Conservation practices induce dialect formation in the endangered Puerto Rican amazon
(***Amazona vittata***)

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Thesis submitted in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE
In
BIOLOGY
UNIVERSITY OF PUERTO RICO
MAYAGUEZ CAMPUS
2016

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ABSTRACT

Captive breeding is a conservation strategy that often results in behavioral changes in animals born and reared in captivity. Culturally transmitted behaviors, such as learned vocal signals, are particularly prone to change because captive animals have limited opportunities to learn behaviors from wild animals. Changes in learned behavior could affect the success of reintroduction programs once captive animals are released into the wild. I tested for the presence of vocal divergence of learned calls in the repertoires of geographically separated populations of Puerto Rican amazons (*Amazona vittata*). I recorded parrots from two captive and two wild populations, representing all existing populations of this species. I also recorded parrots that had been translocated between populations and evaluated their vocal changes over time. Luscinia software was used to compare calls from different populations using a dynamic time warping algorithm. Discriminant function analyses was used to test for the presence of differences between populations. I found evidence of acoustic differences in all four populations and considered these differences to be discrete enough to be classified as separate dialects. Captive parrots that had regular vocal interaction with wild parrots produced calls that were similar to those produced by wild parrots. Parrots that had been translocated between populations were able to adopt the dialect of the foreign population. The emergence of dialects in this species likely resulted from a combination of historical rearing practices, cultural drift, and geographic separation. Managers of this species should consider employing strategies that will facilitate parrots' abilities to acquire foreign vocal signals prior to release.

RESUMEN

La propagación en cautiverio es una estrategia de conservación que muchas veces resulta en cambios en el comportamiento de aquellos animales nacidos y criados en cautiverio. Comportamientos que son transmitidos culturalmente, como las señales acústicas aprendidas, son particularmente susceptibles a cambiar ya que los animales cautivos tienen pocas oportunidades de interactuar con animales silvestres. Cambios en comportamientos aprendidos pueden afectar el éxito de los programas de reintroducción cuando intentan liberar animales que han sido criados en cautiverio. En este estudio se investigaron los cambios acústicos en las vocalizaciones aprendidas de la cotorra puertorriqueña (*Amazona vittata*). Obtuve grabaciones de dos poblaciones cautivas y dos poblaciones silvestres de esta especie. También grabé cotorras que habían sido trasladadas entre poblaciones para poder medir sus cambios acústicos con el paso del tiempo. Utilicé el programa Luscinia para comparar vocalizaciones a través del algoritmo "dynamic time warping". Luego llevé a cabo un análisis discriminante lineal para determinar si existían diferencias entre las poblaciones. Encontré evidencia de diferencias acústicas en las cuatro poblaciones que son suficientemente discretas como para que cada población se considere un dialecto distinto. La población de cotorras cautivas que tenía más contacto vocal con cotorras silvestres producía vocalizaciones que eran más parecidas a la de la población silvestre. Las cotorras que fueron trasladadas entre poblaciones adoptaron el dialecto de la población extranjera. El desarrollo de dialectos en esta especie probablemente se debe a prácticas de avicultura históricas, deriva cultural y separación geográfica poblacional. Se recomienda que los manejadores empleen estrategias que faciliten la habilidad de las cotorras cautivas de aprender vocalizaciones extranjeras antes de ser liberadas.

DEDICATION

To the conservation dream team, the heroes of the Puerto Rican Parrot Recovery Program. Those

who wake up every day to make the world a greener and more boisterous place.

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INTRODUCTION

Captive breeding is a widely used tool in the conservation of threatened and endangered species. Despite its widespread use, the method has many notable limitations particularly when it comes to preserving behaviors essential for survival in the wild (Snyder *et al.* 1996). Behavioral changes in captive reared animals have often hindered the success of releases into the wild (Meretsky *et al.* 2000, Stoinksi et al 2003). Captive environments are drastically different from wild environments and animals in captivity usually lack opportunities to interact with their wild counterparts. For this reason, behavioral traits that are acquired through conspecific learning may be more prone to loss in captivity than traits that are acquired without conspecific learning. For instance, the reintroduction of captive reared whooping cranes (*Grus americana*) required the use of human piloted aircrafts to teach the birds how to migrate, a behavior that is normally acquired through social learning (Mueller *et al*. 2013). Managers of captive populations should be aware of cultural aspects of an animal's behavioral repertoire that could be subject to change and how management actions can directly influence this change.

The continued survival of the Puerto Rican amazon (*Amazona vittatta*) depends on captive breeding. This critically endangered species is endemic to the island of Puerto Rico. At present, the total population numbers less than 500 individuals. Since the 1970's, the species has been the focus of an intensive conservation effort known as the Puerto Rican Parrot Recovery Program. Management efforts have included captive breeding and releases of captive-bred individuals into the wild. Currently, population managers maintain four distinct populations of this species, two in captivity and two in the wild. The first is a relict population of wild parrots in the El Yunque National Forest (hereafter El Yunque). In 1973, managers began capturing individuals from that population to found a captive-breeding facility within El Yunque. Twenty years later, a subset of captive parrots was transferred to a second captive-breeding facility located 100 km away in the Rio Abajo State Forest (hereafter Rio Abajo). In 2006, parrots were released from the Rio Abajo breeding facility into the surrounding forest creating a second population of wild parrots. Except for a small number of dispersal events, mostly in the vicinity of

Rio Abajo, these four populations represent the global distribution of the Puerto Rican amazon (DNER 2015).

The separation of the Puerto Rican amazon into four populations may have unwittingly stimulated the emergence of vocal dialects. Dialects, or geographic variations in learned acoustic signals, are a natural phenomenon that has been well documented in wild parrot populations (Wright 1996). Dialects can emerge in several ways including cultural drift and founder-bottleneck processes (Lemon 1975, Rothstein and Fleischer 1987). Anecdotal reports from conservation practitioners suggest that wild Puerto Rican amazons within the relict El Yunque population produce different vocalizations than parrots in the other populations (White *et al.* 2014). Confirmation of these reports would suggest that one or more dialects has emerged during the 40-years of Puerto Rican parrot conservation efforts.

The presence of vocal dialects in Puerto Rican amazons is cause for concern because acoustic signals are an integral aspect of parrot biology. Parrots use these signals to initiate and coordinate social activities including mating, foraging, and communicating with offspring (Buhrman-Deever *et al.* 2008, Berg *et al.* 2011a, Berg *et al.* 2011b, Bradburry and Balsby 2016). Due to its central nature in parrot social dynamics, vocal communication may influence the survival and reproduction of Puerto Rican parrots in the wild. The presence of dialects could hinder social interaction between individuals from different dialects. For instance, congeneric Yellow-naped amazons (*Amazona auropalliata*) experimentally translocated between dialect regions exhibit limited social interaction with birds from foreign dialects (Salinas-Melgoza and Wright 2012). Nesting pairs of the same species also show a stronger positive response towards playback of calls from the same dialect region compared to playback of a different dialect region (Wright and Dorin 2001).

The considerable distance that separates the two existing wild Puerto Rican parrot populations makes it improbable that parrots would naturally disperse between Rio Abajo and El Yunque. However, members of the different sub-populations do come into contact as a result of population management techniques. Birds are regularly exchanged between the two aviary facilities and are also released into the wild as part of the conservation efforts. Management agencies are also planning to create a third wild

population by reintroducing parrots into the Maricao State Forest by the end of 2016 (DNER 2015). The presence of dialects in different populations could affect the ability of parrots to communicate and integrate socially when they are transferred between dialect regions. Difficulties in social integration could affect the ability of captive-raised and released birds to survive and reproduce once they are released into wild populations.

The overall objective of this project is to determine if different populations of Puerto Rican amazons can be distinguished by their acoustic features. Based on the hypothesis that Puerto Rican amazons emit distinct vocal dialects in one or more of the captive and wild populations, I predicted that calls from different populations could be distinguished by their acoustic features. Lack of regular vocal interaction between the captive and wild population in El Yunque may have resulted in differences in call structure between the relict wild population and its captive descendants. Conversely, regular vocal interaction between the captive and wild populations of Rio Abajo may have maintained similar call structure in these two populations. The hypothesis was tested by recording calls from all four populations, and comparing their acoustic structures. I also recorded birds that had been reared in one population and translocated to another population. If dialects exist between populations, then translocated parrots may adopt the dialect of a foreign population. Alternatively, translocated parrots may be unable to adopt a new dialect once they have learned the dialect of their original population.

The present study is the first to examine dialect creation as a consequence of captive breeding. It is also the first study to examine dialect creation within a known and relatively short time span. Furthermore, while this species has been extensively studied over the past 40 years, the majority of the studies have focused on aspects of the parrot's demography and ecology. Only a handful of studies have attempted to study Puerto Rican amazon behavior with the aim of applying behavioral knowledge to management techniques. This study is part of a program of research aimed at providing critical behavioral information to management agencies as they work towards the conservation of this iconic species.

