Phenotypic Variation in Introduced Rock Pigeons (*Columba livia*) In the Eastern United States

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Abstract

As an introduced species in North America, the Rock Pigeon (*Columba livia*) has established itself in a vast array of climates and niches. Rock Pigeons exhibit great phenotypic variation in their plumage in captivity and in the wild. In the time since the introduction of *C. livia* to North America, this phenotypic variation in feral pigeons established in different regions may have allowed them to adapt to local environmental conditions. To explore this idea, I focused on analyses of plumage and morphological phenotypes in feral Rock Pigeons across the eastern United States of America. I found that northern Rock Pigeon populations had a heavier body mass, longer wing chord, and longer head length than their southern counterparts. This geographic variation in phenotypes observed in feral Rock Pigeons in the eastern United States suggests this species may be poised to respond to local selective pressures.

KEYWORDS: Rock pigeon, *Columba livia*, microevolution, North America

Introduction

Introduced species offer a unique opportunity to understand how quickly populations can change in morphology, behavior, and other aspects of life-history (Johnston and Selander, 1964 Hughey et al. Gilchrist et.al, 2001,Chun et.al, 2007, Hendry, 2008). If an introduced species successfully colonizes a new location and then subsequently expands its range, these species should respond to differences in environmental conditions across their new range, especially if conditions differ from their native ranges. Studies of introduced species have found rapid phenotypic changes across the introduced geographic ranges, but these studies often focus on less mobile species (plants, fruit flies and lizards). Here, I examine for similar phenotypic changes across geography in a mobile bird, the feral Rock Pigeon (*Columba livia*).

Previous work on the near globally-ubiquitous House sparrow (Passer domesticus) has demonstrated significant size variation in its introduced ranges. Introduced populations in North America show greater body length, wing length, and bill length than their European counterparts. Moreover, within the introduced North American populations, significant morphological variation exists. Specimens from Death Valley California had the palest plumage coloration, while specimens from Mexico City had the overall darkest coloration. Similarly, regional variation in body mass showed the heaviest individuals in Quebec, Canada with average masses of ~31 grams, and the lightest individuals in Oaxaca, Mexico with average masses of ~27 grams (Johnston and Selander, 1964). These patterns are consistent with predictions generated by Bergmann's Rule (Ashton, 2008), where the heaviest individuals are furthest north. House sparrows were introduced into North America in 1851, giving them a span of 133 years between their introduction and Johnston and Selander's study to diverge.

Johnston and Selander's (1964) study of introduced House Sparrows suggests that other introduced bird species might show similar levels of phenotypic variation across their introduced ranges. I examine for similar patterns of geographic variation in introduced feral Rock Pigeons within the Eastern United States. Pigeons and humans have a long history of interactions and this history makes pigeons an ideal species to examine for phenotypic changes as a result of range introductions.

A Brief Natural History of the Rock Pigeon

The Rock pigeon (Columba livia) is an old-world pigeon used as a model organism for many processes (Levi, 1996), showing extensive morphological variation in the wild and in captivity. In the bird's native range (Southwest Asia, Northern Africa, and Western Europe), twelve subspecies are recognized, some of which have very limited ranges, such as the Dakhla and Kharga oases of Egypt (C. l dakhlae) and the Canary Islands of Spain (C. l. canariensis) (Gibbs et al., 2001). Changes in the physical traits of Rock Pigeons in the wild can be swift and conspicuous. For instance, the ancestors of the Canary Islands subspecies (C. l. canariensis) likely colonized these islands around 130,000 years ago when islands became habitable for large Columbiformes due to complex soils capable of sustaining grasses and rock structures such as small caves and ledges for nesting (Rando, 1999). The Canary Islands Rock Pigeon differs from their sister taxa (C. l. livia) in its size, coloration of the wing coverts, wing shape , and tail color (Gibbs et al., 2001). These examples of changes in phenotype observed in wild pigeons suggests that feral pigeons might change their phenotypes in response to variable conditions in their introduced ranges. Similar, introduction events of other Columbiformes, where a limited number of escapees have colonized and dominated a landmass, have occurred with the Eurasian Collared Dove (Streptopelia decaocto) in North America (Hengeveld, 1993) and the Zebra Dove (Geopelia striata) in Hawai'i (Richard and Fleischer, 1989).

A Brief Unnatural History of the Rock Pigeon

In captivity, selective breeding creates more dramatic variations to morphology. Pigeons were first kept by humans about 5,000 years ago as a food source, as pets, as messenger, and as religious icons (Gilbert et al., 2020). The first depictions of novel captive bred phenotypes were illustrations of common captive color forms including what are known by modern pigeon keepers as checkered and ash red (Facsimile Painting from the 'Green Room') and white (Scene in the Nile Marshes) birds from Ancient Egyptian tomb paintings, stretching back as far as 1353 BC. However, due to the long history of humans and pigeons, physical modification, especially in coloration, may have occurred earlier. A record of the most dramatic change to the Rock pigeon comes in the year 1238 when ancestral members of the tumbler pigeon breed were recorded by Europeans for the first time as "Syrian" pigeons. It can be noted, however, that these pigeons likely existed long before European documentation (Johnston, 1998). Tumbler pigeons are noted for their ability to perform "somersaults" in the air, often uncontrollably. This leads to either the unusual "flipping" of a flying bird close to the ground or the "cartwheeling" of a bird high in the air. While the reason for this unusual "tumbling" response is unknown, it is widely believed to be the result of either a heritable condition similar to Ménière's disease in humans or a neurological or behavioral alteration (Mowrer, 1940).

