or seizure records during the study.

Quota years[a]: summed number of years (2001-2011) with national commercial harvest (export) quotas for native avian species recorded in the market survey or seizure records during the study.

U.S. import (log-transformed): summed imports of avian species originating from Peru during 1970-1974 (Clapp & Banks 1973b; Clapp & Banks 1973a; Clapp 1975; Greenhall 1977) and 1980-1989 (Nilsson 1985, 1989, 1990, 1992). The United States was the major importer of Neotropical birds during the 1970s and 1980s (Thomsen & Mulliken 1992), and I considered these values more reliable than CITES permit records because CITES permits may be issued but not used.

CITES permit (log-transformed): summed export permit values of native birds from Peru listed in CITES trade database from 1975-1979 and 1990-2006 (CITES 2014b). CITES records were based on gross export reports from Peru and the search criteria included: all import countries, wild sources, all trade purposes and live animals.

Price (U.S. dollar; square-root transformed): selling prices given to us by vendors of native birds (mostly parrot species) in markets during the study period. In most cases, only one value was collected per species; however, whenever multiple values were collected, either in the same city or in different cities, the values were averaged. Values were converted from Peruvian *nuevos soles* to U.S. dollars using the average conversion rate during the study period (http://usd.fx-exchange.com/pen/). For the parrots-only subset model, price and body mass were highly correlated (VIF > 5); I retained the price variable as it contributed more to the model.

CITES Status: a binomial scale to classify native birds recorded in the study as (1) not listed on any CITES Appendix, or (2) listed on either Appendix I or II (CITES 2013). None of the avian species included in the study were listed on CITES Appendix III. For the parrots-only subset model, the CITES Status variable was not included because all species were listed on either Appendix I or II.

[a] The four quota variables (current quota, past quota, total quota and quota years) were highly correlated (VIF > 5); I retained only quota years to reduce multi-collinearity.

AVIAN SPECIES IN MARKETS AND SEIZURES

Table B1. Number of avian species (native, regional, exotic and ornamental) observed for sale in animal markets in nine Peruvian cities, recorded in government seizures, and/ or with commercial harvest (export) quotas (2007–2011). CITES trade status according to Appendices.

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
Accipiter striatus	Sharp-shinned Hawk		1		II
Accipitridae	Hawk	46			
Agapornis fischeri[c]	Fischer's Lovebird	1,560			II
Agapornis personatus[c]	Yellow-collared Lovebird	2,271			II
Agapornis roseicollis[c]	Peach-faced Lovebird	2,512			II
Agapornis sp.[c]	Lovebird	325			
Amazona aestiva[d]	Turquoise-fronted Amazon	19	3		II
Amazona amazonica	Orange-winged Amazon	1,027	120		II
Amazona farinosa	Southern Mealy Amazon	272	51		II
Amazona festiva	Southern Festive Amazon	520	33		II
Amazona mercenarius	Scaly-naped Amazon	12	10		II
Amazona ochrocephala	Yellow-crowned Amazon	351	17		II
Amazona sp.	Amazon Parrot	11	26		
Anatidae	Wild Duck	6			
Andigena hypoglauca	Grey-breasted Mountain-toucan		2		
Anhima cornuta	Horned Screamer	29			
Anisognathus igniventris	Scarlet-bellied Mountain-tanager			500	
Anisognathus somptuosus	Blue-winged Mountain-tanager			200	

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
Ara ararauna	Blue-and-yellow Macaw	115	24		II
Ara chloropterus	Red-and-green Macaw	82	10		II
Ara macao	Scarlet Macaw	47	15		I
Ara militaris	Military Macaw	7	4		I
Ara severus	Chestnut-fronted Macaw	52	3		II
Ara sp.	Macaw	41	17		
Aramides cajaneus	Grey-necked Wood-rail	16			
Aratinga weddellii	Dusky-headed Parakeet	609	217	5,000	II
Ardea alba	Great White Egret	1			
Ardea cocoi	Cocoi Heron	19			
Ardeidae	Heron	4			
Arremon abeillei	Black-capped Sparrow	2			
Asio clamator	Striped Owl	2			II
Athene cunicularia	Burrowing Owl	22	5		II
	Bird		13,285		
Bolborhynchus orbygnesius	Andean Parakeet	49			II
Brotogeris chiriri[d]	Yellow-chevroned Parakeet	5			II
Brotogeris cyanoptera	Cobalt-winged Parakeet	2,568	58	5,000	II
Brotogeris pyrrhoptera	Grey-cheeked Parakeet	216	4		II
Brotogeris sanctithomae	Tui Parakeet	1,349	51	4,350	II
Brotogeris sp.	Parrot	11	1,403		
Brotogeris versicolurus	White-winged Parakeet	12,093	5,012	5,000	II
Bubo sp.	Owl		2		
Bubo virginianus	Great Horned Owl	3	5		II
Burhinus superciliaris	Peruvian Thick-knee	1		100	