LITERATURE REVIEW

Vocal dialects in birds

Dialects were first described in white-crowned sparrows, (*Zonotrichia leucophrys nutallin*) by Marler and Tamura (1962). In this classic study, sparrows from one population sung trills with specific structures that differed from those sung by sparrows in nearby populations. Subsequent studies suggested that both the cultural transmission of songs across generations through vocal imitation (Marler and Tamura 1964), and the limited dispersal of individuals across dialect boundaries (Baker and Mewaldt 1978) contribute to the evolution of dialects in this species. The existence of dialects has been documented in songbirds (Passerines), hummingbirds (Trochilidae), and parrots (Psittaciformes). The abundance of bird species that exhibit geographic variation in their vocal signals is due largely to the fact that many bird species learn vocalizations through imitation, a phenomenon that enables novelties to be generated and transmitted to future generations (Slater 1989).

Origin and biological significance of dialects

There are several hypotheses of avian dialect formation and maintenance. The epiphenomenon hypothesis, states that dialects are non-adaptive by-products of learning and dispersal patterns (Andrew 1962). If birds learn songs by copying conspecifics, and the accuracy of copying varies, then vocal structure may change over space and time resulting in the emergence of regional dialects (Slater 1986).

The local adaptation hypothesis, states that females benefit from mating with males from their natal region rather than males from other regions because this provides offspring with genes that are more adapted to local ecological conditions (Nottebohm 1969). If local male's genomes are adapted to the local environment, then local song structure can serve as an honest signal of mate quality. Selection should favor the divergence of dialects as females select males that produce vocalizations typical of their natal region.

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Another group of hypotheses, termed social adaptation hypotheses, suggest that males gain social benefits by producing vocalizations that are similar to other males in the region, while males that produce differing vocalizations will be subject to social penalties (Payne 1981). Birds benefit from learning and imitating the dialect of the local region to access mates or be allowed entrance into the local group.

Although multiple studies have found evidence for each of these hypotheses, dialect systems exhibit tremendous variety and occur in a range of scales, social systems, and ecological conditions (Podos and Warren 2007). No single hypothesis can account for all the examples of dialect systems.

Changes in cultural traits

Cultural learning is a phenomenon of interest to researchers in the field of conservation and to managers in captive breeding programs. Behaviors that are shared by members of a population and acquired from conspecifics through social learning are considered "cultural traits" (Whitehead et al 2004). Changes in these traits can affect the fitness of segmented subpopulations (Luck *et al.* 2003). The Thick-billed Parrot Program provides an example of how cultural traits can affect the success of captive breeding and reintroduction programs. This short-lived conservation program attempted to reintroduce thick-billed parrots *(Rhynchopsitta pachyrhyncha)* into the wild in southern Arizona. During numerous releases conducted over seven years, captive-reared thick-billed parrots suffered increased mortality when compared to wild-caught thick-billed parrots that were released at the same time (Snyder 1994). The mortality of captive-reared birds was attributed to lack of basic social skills and cultural knowledge such as the location of foraging areas.

Vocal signals in parrots

Parrots, like many social animals, use vocal signals to initiate and coordinate group activities. Among the most important of these is the coordination of activities related to reproduction, including recognizing mates or offspring and defending nesting territories. Green-rumped parrotlets (*Forpus passerinus*) can discriminate between the contact calls of their mates and other conspecifics (Berg *et al.*

2011b). Nesting females are more likely to either emerge or call back to playback of their mate's call than to the call of a male from a different nest. Furthermore, contact calls of nestling green-rumped parrotlets are more similar to contact calls of parental care-givers than non-parental care-givers (Berg *et al.* 2011a). This suggests that nestlings learn calls from parental care-givers. The sharing of calls between parents and offspring facilitates parental care and coordination of movement after the nestlings have fledged. Vocal signals also function as nesting territory defense in parrot species such as the yellow-naped amazon, which vocalize in aggressive pair duets to ward off rival conspecific pairs (Dahlin and Wright 2012).

Vocal signals play an important role in structuring parrot societies, which often exhibit fission-fusion dynamics and variable group composition (Balsby and Adams, 2011). Brown-throated conures (*Aratinga pertinax*) preferentially solicit conspecifics to foraging sites by calling out to some overflying groups while ignoring other groups (Buhrman-Deever *et al.* 2008). Parrots can also use vocal signals to discriminate among individuals in a social group. Orange-fronted conures (*Aratinga canicularis*) can discriminate and respond variably to calls from familiar and unfamiliar individuals (Balsby and Adams, 2011).

Dialects in parrots

Vocal geographic variation has been documented in many species of parrots. The earliest studies of parrot vocal geographic variation described differences in white-tailed black cockatoo (*Calyptorhynchus funereus latirostris*) calls among different regional groups (Saunders 1983). A more thorough study on this topic was conducted by Wright (1996) and examined regional dialects in the contact calls of yellow-naped amazons. Wright compared contact calls from individuals among geographically segregated night roosting sites. The study found evidence of three dialect boundaries throughout the study area with birds in each dialect region producing one of three structural variants of the contact call and birds in border roosts alternating between calls from both dialect regions.

Subsequent studies have also found evidence of vocal geographic variation in orange fronted conures, ringneck parrots *(Barnardius zonarius)*, monk Parakeets *(Myiopsitta monachus),* and the St.

Lucia Parrot *(Amazona versicolor)* (Baker 2000; Bradbury *et al.* 2001; Burhman-Deever *et al.*, 2007; Kleeman and Gilardi, 2005). Vocal geographic variation in orange-fronted conures occurs without the clear dialect boundaries seen in yellow-naped amazons (Bradbury *et al.* 2001). St. Lucia parrots produce regionally distinct calls at relatively small spatial scales of 6-9 km (Kleeman and Gilardi, 2005). At least one species, the thick-billed parrot, has no geographic variation in vocal signals across its studied range suggesting that dialects are not a universal trait among parrots (Guerra *et al.* 2008). No previous study has looked at dialect formation as a consequence of captive breeding.

Dialects and parrot social systems

Dialects affect parrot social behavior by influencing interactions between residents and foreigners in a dialect region. The potential impacts of dialects on parrot social interactions have been tested in two systems. A playback experiment on yellow-naped amazons found evidence that nesting pairs respond more strongly to recordings of local dialects compared to foreign dialects (Wright and Dorin, 2001). Pairs were more likely to move towards the broadcasting speaker and vocalize if the dialect being played originated from the same dialect region as the nesting pair. In contrast, pairs did not respond if the vocalization being played originated from a foreign dialect region.

Studies on orange-fronted conures tested the response of wild birds to playback of conspecific vocalizations obtained from regions of gradually increasing geographic distances (Vehrencamp *et al.* 2003). The strength of response was negatively correlated with geographic distance. Conures were less likely to land, approach and interact with the loudspeaker if the stimulus originated from a more distant site.

To date, only one study has empirically examined how dispersing parrots in the wild may interact socially with parrots from foreign dialect regions. During the study both adult and juvenile wild yellow-naped amazons were translocated between dialect regions (Salinas-Melgoza and Wright 2012). Only one juvenile parrot imitated the contact call of the region to which it was translocated, while all translocated adult parrots retained their original contact call structures. The imitating juvenile also showed complete

integration into the flock of the new dialect region. The translocated adults showed fewer signs of flock integration and preferentially roosted with other translocated adults. These studies suggest that the presence of dialects may impact social dynamics when parrots from different dialects come into contact.

Researchers have posited two hypotheses to explain why birds exhibit differential responsiveness to conspecific vocal signals from different geographic locations. Dialect recognition may be a form of species recognition in which birds compare the vocal signal to an internal standard for the species and respond more strongly to the signal that most closely resembles this standard (Nelson, 1998). Alternatively, dialect recognition may be a type of threat-level assessment in which birds that produce local vocalizations are considered more threatening because they have greater experience with the local area and more potential to take over a territory (Wright and Dorin 2001).

METHODS

Study Area

The study took place within the El Yunque National Forest (18°18'N, 65°47'W) managed by the United States Forest Service and the Rio Abajo State Forest (18°20'N, 66°42'W) managed by the Puerto Rico Department of Natural and Environmental Resources. The 1,9656 ha El Yunque National Forest consists mostly of subtropical wet and subtropical montane rainforests. The 2,340 ha Rio Abajo State Forest consists of subtropical moist forests (Ewel and Whitmore, 1973).