In modern pigeon keeping, new breeds can arise within a few years in the hands of a single dedicated breeder. One example of this phenomenon is the origin of the breed known as the "almond brown". This bird was bred exclusively by a keeper named W.F Hollander at Iowa State University from a "mixed stock" of birds and was used to study the sex-linkage of traits. The almond brown breed is known for its dark eyes as an adult, pink eyes as a juvenile, and pale brown plumage (Levi, 1996). Changes like these give further testament to how quickly (i.e. within a human lifespan) pigeon phenotypes can change.

In captivity, the number of extant domestic breeds is around 314. Some breeds have been selected for flying ability, others have been rendered flightless, while others can fly for 22 hours straight. Other breeds, bred for meat production, can weigh the same as Common ravens (Corvus corax) with weights up to 1400 grams, compared to the 238-302 gram weight of wild-type pigeons (Gibbs et al., 2001). Pigeons bred for showing and the pigeon fancy can have a variety of traits such as erect fanned tails, elongated and shortened bills, flight feathers on feet, hoodlike crests, and high-pitched calls (Levi, 1996). Among these modern breeds, birds have been produced with traits so foreign to their wild ancestors they often appear to be from a completely different family. It seems, given the right artificial selective pressures, that the plumages, vocalizations, behaviors, and anatomy of domestic Rock Pigeons have diversified to such a great degree that their multiplicity of forms, within this single species, surpasses even that of the entire family of the famously variable and bizarre birds-of-paradise (Paradisaeidae).

Rock Pigeons in North America

The history of pigeons in North America is vivid, rich and well recorded. The first Rock pigeons in North America were introduced in 1606 to Nova Scotia as free-flying birds by some of the first French colonists of the region. The English later separately introduced pigeons to the Virginia colony in 1621. While the exact reason for bringing these birds overseas is unknown, it may have been similar to the reasons pigeons were domesticated in the first place––for use as pets, messengers or food; or to produce guano. By 1773, Rock Pigeons could be found free-flying in some capacity (either as true feral birds or as captives kept in open dovecotes) from Nova Scotia south to what is now Florida and west to Illinois (Schorger, 1952).

Based on the folk-art depictions of pigeons and pigeon-like birds as well as dovecote designs from North America in the 1700s, the Rock Pigeons introduced to North America by the English and French were likely a form of the common utility and flying breeds kept in Europe at the time. These illustrations show popular pigeon breeds of the time without atypical plumage structures (Chimney Piece with Images of Adam and Eve). Pigeons were depicted in the air (Stone, Anstiss. "Memorial Brooch.") and dovecotes rather than closed lofts were used for their housing (Kryder-Reid, 2020). These depictions show the early American pigeons as either pure white, implying the presence of at least some white domestic birds (Starr, Sarah. "Embroidered Sampler: Starr Coat of Arms.") or gray with banded tails (Birth and Baptismal Certificate 1769). Although the exact breed or breeds that populated the Americas is unknown, depictions of commonly kept birds in France and England, showed that they may have been a mix of what is now called the Baghdad, dragoon, carrier, and, most likely an ancestral homer breed known as the "dovecote pigeon" (Levi, 1996). Other breeds such as barbs, pouters, (London Trade Card with Three Pigeons) and short-crested breeds, such as the archangel (Barlow, Diverse Pigeon Species) are also commonly depicted in the avian illustrations of Europe at the time (Buffon, "Little Dove, Powter And Dovehouse Pigeon"). Pigeons of these varieties were not recorded in the Americas until much later. Even if released in North America, the exaggerated physical traits of these breeds would make it unlikely they would survive and reproduce as other, less ornamented breeds might have. It can be reasonably assumed that the modern feral pigeons of North America are the descendants of these first European birds.

Rock pigeons, being introduced earlier than House Sparrows and having nearly the same range as introduced House Sparrows, could show similar levels of geographic variation in phenotypic traits. Feral Rock Pigeons in North America have been shown to be morphologically and genetically distinct from those in Europe. This is likely due to different source populations, rather than adaptive microevolution, as the “feral” European source population is likely a combination of domestic birds and true wild “Rock Pigeons” that the domestic birds may have bred with (Johnson, 1992). Different populations of feral Rock Pigeons from eastern North America have been shown to be genetically distinct (Carlen, 2020). This shows that at least at a genetic level, some geographic separation of populations has occurred, since the introduction of a possibly homogenous population. Despite the phenotypic variation expressed in both free-living wild pigeons and captive-bred individuals, no study so far has shown any distinct physical variation between populations of feral pigeons within North America.