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
Busarellus nigricollis	Black-collared Hawk	7			II
Buteo sp.	Hawk	1			
Buteogallus meridionalis	Savanna Hawk	7			II
Buteogallus solitarius	Black Solitary Eagle		1		II
Butorides striata	Striated Heron	31			
Cacicus cela	Yellow-rumped Cacique			500	
Capito auratus	Gilded Barbet			60	
Capito aurovirens	Scarlet-crowned Barbet	7			
Caprimulgidae	Nightjar	2			
Caracara plancus	Southern Caracara		1		II
Carduelis atrata	Black Siskin			15,000	
Carduelis magellanica	Hooded Siskin			15,300	
Carduelis sp.	Siskin	283	7		
Carduelis uropygialis	Yellow-rumped Siskin			150	
Catamenia analis	Band-tailed Seedeater	3		900	
Cathartes aura	Turkey Vulture			600	
Celeus sp.	Woodpecker	8			
Cephalopterus ornatus	Amazonian Umbrellabird	1			
Chloroceryle amazona	Amazon Kingfisher	1			
Chloroceryle sp.	Kingfisher	18			
Chlorophanes spiza	Green Honeycreeper			300	
Chlorophonia cyanea	Blue-naped Chlorophonia			1,200	
Chrysomus icterocephalus	Yellow-hooded Blackbird	4		1,200	
Ciccaba virgata	Mottled Owl		1		II
Cissopis leverianus	Magpie Tanager			300	

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
Claravis pretiosa	Blue Ground-dove	16		2,700	
Cochlearius cochlearius	Boat-billed Heron	3			
Coereba flaveola	Bananaquit			1,200	
Colonia colonus	Long-tailed Tyrant			60	
Columbidae	Dove	18			
Columbina cruziana	Croaking Ground-dove	311		8,500	
Columbina minuta	Plain-breasted Ground-dove			900	
Columbina talpacoti	Ruddy Ground-dove	5		2,000	
Coragyps atratus	Black Vulture	1	2	1,400	II
Coryphospingus cucullatus	Red-crested Finch	10		300	
Crotophaga major	Greater Ani	18		120	
Crypturellus undulatus	Undulated Tinamou	36	8		
Cyanerpes caeruleus	Purple Honeycreeper			1,200	
Cyanocorax mystacalis	White-tailed Jay	71		2,400	
Cyanocorax sp.	Jay	4			
Cyanocorax violaceus	Violaceous Jay	5			
Cyanocorax yncas	Green Jay	6		3,000	
Dacnis flaviventer	Yellow-bellied Dacnis			120	
Dacnis lineata	Black-faced Dacnis			150	
Dives warszewiczi	Scrub Blackbird	2,041			
Erythrura gouldiae[c]	Gouldian Finch	157			
Euphonia chlorotica	Purple-throated Euphonia			800	
Euphonia minuta	White-vented Euphonia			1,200	
Euphonia saturata	Orange-crowned Euphonia	1			
Euphonia sp.	Euphonia	8			

Table B1. Continued

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
Euphonia xanthogaster	Orange-bellied Euphonia			1,200	
Eurypyga helias	Sunbittern	38			
Falco femoralis	Aplomado Falcon		9		II
Falco peregrinus	Peregrine Falcon	3	15		I
Falco sp.	Falcon		6		
Falco sparverius	American Kestrel	43	15		II
Falconidae	Falcon		8		
Forpus coelestis	Pacific Parrotlet	3,504	70	600	II
Forpus sp.	Parrotlet	29	110		
Forpus xanthops[e]	Yellow-faced Parrotlet	24	22		II
Forpus xanthopterygius	Blue-winged Parrotlet	46			II
Gampsonyx swainsonii	Pearl Kite	1			II
Geothlypis aequinoctialis	Masked Yellowthroat			60	
Geranoaetus melanoleucus	Black-crested Buzzard-Eagle	3	13		II
Geranoaetus polyosoma	Variable Hawk	11	10		II
Geranoaetus sp.	Hawk		2		
Glaucidium brasilianum	Ferruginous Pygmy-owl	1			II
Glaucidium sp.	Pygmy Owl	7			
Graydidascalus brachyurus	Short-tailed Parrot	279	1		II
Harpagus bidentatus	Double-toothed Kite		4		II
Harpia harpyja	Harpy Eagle		1		II
Herpsilochmus sp.	Antwren	3			
Hylatomus lineatus	Lineated Woodpecker	2			
Icterus croconotus	Orange-backed Troupial			300	
Icterus graceannae	White-edged Oriole	180		1,500	