These two government-managed forest reserves contain the entire global population of Puerto Rican amazons. I recorded adult parrots from the Rio Abajo captive (RAC) and Rio Abajo wild (RAW) populations as well as the El Yunque captive (EYC) and El Yunque wild (EYW) populations (Figure 1). I then used automated sound analysis software to compare their structure. I also recorded a group of parrots that were transferred between populations and analyzed changes in the acoustic structure over time.
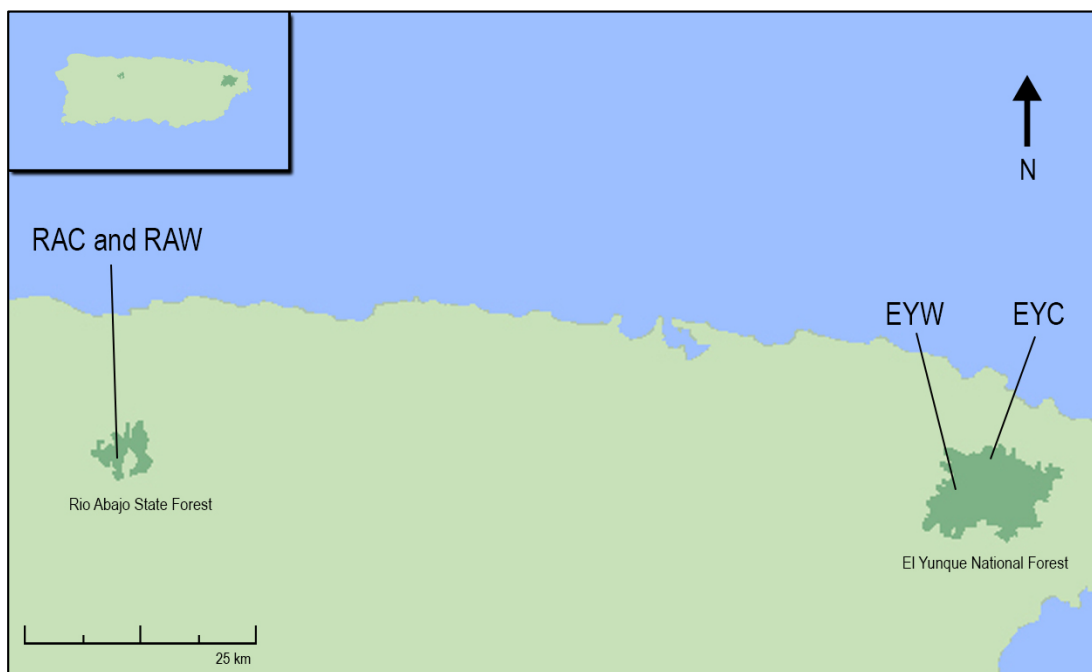

Figure 1. Map of Puerto Rico showing boundaries of the El Yunque National Forest and Rio Abajo State Forest reserves. Black lines indicate the geographic locations of the four study populations: Rio Abajo captive (RAC), Rio Abajo wild (RAW), El Yunque Captive (EYC) and El Yunque Wild (EYW).

Captive populations

Parrots from the EYC population are housed at a captive breeding facility called the Iguaca Aviary within the El Yunque National Forest. Captive breeding was initiated during the 1970's by capturing wild parrots from the relict population of Puerto Rican amazons in El Yunque. Parrots from the RAC population are housed at a second captive breeding facility called the Jose Vivaldi Aviary within the Rio Abajo State Forest. RAC was founded by 13 captive birds transferred from EYC in 1993. The captive breeding facilities currently house approximately 200 Puerto Rican amazons each. Both facilities also house a number of Hispaniolan amazons *(Amazona ventralis)* which are sometimes used as foster parents for rearing Puerto Rican amazon nestlings. Parrots are occasionally exchanged between the two captive populations to provide candidates for release into the wild, provide veterinary care, or manage population genetics. Usually only a small number of captive birds are transferred between the two aviaries in any given year. Once a parrot departs a facility it is never brought back to its facility of origin.

Wild populations

The relict wild population, EYW, became restricted to the El Yunque area during the 1940's when the species was extirpated from the rest of the island. Since the year 2000, wildlife managers have been releasing captive-reared parrots in attempts to augment this population. Despite this effort, population numbers have dwindled in recent years. At the time of this study, the number of parrots in EYW was estimated at no more than 9-11 individuals. EYW is in a secluded region of the forest, approximately 6 km away from the site of the Iguaca Aviary. Interaction between EYW and EYC is uncommon, although, recently-released parrots may occasionally fly back to the vicinity of the Iguaca Aviary. If a released parrot flies back to the aviary it is usually recaptured. Recaptured birds are either re-released in the future or integrated into the captive breeding program.

In 2006, efforts to create a second wild population of Puerto Rican amazons in the Rio Abajo State Forest commenced. Additional releases of captive-reared parrots have taken place every year since. At the time of this study, the number of wild parrots in Rio Abajo was estimated at 80-90 individuals.

Unlike in El Yunque, parrots in Rio Abajo are released onsite at the captive breeding facility. As a result, parrots from RAW flock and nest within close proximity of the parrots from RAC. Captive birds regularly engage in vocal interactions with overflying wild flocks.

Captive bird recordings

Recordings from EYC and RAC were collected on-site at both the Jose Vivaldi Aviary and the Iguaca Aviary. My assistants and I recorded at the Jose Vivaldi Aviary between September 2013 and December 2015 during the hours of 06:00-10:00 and 15:30-18:00 (UTC-4). These time periods correspond to the periods of greatest vocal activity for Puerto Rican parrots both in captivity and in the wild. Recordings at the Iguaca Aviary took place between January 2014 and November 2015 during the hours of 06:00-15:00 (UTC-4). The difference in recording period at the Iguaca Aviary was due differences in staffing schedules between the two aviaries, which resulted in restricted access to the facility during later times of the day. We recorded birds using a Sennheiser (ME67, Wedemark, Germany) directional microphone and a Marantz (PMD661, Sagamihara, Japan) digital recorder. Recordings were digitized at 44.1 kHz and at 16 bit accuracy.

Captive parrots were either isolated for recording within individual cages or recorded within group flight enclosures. Parrots were isolated if their normal enclosures were too close to other parrot enclosures making recording difficult because of the high levels of noise contamination. A stratified random rule was used to select recording subjects from the population database. Birds selected as recording subjects were transferred to an individual recording cage. Because parrots are more likely to vocalize in the presence of conspecifics, isolated parrots were recorded in pairs. Each bird was housed individually within one of two cages located 10 m apart. Mated pairs were always recorded next to their pair-mate and non-mated birds were recorded next to a conspecific of the opposite sex. Because birds would sometimes refuse to vocalize if they detected humans in close proximity, the recording equipment and recordist hid behind a black screen or observation blind located approximately 5 meters away from the recording cage. All recording subjects were given food and water on a daily basis. Parrots were

housed in the recording cages for 2-7 days before being returned to their regular enclosure within the aviary.

Some parrots were also recorded within large flight enclosures housing 20-40 parrots at a time. This was mostly done in cases in which capturing a parrot would have resulted in unacceptable levels of stress or injury to the parrot or its flock mates. Parrots within flight enclosures produced the same kinds of vocalizations as isolated parrots. All parrots housed in flight enclosures were individually marked with unique colored pet tags attached with a cable around the neck. While recording at flight cages, recordists did not hide behind screens or blinds. However, birds in flight cages were acclimated to aviary personnel around the cages and vocalized freely despite detecting human presence.

Wild bird recordings

Recordings from RAW were collected at the Rio Abajo State Forest 06:30-10:00 and 15:30-18:00 (UTC-4) between July 2013 to May 2015. My assistants and I recorded vocalizations opportunistically as we encountered wild parrots in the forest. Most wild parrots could be individually identified by the colored markings on their radio collars and colored leg bands. We also recorded parrots from observation blinds adjacent to parrot nest sites. Individual parrots could be identified using a spotting scope and a Nikkon D7100 digital camera with 150-500 mm zoom lens. Parrots were recorded as they vocalized spontaneously and were not presented with any stimuli to incite vocalization. To avoid pseudoreplication in the results, I only included recordings from parrots with known identities in the analysis.

Recordings from EYW were collected at El Yunque National Forest in July 2014 and July 2015. Owing to the low population size and the lack of individual markings in the EYW birds, recordings of known individuals could only be reliably obtained from the vicinity of their nesting sites. Recordings were obtained from two of the three nest sites in 2014 and two of the three nest sites in 2015. One of the nesting pairs recorded in 2015 had been previously recorded in 2014. A total of three nesting pairs (6 birds) were recorded, which at the time represented just over 50% of the existing wild population. Because of the risk of disturbing nesting parrots, all recordings were obtained from observation blinds

located approximately 50 meters away from parrot nests. Recording took place during a 12-hour period beginning at approximately 07:00 (UTC-4). Nesting pairs regularly return to the nest 3-6 times throughout the day to feed the nestlings and often vocalize as they approach and just after exiting the nest, providing multiple opportunities to obtain recordings from pair mates.