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
Icterus mesomelas	Yellow-tailed Oriole			750	
Jacana jacana	Wattled Jacana	40			
Knipolegus aterrimus	White-winged Black-tyrant			60	
Leptotila pallida	Pallid Dove	3			
Leptotila sp.	Dove	33			
Leptotila verreauxi	White-tipped Dove	2		1,000	
Lonchura striata[c]	White-rumped Munia	747			
Megaceryle torquata	Ringed Kingfisher	47			
Megascops choliba	Tropical Screech-owl	3			II
Megascops watsonii	Tawny-bellied Screech-owl	1			II
Melanerpes cruentatus	Yellow-tufted Woodpecker			100	
Melopsittacus undulatus[c]	Budgerigar	43,521			
Mesembrinibis cayennensis	Green Ibis	4			
Metriopelia ceciliae	Bare-faced Ground-dove	4		3,000	
Metriopelia melanoptera	Black-winged Ground-dove			1,500	
Milvago chimachima	Yellow-headed Caracara	2			II
Mimus longicaudatus	Long-tailed Mockingbird	195		1,200	
Mitu tuberosum	Razor-billed Curassow	21			
Molothrus bonariensis	Shiny Cowbird	65			
Momotus momota	Amazonian Motmot			300	
Myiopsitta monachus[d]	Monk Parakeet	2			II
Myiozetetes similis	Social Flycatcher			280	
Neopsephotus bourkii[c]	Bourke's Parrot	2			II
Nothocrax urumutum	Nocturnal Curassow	1			
Nothoprocta ornata	Ornate Tinamou			800	

Table B1. Continued

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
Nothoprocta sp.	Tinamou	8			
Nyctibius grandis	Great Potoo		1		
Nyctibius griseus	Common Potoo	1			
Nyctibius sp.	Potoo	1			
Nycticorax nycticorax	Black-crowned Night-heron		4		
Nyctidromus albicollis	Pauraque	1			
Nymphicus hollandicus[c]	Cockatiel	2,172			
Opisthocomus hoazin	Hoatzin	4		50	
Ortalis guttata	Speckled Chachalaca	81	1		
Orthopsittaca manilatus	Red-bellied Macaw	40			II
Oryzoborus angolensis	Lesser Seed Finch			400	
Padda oryzivora[c]	Java Sparrow	212			II
Pandion haliaetus	Osprey		1		II
Parabuteo unicinctus	Harris's Hawk	8	25		II
Paroaria coronata[d]	Red-crested Cardinal	279			II
Paroaria gularis	Red-capped Cardinal	28		1,500	
Passer domesticus[d]	House Sparrow	17			
Passeridae	Songbird	69			
Patagioenas albilinea	Southern Band-tailed Pigeon	7		1,000	
Patagioenas cayennensis	Pale-vented Pigeon	11			
Patagioenas oenops	Peruvian Pigeon	4			
Pelecanus sp.	Pelican		1		
Penelope jacquacu	Spix's Guan	70			
Penelope sp.	Guan		1		
Phalacrocorax	Guanay Cormorant		2		

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Table B1. Continued

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
bougainvilliorum					
Phalacrocorax brasilianus	Neotropical Cormorant	6	2		
Phalcoboenus megalopterus	Mountain caracara		5		II
Phalcoboenus sp.	Caracara		1		
Pheucticus aureoventris	Black-backed Grosbeak			3,000	
Pheucticus chrysogaster	Golden-bellied Grosbeak	155		6,000	
Pheucticus sp.	Grosbeak	4			
Phoenicopterus chilensis	Chilean Flamingo		1		II
Phrygilus fruticeti	Mourning Sierra-finch			800	
Picidae	Woodpecker	15			
Piezorhina cinerea[e]	Cinereous Finch	64		600	
Pionites melanocephalus	Black-headed Parrot	74	1		II
Pionites sp.	Parrot	33	6		
Pionites xanthomerius	Black-legged Parrot	17	7		II
Pionus chalcopterus	Bronze-winged Parrot	89	5		II
Pionus menstruus	Blue-headed Parrot	232	34		II
Pionus sordidus	Red-billed Parrot	3			II
Pionus sp.	Parrot		2		
Pionus tumultuosus	Plum-crowned Parrot	1			II
Pipile sp.	Piping-guan		2		
Pipra erythrocephala	Golden-headed Manakin			60	
Pitangus sulphuratus	Great Kiskadee	9			
Plegadis ridgwayi	Puna Ibis			100	
Poephila acuticauda[c]	Long-tailed Finch	1			
Poephila personata[c]	Masked Finch	4			

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Table B1. Continued

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
Poospiza hispaniolensis	Collard Warbling-finch	183		5,550	
Porphyrio martinicus	Purple Gallinule	2			
Psarocolius angustifrons	Russet-backed Oropendola			800	
Psarocolius decumanus	Crested Oropendola			120	
Pseudastur occidentalis	Grey-backed Hawk	2			II
Psilopsiagon aurifrons	Mountain Parakeet	202			II
Psittacara erythrogenys	Red-masked Parakeet	1,072	73		II
Psittacara frontatus	Cordilleran Parakeet	493	50	6,050	II
Psittacara leucophthalmus	White-eyed Parakeet	775	146		II
Psittacara mitratus	Mitred Parakeet	126	7	5,000	II
Psittacara sp.	Parakeet	35	95		
Psittacidae	Parrot	117	106		
Psophia crepitans	Grey-winged Trumpeter	16	2		
Pteroglossus azara	Ivory-billed Aracari			50	
Pteroglossus castanotis	Chestnut-eared Aracari	25	1	60	
Pteroglossus inscriptus	Lettered Aracari	4			
Pteroglossus sp.	Aracari	48			
Pulsatrix perspicillata	Spectacled Owl	1			II
Pyrilia barrabandi	Orange-cheeked Parrot	19			II
Pyrrhura roseifrons	Rose-fronted Parakeet	4			II
Pyrrhura sp.	Parakeet	15			
Rallidae	Rail	1			
Ramphastos ambiguus	Yellow-throated Toucan		1		
Ramphastos culminatus	Yellow-ridged Toucan	1			II
Ramphastos cuvieri	Cuvier's Toucan	12	3		II

Table B1. Continued

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
Ramphastos sp.	Toucan	24	1		
Ramphastos toco	Toco Toucan		1		II
Ramphocelus carbo	Silver-beaked Tanager	95		1,500	
Ramphocelus nigrogularis	Masked Crimson Tanager			160	
Rhodospingus cruentus	Crimson-breasted Finch			150	
Rostrhamus sociabilis	Snail Kite	3			II
Rupicola peruvianus	Andean Cock-of-the-Rock		1		II
Rupornis magnirostris	Roadside Hawk	5	1		II
Saltator aurantiirostris	Golden-billed Saltator	8		300	
Serinus canaria[c]	Island Canary	2,080			
Sicalis flaveola	Saffron Finch	1,741	441	11,000	
Sicalis luteola	Grassland Yellow-finch			7,500	
Sicalis sp.	Finch	6			
Spheniscus humboldti	Humboldt Penguin		9		I
Spizaetus sp.	Hawk-eagle	3			
Sporophila castaneiventris	Chestnut-bellied Seedeater			11,000	
Sporophila corvina	Variable Seedeater			450	
Sporophila lineola	Lined Seedeater			600	
Sporophila luctuosa	Black-and-white Seedeater	569		10,500	
Sporophila peruviana	Parrot-billed Seedeater	13		8,000	
Sporophila sp.	Seedeater	5			
Sporophila telasco	Chestnut-throated Seedeater			7,000	
Strigidae	Owl	38	8		
Sturnella bellicosa	Peruvian Meadowlark	306		1,200	
Sula variegata	Peruvian Booby		1		