Translocated parrot recordings

To test for the adoption of foreign dialects, I recorded birds that had been reared at one breeding facility and translocated to the other facility. I divided these translocated birds into two groups. I refer to all translocated birds as "previously" or "recently" translocated followed by the acronym for the population they were bred in (e.g., previously-translocated EYC). Previously-translocated birds were translocated between 1993 and 2014 and had been living at the foreign facility for 6 months or more when they were recorded. Recently-translocated birds were transferred in July 2014 and had been living at the foreign facility less than 6 months when they were recorded. Recently-translocated birds were recorded multiple times throughout the study to track acoustic changes.

I recorded 11 previously-translocated EYC birds at the Jose Vivaldi Aviary and 1 previously-translocated RAC bird at the Iguaca Aviary. I also recorded a group of recently-translocated EYC birds at the Jose Vivaldi Aviary. In late July 2014, a group of 12 birds was transferred from the Iguaca Aviary to the Jose Vivaldi Aviary as candidates for release into the Rio Abajo State Forest. The translocated parrots were all hatched and raised at the Iguaca Aviary. After being translocated, the birds were housed in a large flight cage along with a group of local birds. One of the translocated parrots suffered an injury shortly after arriving at the aviary and had to be removed from the flight enclosure. This bird was later diagnosed with neurological problems by a veterinarian and was excluded from future recording. My assistants and I began recording the remaining parrots in December 2015. Seven of the recently-translocated birds were released into the wild on January 21, 2015 along with a group of 8 local birds. The 5 remaining recently-translocated birds continued to be housed in group enclosures with local birds

for the following year. Three of them were released into the wild on January 21, 2016 along with a group

of 13 local birds. All released birds were equipped with radio collars and were tracked 3 times per week

every other week. I continued to record translocated birds after they were released until February 2016.

Table 1. Number of parrots recorded in El Yunque captive (EYC), El Yunque wild (EYW), Rio Abajo captive (RAC), and Rio Abajo wild (RAW).

Population	Local birds	Previously-translocated birds	Recently-translocated birds
EYC	37	1	0
EYW	6	-	-
RAC	37	11	9
RAW	29	-	-

Acoustic analysis

I visualized recordings as spectrograms in Syrinx (http://syrinxpc.com , FFT window type:

Blackman, transform size: 512 points) and extracted individual calls from recording tracks. Vocalizations

were divided into general call "classes" based on the broad behavioral context under which they were

produced. I also divided vocalizations within some call classes into "structural variants". Structural

variants are calls produced under similar behavioral contexts but with varying acoustic structure.

This study focuses on vocalizations belonging to the compound call class. Calls in this class

consist of multiple syllables produced in succession. These calls are produced by perching birds engaging

in vocal exchanges with other parrots. I analyzed two structural variants within the compound call class. I

refer to these two structural variants with the onomatopoeic names *caw* and *chi*. The general syntax of a

caw or *chi* call consists of an introductory syllable followed by one or more repetitions of a *caw* or *chi*

syllable. The acoustic structure of the introductory syllable was highly variable and individual parrots

could produce several dissimilar types of introductory syllables.

The *caw* and *chi* syllables possessed more uniform characteristics and equivalent calls could be

identified in different populations. Some parrots produced variations of these calls that swapped syllable

positions, alternated between *caw* and *chi* syllables, duplicated introductory syllables, or excluded the introductory syllable. These variations were rare and were not included in the analysis.

The *caw* syllable begins as an ascending or descending harmonic series that levels out and then terminates with a rapid drop in frequency (Figure 2). The *chi* syllable has three sections. The first and third sections initiate as short harmonic series that either descend or remain constant. The middle section is frequency modulated and includes a jump to a higher frequency (Figure 3).

Chi and *caw* syllables vary in their degree of frequency modulation. Some syllables had little or no frequency modulation, giving them a linear quality. Others contained rapid modulation throughout some or all of the syllable. Syllables with greater frequency modulation sounded rougher and harsher than those with smoother appearances. Some syllables also contained a chaotic portion at the end. Both syllables sometimes contained subharmonics, although this was more common in unmodulated *ca* syllables. An individual parrot's repertoire could include syllables with one or more of these structural features and parrots sometimes included syllables with more than one of these features within a single call.

Caw calls were present in the repertoires of parrots from RAC, RAW, and EYC. *Chi* calls were only present in RAC and EYC repertoires. *Chi* calls were uncommon in RAW birds and the population was excluded from the *chi* call analysis. EYW did not contain either *caw* or *chi* calls in its repertoire and was excluded from both analyses.

Figure 2. Spectrograms of *caw* calls with different introductory syllables produced by Puerto Rican amazons. (a-b) *Caw* calls produced by two different birds in the El Yunque captive population (EYC). (c-d) *Caw* calls produced by two different birds in the Rio Abajo captive population (RAC). (e-f) *Caw* calls produced by two different birds in the Rio Abajo wild population (RAW) (e-f).
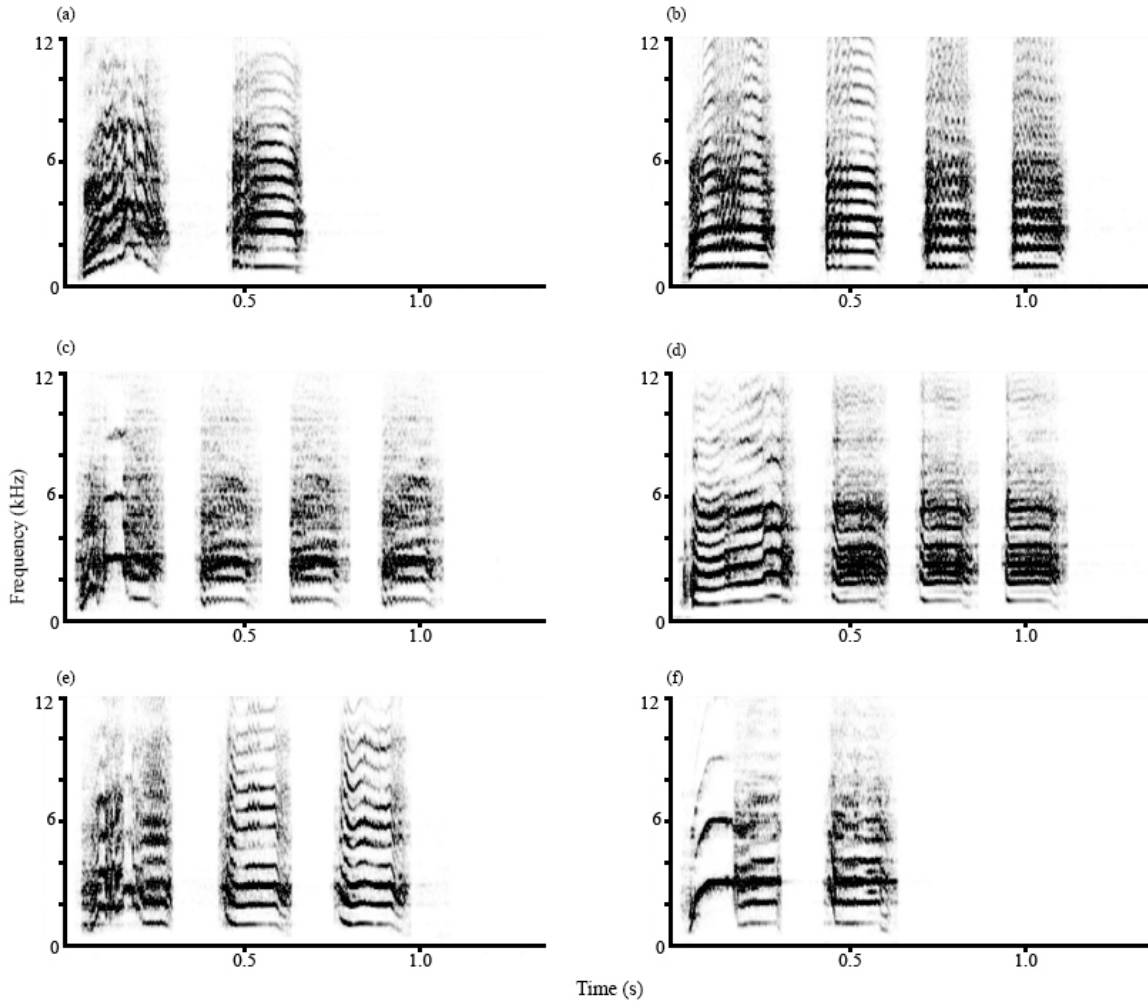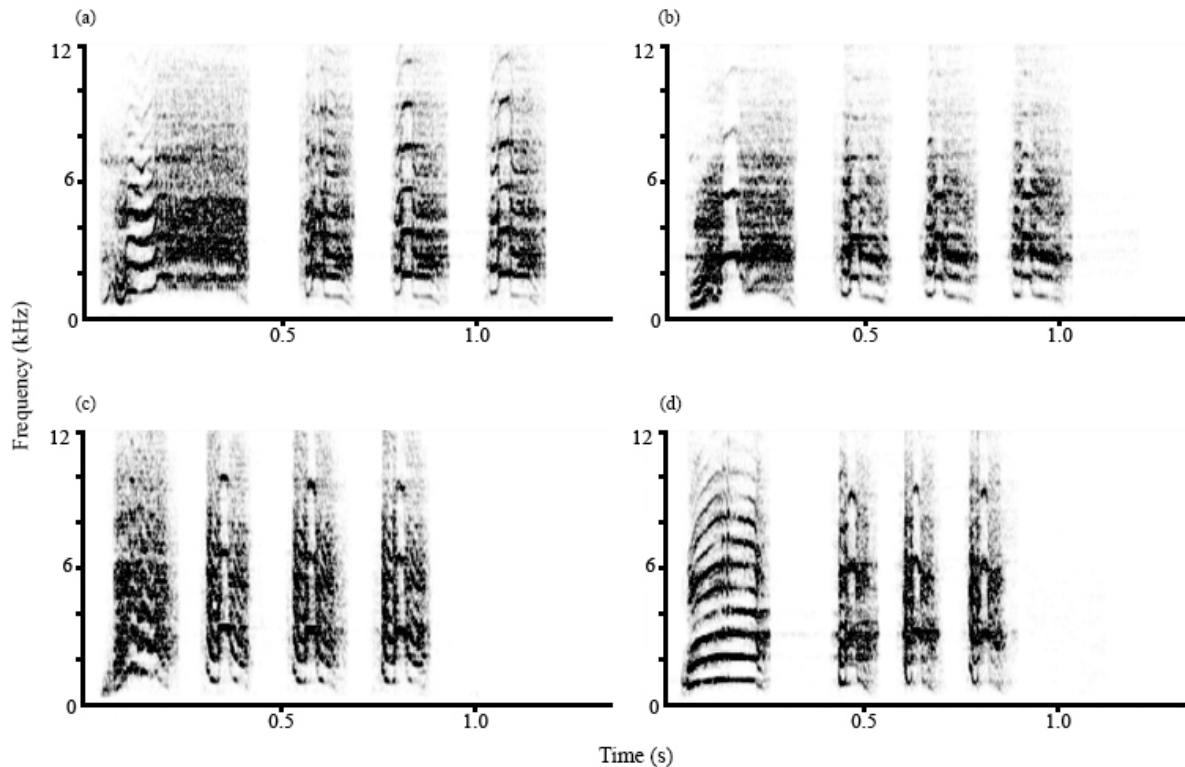
Figure 3. Spectrograms of *chi* calls with different introductory syllables produced by Puerto Rican amazons. (a-b) *Chi* calls produced by two different birds in the Rio Abajo captive population (RAC). (c-d) *Chi* calls produced by two different birds in the El Yunque captive population (EYC).