Table B1. Continued

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
Tachuris rubrigastra	Many-coloured Rush-tyrant			300	
Taeniopygia guttata[c]	Zebra Finch	1,596			
Tangara arthus	Golden Tanager			1,400	
Tangara chilensis	Paradise Tanager	1		1,500	
Tangara chrysotis	Golden-eared Tanager			800	
Tangara cyanicollis	Blue-necked Tanager	8		1,500	
Tangara gyrola	Bay-headed Tanager	1		2,400	
Tangara mexicana	Turquoise Tanager			2,000	
Tangara nigrocincta	Masked Tanager			1,000	
Tangara nigroviridis	Beryl-spangled Tanager	1		2,100	
Tangara parzudakii	Flame-faced Tanager			1,800	
Tangara schrankii	Green-and-gold Tanager			1,800	
Tangara sp.	Tanager	27			
Tangara velia	Opal-rumped Tanager			240	
Tangara xanthocephala	Saffron-crowned Tanager			1,800	
Tersina viridis	Swallow Tanager			800	
Thraupis bonariensis	Blue-and-yellow Tanager	1		7,500	
Thraupis episcopus	Blue-grey Tanager	343		7,850	
Thraupis palmarum	Palm Tanager			800	
Thryothorus superciliaris	Superciliated Wren	3			
Tigrisoma lineatum	Rufescent Tiger-heron	11			
Tinamidae	Tinamou	25			
Trochilidae	Hummingbird	8			
Trogon melanurus	Black-tailed Trogon			30	
Trogon personatus	Masked Trogon			45	

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Table B1. Continued

Scientific name[a]	English name	Market counts	Seizure counts	Export quotas[b]	CITES Appendix
Turdus fuscater	Great Thrush			300	
Turdus serranus	Glossy-black Thrush			180	
Turdus sp.	Thrush	7			
Tyto alba	Barn Owl	11	3		II
Volatinia jacarina	Blue-black Grassquit	9		15,000	
Vultur gryphus	Andean Condor		9		I
Zenaida auriculata	Eared Dove	74		2,000	
Zenaida meloda	West Peruvian Dove	413			
Zenaida sp.	Dove	9			
Zonotrichia capensis	Rufous-collared sparrow	218		3,000	
Total		**92,761**	**21,745**	**241,005**	

[a] Includes recent taxonomic changes according to: del Hoyo, J.; Collar, N. J.; Christie, D. A.; Elliott, A.; Fishpool, L. D. C. 2014. HBW and BirdLife International Illustrated Checklist of the Birds of the World. Barcelona, Spain and Cambridge UK: Lynx Edicions and BirdLife International

[b] No export quotas were published for 2010

[c] Captive-bred ornamental species

[d] Regional or exotic species

[e] Endemic species

APPENDIX C

DERIVATION OF R_0

Derivation of the basic reproduction number (R_0) using the next-generation matrix method.

The expressions for the basic reproduction number (R_0) were derived using the next-generation matrix method (van den Driessche & Watmough 2002). To construct the next-generation matrix, (FV^{-1}), I defined the matrices F and V as:

$$F = \left[\frac{\partial F_i(x)}{\partial x_j}\right] x = x_0 \text{ and } V = \left[\frac{\partial V_i(x)}{\partial x_j}\right] x = x_0,$$

where the (i, j) entry of matrix F was the rate at which infected individuals in compartment j produce new infections in compartment i and the (i, j) entry of V was the net rate of change of animals in the compartment by any other means. I considered that E, I_A and I_C were the infected states but that new infections occurred only in the E compartment. The rates were evaluated at the disease-free equilibrium (DFE) $x = x_0$.

Setting $\vec{I} = (E, I_A, I_C)^T$ for model 1, it follows that

$$\frac{d\vec{I}}{dt} = J\vec{I} = (F - V)\vec{I},$$

where J denotes the Jacobian matrix evaluated at the DFE and F and V matrices are:

$$F = \begin{bmatrix} 0 & \beta_A S0 & \beta_C S0 \\ 0 & 0 & 0 \\ 0 & 0 & 0 \end{bmatrix}$$

$$V = \begin{bmatrix} d + h + \alpha & 0 & 0 \\ -\alpha p_1 & d + h + \mu_A + \delta & 0 \\ -\alpha(1 - p_1) & -\delta(1 - p_2) & d + h + \mu_C + \gamma \end{bmatrix}$$

Following (Diekmann et al. 1990; van den Driessche & Watmough 2002), the basic reproduction number R_0 is defined as the spectral radius (dominant eigenvalue) of matrix FV^{-1}. That is,

$$R_0 = \rho(FV^{-1}) = R_{0A} + R_{0C}, \tag{C1}$$

where

$$R_{0A} = \frac{\alpha p_1 \beta_A S0}{(d + h + \alpha)(d + h + \mu_A + \delta)}$$

$$R_{0C} = \left[\frac{\alpha(1 - p_1)}{(d + h + \alpha)} + \frac{\alpha p_1(1 - p_2)}{(d + h + \alpha)(d + h + \mu_A + \delta)}\right] \frac{\beta_C S0}{(d + h + \mu_C + \gamma)}$$

The expression for R_{0A} can be interpreted as follows: a fraction $\alpha p_1/(d + h + \alpha)$ of exposed hosts E progress to state I_A and spend an average of $1/(d + h + \mu_A + \delta)$ days in state I_A over the expected duration of infection. Multiplying by $\beta_A S0$ gives the expected number of secondary infections resulting from interactions between susceptible and acutely infected hosts.

Similarly, the expression for R_{0C} can be interpreted as follows: a fraction $\alpha p_1/(d + h + \alpha)$ of exposed hosts E progress to state I_A, and of these acutely infected hosts, a fraction $\delta(1 - p_2)/(d + h + \mu_A + \delta)$ progress to state I_C spending an average of $1/(d + h + \mu_C + \gamma)$ days in state I_C over the expected duration of infection. Alternatively, a fraction $\alpha(1 - p_1)/(d + h + \alpha)$ of exposed hosts progress directly to state I_C and spend an average of $1/(d + h + \mu_C + \gamma)$ days in state I_C. Multiplying by $\beta_C S0$ gives the expected number of secondary infections resulting from interactions between susceptible and chronically infected hosts.

For model 2, setting $\vec{I} = (E_j, I_{Aj}, I_{Cj}, E_a, I_{Aa}, I_{Ca})^T$, it follows that

$$\frac{d\vec{I}}{dt} = J\vec{I} = (F - V)\vec{I},$$

where J denotes the Jacobian matrix evaluated at the DFE. I assumed that new infections only occur when a susceptible bird (S_j or S_a) becomes exposed (E_j or E_a) after direct contact with an infectious juvenile or adults. Thus, F and V matrices are:

$$F = \begin{bmatrix} 0 & \beta_{Aj}S_{j0} & \beta_C S_{j0} & 0 & \beta_{Aa}S_{j0} & \beta_C S_{j0} \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \beta_{Aj}S_{a0} & \beta_C S_{a0} & 0 & \beta_{Aa}S_{a0} & \beta_C S_{a0} \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix},$$

$$V = \begin{bmatrix} c_1 & 0 & 0 & 0 & 0 & 0 \\ -\alpha p_1 & c_2 & 0 & 0 & 0 & 0 \\ -\alpha(1-p_1) & -\delta(1-p_1) & c_3 & 0 & 0 & 0 \\ -\Omega & 0 & 0 & c_4 & 0 & 0 \\ 0 & -\Omega & 0 & -\alpha p_1 & c_5 & 0 \\ 0 & 0 & -\Omega & -\delta(1-p_1) & -\delta(1-p_2) & c_6 \end{bmatrix},$$

where
$$c_1 = d_j + h_j + \Omega + \alpha,$$
$$c_2 = d_j + h_j + \Omega + \mu_{Aj} + \delta,$$
$$c_3 = d_j + h_j + \Omega + \mu_{Cj} + \gamma,$$
$$c_4 = d_a + h_a + \alpha,$$
$$c_5 = d_a + h_a + \mu_{Aa} + \delta,$$
$$c_6 = d_a + h_a + \mu_{Ca} + \gamma.$$

Thus, R_0 is defined as:

$$R_0 = \rho(FV^{-1}) = \tfrac{1}{2}\left[R_{01} + R_{02} + \sqrt{(R_{01} - R_{02})^2 + 4R_{03}R_{04}}\right], \qquad (C2)$$