Because of the variable nature of the introductory syllable in compound calls, I chose to only

examine structural differences in the repeated *caw* or *chi* syllable. One call from each individual was

selected for the analysis of *caw* and *chi* vocalizations. I visualized calls as sonograms using the program

Luscinia (http://luscinia.sourceforge.net). I used visual inspection to rate recording quality hierarchically

as bad, fair, or good based on signal to noise ratio. I then randomly selected one call from the highest

quality category for each individual. Because the number of repetitions of the secondary syllables varied

between calling bouts, I only analyzed one syllable in each of the selected calls. If a call had more than

one repetition of the secondary syllable, I randomly selected the syllable to be analyzed. I compared

syllables using the dynamic time-warping (DTW) algorithm in Luscinia. Syllables were individually

highlighted (dynamic range: 35, high pass threshold: 300, FF jump suppression: 20, FF bias: 0.1) and

analyzed with DTW on the basis of the following parameters: time, mean frequency, fundamental

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frequency, harmonicity, and FF norm (compression ratio: 0.001, minimum element length: 10, Time SD weighting: 1, cost for stitching syllables 0, cost for alignment error: 0).

Statistical analysis

To test for geographic variation of *caw* and *chi* calls among populations I used Luscinia's built in non-metric multidimensional scaling ordination (NMDS) to convert the dissimilarity matrix generated by the DTW into Euclidian dimensions. I used DFA to determine if populations could be correctly classified by the acoustic structure of calls. I used five principal axes generated by the NMDS to test for group separation using discriminant function analyses (DFA) in the program Infostat (http://infostat.com). Only parrots considered residents of their population were included in the DFA. Captive parrots were considered residents if they had lived their entire lives at a single breeding facility. Unlike the captive populations, wild populations consist of one-time captive birds released into the wild as well as birds that were born in the wild. Released birds were considered residents of the wild population if they had been living in the wild for a year or more. Otherwise, they were treated as translocated birds.

I had no *a priori* reason to classify translocated birds as members of the population they were born in rather than the population they were translocated to. Therefore, all translocated birds were excluded from classification by the DFA. The group membership for translocated birds was instead determined by calculating the distance to each population centroid and assigning the bird to its closest population.

RESULTS

Resident birds

Vocalizations produced by birds in EYW differed from calls from all other populations in overall structure. Calls recorded from birds in EYW did not appear to be equivalent to calls in the other populations even when they occurred under similar behavioral contexts. Calls in the EYW repertoire did not follow the typical structure of the other populations in which an introductory syllable is followed by variable repetitions of a secondary syllable. Instead, EYW compound calls commonly consisted of single syllables repeated in succession or alternating syllables produced in pairs (Figure 4). These calls were not analyzed further.
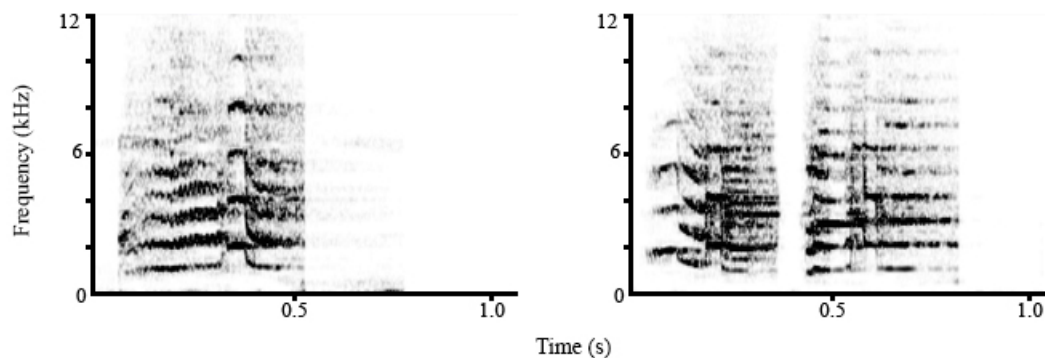
Figure 4. Two common calls obtained from birds in the El Yunque wild population (EYW).

Chi calls were recorded from 18 birds in RAC and 13 birds in EYC. The DFA performed on *chi* calls from EYC and RAC indicated significant group discrimination (p= 0.0004). The DFA assigned 12 of 13 EYC *chi* calls and 17 of 18 RAC *chi* calls to the correct population for a correct classification of 92% and 94% respectively (Figure 5, Figure 6).