where

$$R_{01} = \frac{\alpha p_1 \beta_{Aj} S_{j0}}{c_1 c_2} + \frac{\alpha(1-p_1)\beta_C S_{j0}}{c_1 c_3} + \frac{\alpha p_1 \delta(1-p_2)\beta_C S_{j0}}{c_1 c_2 c_3} + \frac{\Omega \alpha p_1 \beta_{Aa} S_{j0}}{c_1 c_4 c_5} + \frac{\Omega \alpha p_1 \beta_{Aa} S_{j0}}{c_1 c_2 c_5} +$$
$$\frac{\Omega \alpha (1-p_1)\beta_C S_{j0}}{c_1 c_4 c_6} + \frac{\Omega \alpha (1-p_1)\beta_C S_{j0}}{c_1 c_3 c_6} + \frac{\Omega \alpha p_1 \delta(1-p_2)\beta_C S_{j0}}{c_1 c_4 c_5 c_6} + \frac{\Omega \alpha p_1 \delta(1-p_2)\beta_C S_{j0}}{c_1 c_2 c_5 c_6} +$$
$$\frac{\Omega \alpha p_1 \delta(1-p_2)\beta_C S_{j0}}{c_1 c_2 c_3 c_6},$$
$$R_{02} = \frac{\alpha p_1 \beta_{Aj} S_{a0}}{c_1 c_2} + \frac{\alpha(1-p_1)\beta_C S_{a0}}{c_1 c_3} + \frac{\alpha p_1 \delta(1-p_2)\beta_C S_{a0}}{c_1 c_2 c_3} + \frac{\Omega \alpha p_1 \beta_{Aa} S_{a0}}{c_1 c_4 c_5} + \frac{\Omega \alpha p_1 \beta_{Aa} S_{a0}}{c_1 c_2 c_5} +$$
$$\frac{\Omega \alpha (1-p_1)\beta_C S_{a0}}{c_1 c_4 c_6} + \frac{\Omega \alpha (1-p_1)\beta_C S_{a0}}{c_1 c_3 c_6} + \frac{\Omega \alpha p_1 \delta(1-p_2)\beta_C S_{a0}}{c_1 c_4 c_5 c_6} + \frac{\Omega \alpha p_1 \delta(1-p_2)\beta_C S_{a0}}{c_1 c_2 c_5 c_6} +$$
$$\frac{\Omega \alpha p_1 \delta(1-p_2)\beta_C S_{a0}}{c_1 c_2 c_3 c_6},$$
$$R_{03} = \frac{\alpha p_1 \beta_{Aa} S_{j0}}{c_4 c_5} + \frac{\alpha(1-p_1)\beta_C S_{j0}}{c_4 c_6} + \frac{\alpha p_1 \delta(1-p_2)\beta_C S_{j0}}{c_4 c_5 c_6},$$
$$R_{04} = \frac{\alpha p_1 \beta_{Aa} S_{a0}}{c_4 c_5} + \frac{\alpha(1-p_1)\beta_C S_{a0}}{c_4 c_6} + \frac{\alpha p_1 \delta(1-p_2)\beta_C S_{a0}}{c_4 c_5 c_6}.$$

The terms R_{01} and R_{02} represent the average number of secondary juvenile or adult infections, respectively, produced by one exposed juvenile E_j during its entire infection period. The terms R_{03} and R_{04} represent the average number of secondary juvenile or

adult infections produced by one exposed adult E_a during its entire infection period, respectively.
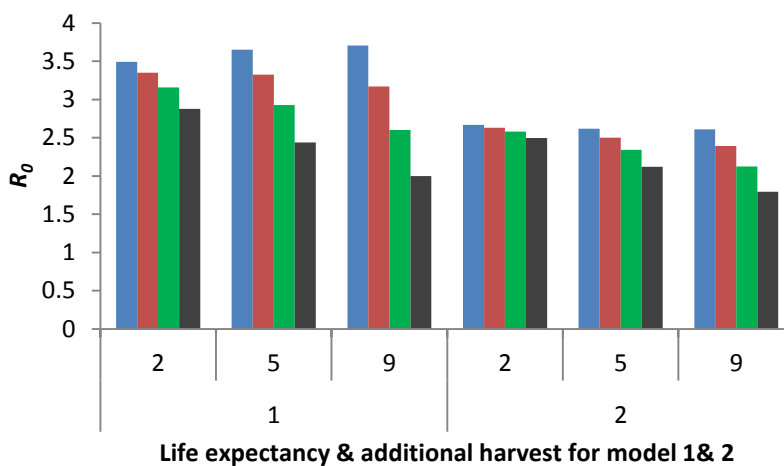
APPENDIX D

LIFE EXPECTANCY SCENARIOS

Figure D1. Mean basic reproductive number (R_0) estimates from 10,000 simulations of Newcastle disease transmissions for homogenous (model 1) and age-structure (model 2) populations of white-winged parakeets with no additional harvest ($h1$=0 blue), and three additional uncompensated harvest rates. ($h1$=2% red, $h1$=5% green, and $h1$=10% black) and for three life expectancies (D_d = two, five, and nine years).

Figure D2. Population size at two years post Newcastle disease introduction for homogeneous (model 1) and age-structure (model 2) populations of white-winged parakeets with no additional harvest ($h1$=0 blue), and three additional uncompensated harvest rates. ($h1$=2% red, $h1$=5% green, and $h1$=10% black) and for three life expectancies (D_d = two, five, and nine years).