Figure 5. Classification of *caw* calls from El Yunque captive (EYC), Rio Abajo captive (RAC), and Rio Abajo wild (RAW) populations compared using discriminant function analysis.
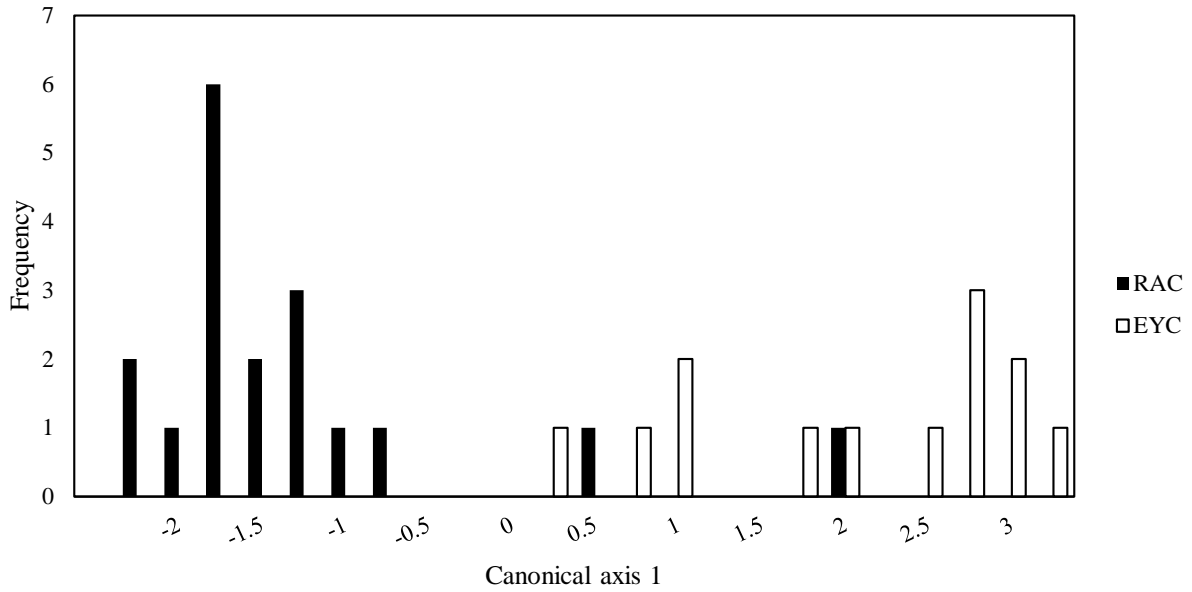
Figure 6. Histogram of canonical variate obtained from discriminant function analysis of *chi* calls obtained from the Rio Abajo captive (RAC) and El Yunque captive populations.

Caw calls were recorded from 20 birds in EYC, 30 birds in RAC, and 22 birds in RAW. The DFA performed on *caw* calls from EYC, RAC, and RAW indicated significant group discrimination (p <0.0001). EYC calls were assigned to the correct group in 90% of cases. Two EYC calls were misclassified as RAC. *Caw* calls from RAC were correctly classified in 67% of cases. Three RAC calls were misclassified as EYC and 7 RAC calls were misclassified as RAW (Figure 7). *Caw* calls from RAW were assigned to the correct category in 100% of cases. A scatter plot of canonical variates 1 and 2 extracted by the DFA reveal the degree of separation in the three sub-populations (Figure 8).
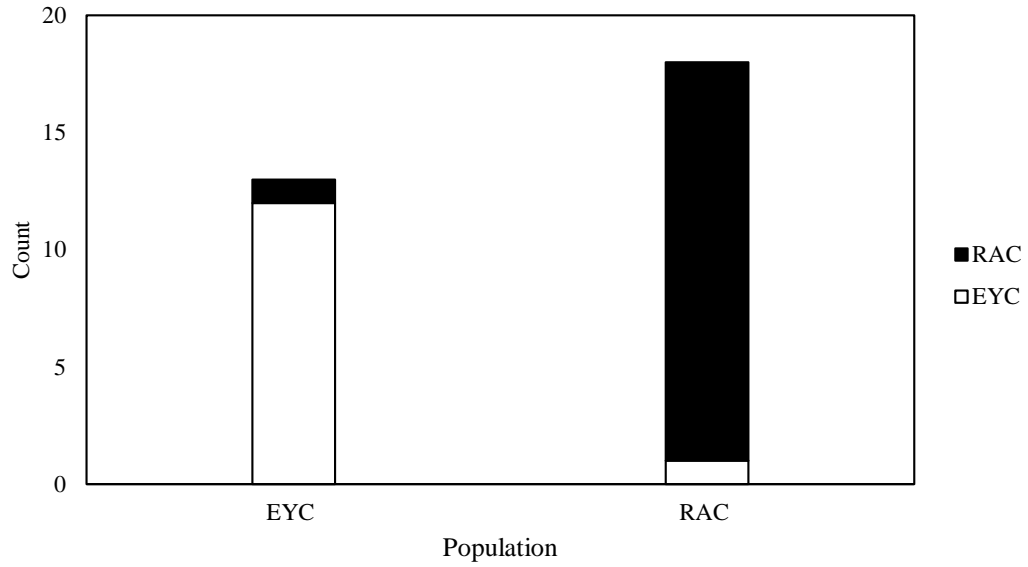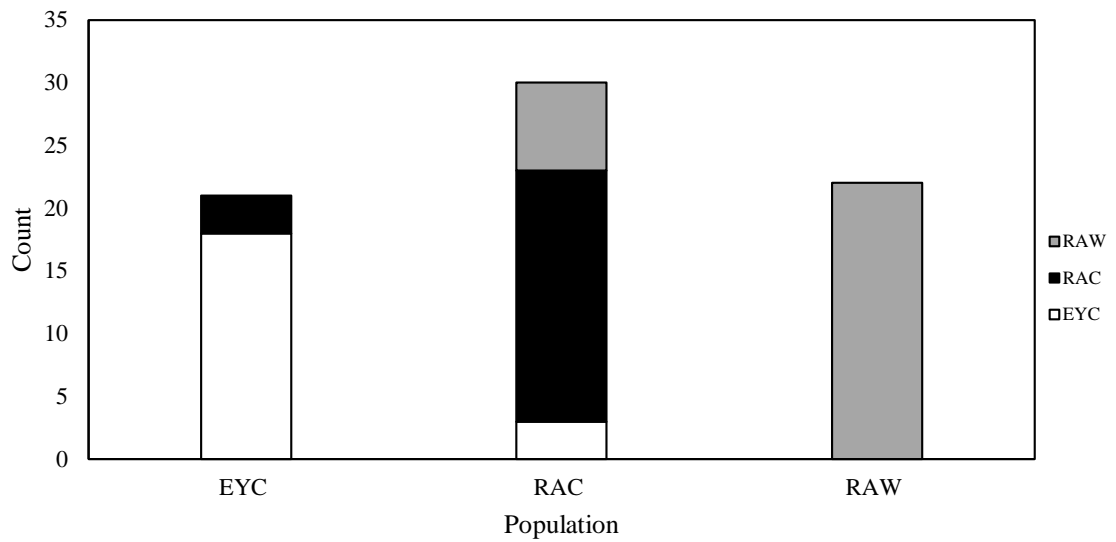

Figure 7. Classification of *caw* calls from El Yunque captive (EYC), Rio Abajo captive (RAC), and Rio Abajo wild (RAW) populations compared using discriminant function analysis.
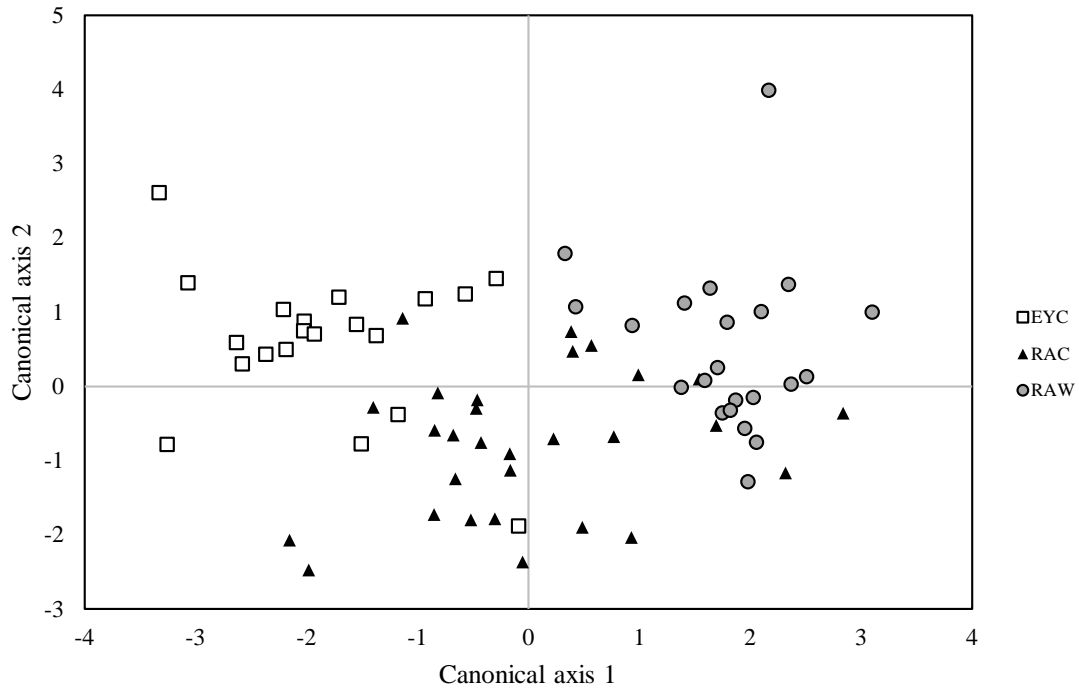
Figure 8. Plot of canonical variates 1 and 2 obtained from discriminant function analysis of *caw* calls from the El Yunque captive (EYC), Rio Abajo captive (RAC), and Rio Abajo wild (RAW) populations.