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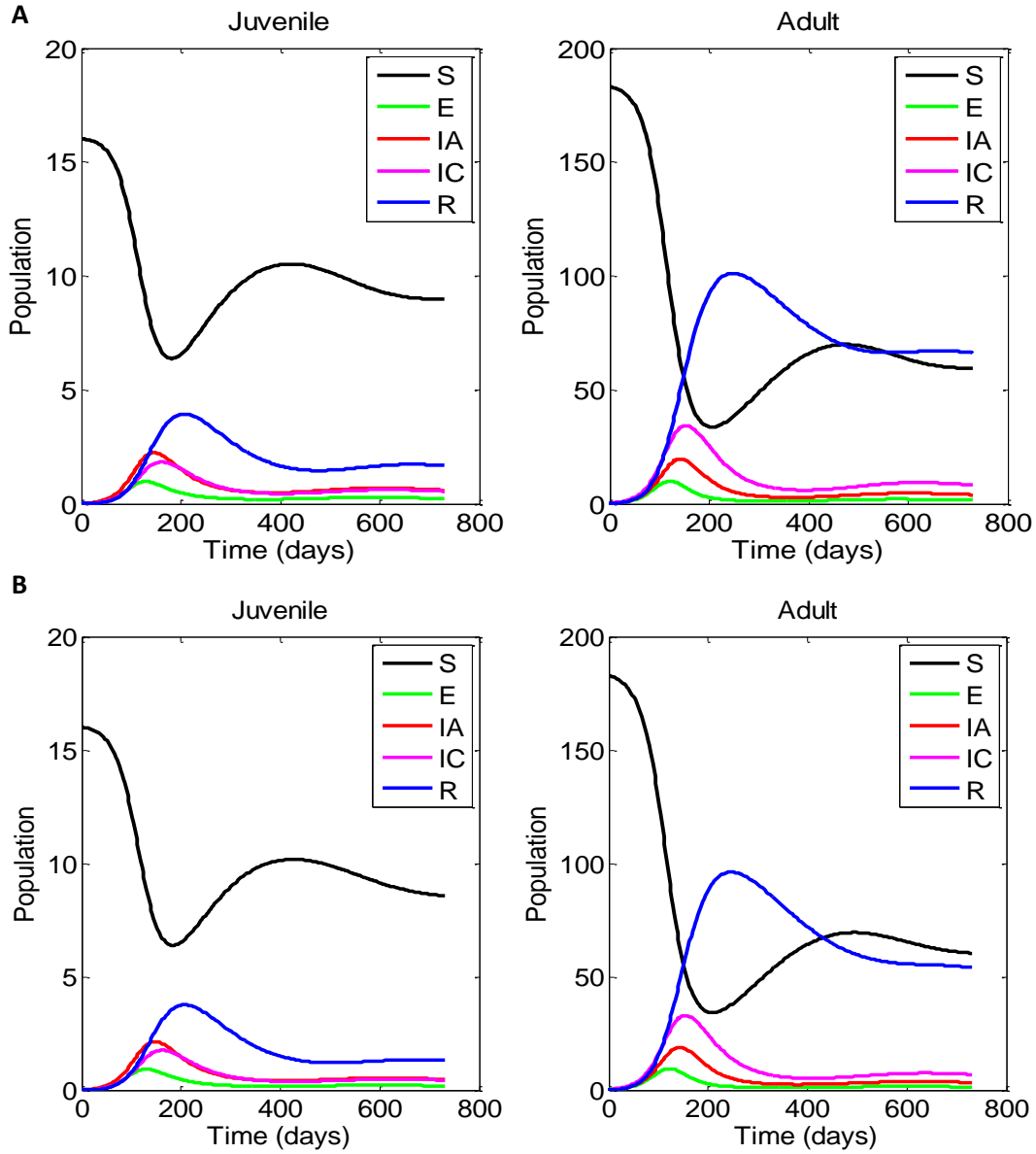## JUVENILE AND ADULT TRAJECTORIES

Figure E1. Deterministic two-year time trajectories for Newcastle disease transmission for juvenile and adult white-winged parakeets (model 2). Panel (A) shows results with no additional harvest ($hl = 0$) and (B) 10% additional (uncompensated) harvest ($hl = 10\%$). Depicted are susceptible (S), exposed (E), acutely-infected (IA), chronically-infected (IC) and recovered (R) classes for juveniles and adults.