After completing the DFA analysis of *ca* calls, I noticed that all RAC birds misclassified as RAW were relatively young birds born after 2007. This finding suggests that vocalizations from RAC parrots born after 2006, the year RAW was founded, were more similar to RAW vocalizations. To test this hypothesis, I used a *post hoc* analysis to compare vocalizations from RAC parrots born after the founding of RAW and RAC parrots born before the founding of RAW. I calculated the distance to the RAC and RAW group centroids for each bird. I then calculated a bias score for each individual by subtracting the distance to the RAC centroid from the distance to RAW centroid. A t-test comparing the bias score of birds born before 2006 to birds born after 2006 found that birds born after 2006 were significantly closer to the RAW centroid (p = 0.0025).

Translocated birds

  I recorded *caw* calls from 10 previously-translocated EYC birds and 1 previously-translocated RAC bird. The DFA for the previously-translocated EYC birds classified 8 birds as RAC and 2 birds as EYC. The previously-translocated RAC bird was classified as RAC. I obtained *chi* calls from only 4 previously-translocated EYC birds and all 4 were classified as RAC. No *chi* calls were recorded from the previously translocated RAC bird.

  I recorded *caw* calls from 9 of the 12 recently-translocated EYC birds. Initial recordings were obtained between December 1, 2014 and February 4, 2015. This period spans the last month prior to release until the first 2 weeks post release. Comparison to the population centroids generated by the DFA from earlier analyses revealed that 2 birds were producing *caw* calls that were classified both as RAC and EYC during this period. The remaining birds were only producing EYC *caw* calls. The bi-lingual birds were among the 7 recently-translocated EYC birds released in 2015. A *caw* call obtained on March 31, 2015 from another of the released recently-translocated EYC birds was classified as RAW. One of the released recently-translocated EYC birds disappeared from the population in July and is assumed to have died or dispersed. Only EYC calls had been obtained from this bird by the end of March 2015. Another of the released recently-transferred EYC birds only produced EYC calls the last time it was recorded in late May 2015. I was unable to obtain post-release recordings for another of the birds for which I had obtained pre-release *caw* recordings. In January and February 2016, I obtained recordings of *caw* calls from 3 of the 5 recently-transferred EYC birds that remained in captivity after the 2015 release. All three birds were classified as RAC (Figure 9).
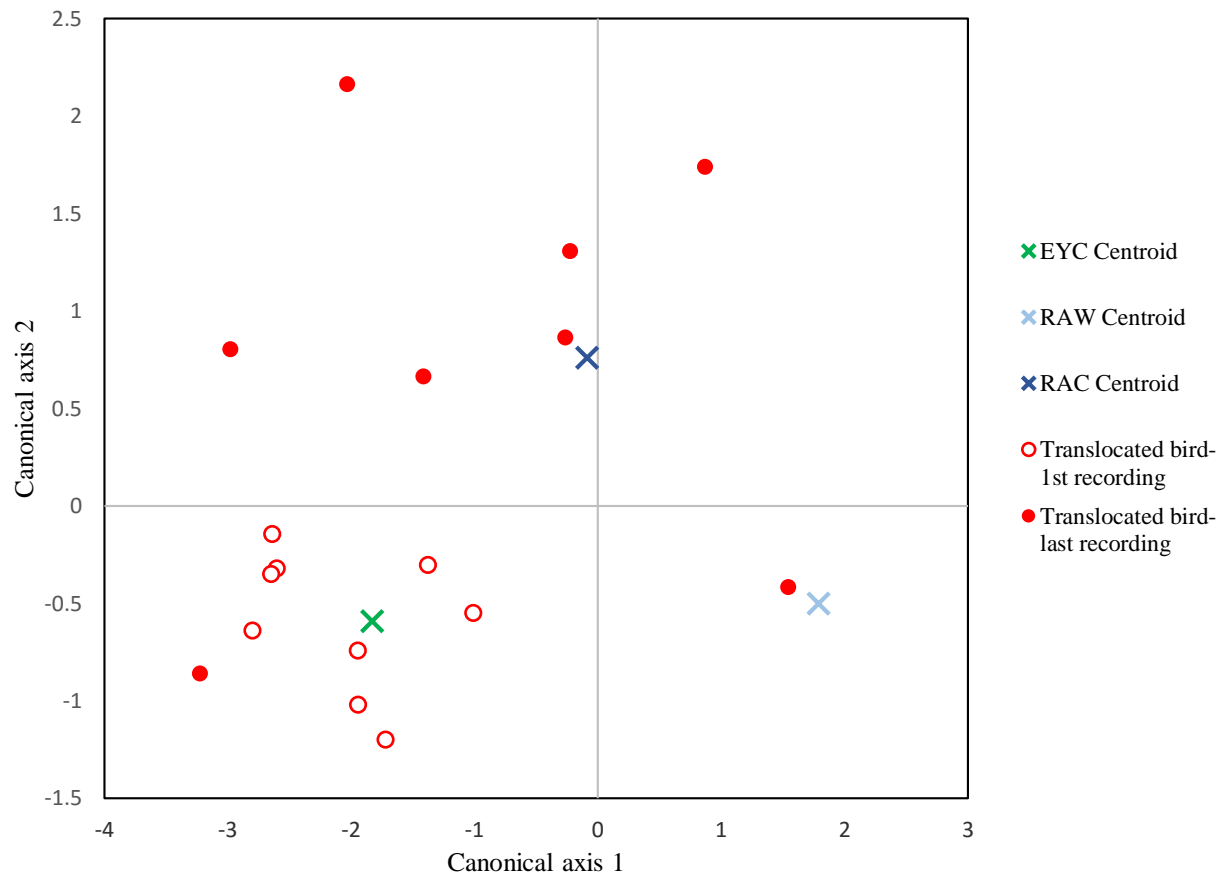
Figure 9. Plot of canonical variates 1 and 2 showing 1st and last recordings obtained for parrots translocated between populations. Population centroids for El Yunque captive (EYC), Rio Abajo Wild (RAW), and Rio Abajo captive (RAC) are represented by colored 'X'.

DISCUSSION

I found evidence of acoustic differences in all four Puerto Rican amazon populations. The differences in acoustic structure of compound calls could be perceived both audibly and through visual inspection of spectrograms. Calls in the EYW repertoire were not equivalent to calls from the repertoires of other populations. I was able to distinguish EYC, RAC, and RAW by the equivalent *caw* and *chi* calls in these populations' repertoires. The differences in repertoires between populations warrant classification as dialects because vocal parameters vary discretely instead of clinally between geographic localities (Podos and Warren 2007).

Acoustic differences were most evident in parrot calls from EYW. Although no statistical comparison could be performed between EYW and other populations, the lack of equivalent calls within the population repertoire indicates dialect emergence. In comparison to EYC, RAC, and RAW, compound calls in EYW had a different overall structure and were composed of syllables with different acoustic features. The captive parrots in EYC have been separated from the relict population of EYW for more than 40 years. While it is unclear when during this relatively short time-frame dialects emerged, the isolation of other populations from EYW has resulted in dramatic changes within the species repertoire.

Early captive-breeding practices may have influenced the divergence of EYC from the relict dialect. With the exception of two mist-netted EYW relict birds, the founders of the EYC population were all harvested as nestling or eggs from wild parrot nests within El Yunque between 1973 and 1979 (Snyder *et al.* 1987). The first captive-breeding facility was located away from wild parrot nesting and foraging sites and members of the relict EYW population rarely flocked close to the aviary. The remoteness of the facility and the age of the founders would have resulted in an abundance of vocally naïve parrots with a lack of exposure to relict dialect learning models. Early captive parrots may have modeled their vocal behavior on other sources. Many of the early EYC founders were hand-reared by humans. The ability of parrots to mimic human speech is well known in the pet trade and has also been extensively studied in captive African greys (*Psittacus erithacus*) (Pepperburg 2010). The fostering of Puerto Rican amazons to

Hispaniolan amazons was also initiated in the early years of the captive breeding program. Hispaniolan amazons made up 40% (10/25) of the captive breeding population in 1979. Evidence of parrots modeling vocal behavior on foster parents has been observed in the wild for two species. Experimental cross-fostering studies of wild green-rumped parrotlets found evidence of vertical transmission of calls between foster parents and nestlings (Berg 2011a). Vocal imitation of foster parents has also been observed in nestling galah cockatoos (*Cacatua roseicapilla*) that were accidentally cross-fostered by Major Mitchell's cockatoos (*Cacatua leadbeateri*) during nest cavity take-overs (Rowley and Chapman 1986). Young Puerto Rican amazons in EYC may have modeled their vocalizations on their human and parrot surrogates. These learning models could have provided additional sources of vocal variation leading to a greater divergence from the relict dialect.

Despite the shorter twenty-year time span between the separation of RAC from EYC, I found evidence of differences in acoustic structure in calls from both populations. In contrast to EYW, equivalent calls were identified in the repertoire of both captive populations. *Caw* calls and *chi* calls were common in the repertoire of birds from both aviaries. Both *caw* calls and *chi* calls were significantly different between populations.

Unlike the founders of the first captive-breeding program at EYC, the first Puerto Rican amazons transferred to RAC in 1993 were adult parrots bred and reared in captivity. Call learning from the more abundant adult conspecific learning models in RAC may account for the similarities to the EYC repertoire. Vocal divergence between the two populations likely resulted from geographic separation. Differences in culturally inherited acoustic signals can result from small innovations and inconsistencies in copying that occur during song learning (Grant and Grant 1996). Cultural drift can lead to changes in the way individual syllables are produced, the emergence of novel syllables, or the reordering of existing syllables (Lemon 1975). Founders of RAC likely produced calls with varying acoustic features and these variations would have served as the models for future generations of RAC vocal learners.

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The populations of RAC and RAW are essentially sympatric, although interaction between the two populations is limited by the presence of cages. I found evidence of acoustic differences between RAC and RAW. RAW *caw* calls were significantly different from the other two populations. *Chi* calls were rarely present in RAW and were only obtained from birds that had been released from RAC. No bird that had fledged in the wild was recorded producing *chi* calls (n = 15). I also found evidence of similarities between RAC and RAW *caw* calls. *Caw* calls from RAC were misclassified as RAW in 23% of cases but no RAW calls was misclassified as RAC. Birds born in 2006 or later were significantly more similar to birds in RAW than birds born before 2006. No RAW *caw* call was classified as RAC, even though released birds made up 41% (9/22) of the RAW *caw* call sample.

A vocal divergence process similar to the one that occurred during the founding of RAC may account for the differences present in RAW. Cultural drift may have occurred after the initiation of the 2006 releases of captive RAC parrots into the Rio Abajo Forest. The creation of a unique RAW dialect may have been reinforced by social interactions between wild birds. Birds in RAW are free to interact vocally with and model their vocalizations on either wild or captive individuals. However, the nature of parrot foraging systems would make vocal interaction with other wild birds more beneficial. Like other parrot species, Puerto Rican amazons forage on a mixed diet of both ripe and immature fruits and other plant parts spread over large indefensible areas (Snyder *et al.* 1987). Social foraging and the mediation of fission-fusion dynamics has been posited as an explanation for the vocal imitative abilities of parrot species (Bradbury and Balsby 2016). The efficient exploitation of unevenly distributed resources spread over large areas may require the exchange of cultural knowledge between members of different flocks (Bradbury and Balsby 2016). Imitation of vocal signals is believed to mediate this dynamic by soliciting the attention of desired individuals (Balsby *et al.* 2012). Hence, wild birds in RAW may be more prone to interact vocally with their fellow RAW members since these birds possess cultural knowledge of exploitable food resources. Newly integrated members of this population (either released or wild-fledged) may be more likely to choose RAW birds as vocal models over RAC birds for this reason.

The similarity of *caw* calls from RAC birds born before the founding of RAW (2006) to RAW *caw* calls suggests that some birds in RAC modeled their vocalizations on wild birds after the emergence of the RAW dialect. Unlike their wild counterparts, captive parrots in RAC have no need to forage or to mediate fission-fusion dynamics. As a result, these birds may discriminate less when selecting vocal learning models. Furthermore, some RAC birds were recorded imitating wild flight calls and take-off calls while perching and remaining stationary. This suggests that captive birds do not know the proper context of the wild calls they chose to imitate. All released parrots recorded in RAW produced the local RAW dialect. Whether they learned the dialect prior or post release could not be determined in this study.

Parrots that were translocated across dialect boundaries were able to acquire the foreign dialect. Most of the previously-translocated EYC birds (8/10) produced *caw* calls that were classified as RAC. Fewer previously-translocated EYC birds produced *chi* calls but all of them were classified as RAC. It is unclear whether the same dialect learning occurs when birds are transferred from RAC to EYC. I only obtained recordings from one such individual and it was classified RAC. Recordings of more translocated RAC birds would be required to better understand this process.

I also found evidence of dialect learning in the group of recently-translocated EYC parrots. Six of the nine parrots from which I obtained *caw* calls eventually switched dialects to either RAC or RAW. One parrot disappeared from the population before a dialect switch was detected. A dialect switch was not detected in another parrot more than four months after its release. This bird remains in RAW but I have been unsuccessful in acquiring additional recordings. I was also unsuccessful in getting post-release recordings of one of the 9 parrots for which I had had obtained pre-release recordings. This bird had not switched dialects prior to its release in 2015. Only one bird was detected producing the RAW dialect but this after it was released.

While the tendency to acquire the foreign dialect is clear, fewer conclusions can be drawn about the time required to learn a new dialect. The amount of time that recently-translocated parrots took to

acquire a foreign dialect varied by individual. However, recordings were obtained inconsistently for most birds and the time the dialect change was detected may not actually reflect the time in which it occurred. Only two birds had acquired either of the local dialects 6 months after the initial translocation. Acquisition of a local dialect was not detected for one bird until 8 months after translocation. The two birds for which a dialect switch was not detected were last recorded 8 and 10 months after the initial translocation. Dialect switches were also detected for 3 birds remaining in captivity after 2015. However, these recordings were not obtained until 2016 (over a year after the initial translocation) and it is not clear when during this time-span the dialect switch occurred.

Although dialect emergence in this species seems to have resulted from anthropogenic forces, dialects are a natural and widely occurring phenomenon in many parrot species. Studies in yellow-naped amazons demonstrated that dialects do not impede dispersal between dialect regions and post-dispersal learning of a new dialect is possible for immigrants (Wright and Wilkinson 2001; Salinas-Melgoza and Wright 2012). Hence, it is not surprising that translocated Puerto Rican amazons were capable of learning a new dialect. However, the same study also suggested that age may affect the ability of translocated parrots to learn a foreign dialect and that translocated parrots had trouble adapting socially to a new dialect region (Salinas-Melgoza and Wright 2012). Whether Puerto Rican amazons that are artificially translocated across dialect boundaries suffer any costs to fitness or survival as a result of the translocation is not yet clear. No mortalities were confirmed for any of the released recently-translocated EYC birds but one birds could not be accounted for less than a year after release. Directly testing the survival and fitness costs of translocations across dialect boundaries may be risky and impractical when managing an endangered species. Therefore, I recommend that managers employ strategies that would facilitate parrots' acquisition of foreign dialects prior to release.

Parrots in RAC have regular vocal exposure to parrots from RAW and, as a result, regularly imitate RAW vocal signals. In contrast to the dynamic of wild and captive populations in Rio Abajo, parrots in EYC and EYW have no regular interaction because of the distance that separates the two

populations. I found no evidence that captive parrots in EYC produce vocalizations from EYW. Although geographic isolation promotes divergence in vocal signals, exposure to local learning models may facilitate transmission of these signals. Conservation practitioners should be aware of this when managing populations of this species. The reintroduction of wild Puerto Rican amazons into Maricao State Forest is set to occur at the end of 2016. Given the history of dialect emergence in this species, managers should expect to discover vocal divergence at some point in this new population as a result of cultural drift. Once the third wild population has been established, housing captive release-candidates in proximity to reintroduction sites may facilitate the acquisition of emerging dialects. I also recommend that the transfer of release-candidates from RAC and EYC to Maricao take place as early as possible to allow birds sufficient time to acquire local signals. Future studies could examine whether there is an ideal age of transfer that would facilitate acquisition of new vocal signals.

The initiation of the captive breeding program and the reintroduction of parrots into the wild are essential strategies that have helped bring the Puerto Rican amazon back from the brink of extinction. The geographic isolation of new populations has also been necessary to protect populations from stochastic factors. However, the unintended consequence of these classic conservation strategies has been the vocal divergence of both captive and wild populations. To my knowledge this is the first evidence of captive breeding resulting in the creation of vocal dialects in any species. Conservation practitioners in other breeding and reintroduction programs should be aware of how culturally transmitted behaviors can change when animals are cut off from exposure to their wild predecessors. If a cultural change is likely to occur, then managers should evaluate what impact this change could have on the eventual release of captive reared animals and develop cost-effective strategies to mitigate these problems.

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