The possibility for geographic variation in feral Rock Pigeons is evident in their ability to form subspecies in the wild and breed in captivity. This is further supported by the occurrence of phenotypic variation in species with similar patterns of introduction. There is already evidence of variation within Eurasian Rock Pigeon populations. The purpose of this study is to determine if similar variation is occurring within Eastern North America as well.

Methods

I captured feral pigeons from 19 different sites. Collection sites refer to places where at least one specimen used for this study originated. All applicable measurements (Figure 1) were taken on every captured or reviewed specimen. In both live and preserved specimens, some structures were not present (ie. cracked bills, missing primary feathers) values for measurements of these were simply left as ‘null’ for these specimens.

Table 1. The different measurements taken from the collected pigeons, and how they were done.

Measurement	Method	Description
Bill length	Electronic calipers (mm)	from the anteriormost point of nare opening to bill tip
Bill depth	Electronic calipers (mm)	from the ventral side of the lower mandible to the dorsal side of the upper mandible, taken at the deepest point
Head length	Electronic calipers (mm)	from the posterior-most point of the head to the tip of the bill
Tarsus length	Electronic calipers (mm)	from the joint of the tibiotarsus and tarsometatarsus to the hallux.
Grouse length	Electronic calipers (mm)	length of feathering from the joint of the tibiotarsus and tarsometatarsus to the phalanges
Wing chord	Wing ruler (mm)	from the carpal joint to the end of the primary feathers
Tail length	Wing ruler (mm)	from the beginning of under tail coverts to the tip of the longest present retrice
Overall body weight	Gram scale (g)	Highest recorded weight in the “weigh box”

Capture of Live Speciments

For individuals captured by researchers, four trapping methods were used: a commercial mechanical bow-net (Mikes Falconry, Gresham, Oregon, USA https://www.mikesfalconry.com), commercial Wire swinging-door cages (Tomahawk Livetrap, Hazelhurst, Wisconsin, USA https://www.livetrap.com/index.php?dispatch=pages.view&page_id=3), hand nets, and noose-carpets.

The bow net was staked down in a regular feeding and congregating area on the ground, then baited with the various foodstuffs (mostly commercial birdseed, but also bread crumbs and fried potato in some cases). A similar approach was taken with the wire swinging-door cages, but trails of bait were used instead of piles. Shade covers were applied to the traps when needed and water bowls were Provided. The noose carpet only captured one bird. In this case, the carpet was attached to a preferred perch, when the bird landed on the perch, its feet became tangled and could be easily removed. The hand net was only used in instances of heavy rain, when some birds were rendered flightless due to waterlogging of feathers. Any bird with poor flight abilities was captured on foot, measured, dried off, and released. On live birds, weight was measured by placing the captured bird in a 27x13x13.5 cm cardboard box with velcro on its opening flaps. The box was tared on a gram scale, the bird placed inside. Once live birds were captured, they were brought to a measurement site. This site was walking distance from the capture site, but obscured from the view of a bird at the capture site. Birds were transferred in a commercial dog carrier. The bottom of the carrier was covered in paper, which was changed for each group of pigeons captured. The carrier was also cleaned with vinegar every day after trapping was completed. After measurement, a V-shaped mark was cut into the bird's first pair of rectrices, so if recaptured, the bird could be identified and not re-measured. If a bird was captured missing the first pair of rectrices, it was released and not measured. All capture was approved by local agencies if applicable:

- Massachusetts Department of Conservation and Recreation no. R-149
- Maryland Department of Natural Resources permit no. 57400

Florida Fish and Wildlife Conservation Commission Permit no. EXOT-19-105

Deceased specimens

Frozen specimens were not weighed due to desiccation and added ice weight. If weight while living/recently deceased was noted on the label of a specimen, then it was recorded and treated as a measurement gathered by the researchers. Round skins, wet specimens, frozen specimens, and skeletons were utilized from the following institutions:

- *The Field Museum of Natural History (FMNH),*
- *The American Museum of Natural History (AMNH),*
- *The Academy of Natural Sciences in Philadelphia (ANSP),*
- *The National Museum of Natural History (Smithsonian) (NMNH),*
- *The North Carolina Museum of Natural Sciences (NCMNS),*
- *The Florida Museum of Natural History (FLMNH)*

Additional frozen specimens were utilized from Avian Haven, a wildlife rehabilitator in Freedom (near Augusta), Maine. No specimen older than 1970 or bearing yellow juvenile "fuzz" was used.

Statistical approach

With the exception of one site (Chicago, Illinois), I measured feral Rock Pigeon traits along a north-south transect from Augusta, Maine in the north to Key West, Florida in the south (Fig. 2). To test for differences in pigeon phenotypes across sampling sites, I regressed the phenotypic trait of interest on the latitude where the pigeon originated. Significant differences in traits across geography were revealed by trend lines with slopes that differed significantly from zero. I present regression plots for all traits examined and add lines to plots to illustrate statistically significant (or near significant) patterns in traits across sampling sites. To account for running a series of tests on multiple traits, many of which are related to one another, I corrected for the increased probability of detecting a significant relationship using false discovery rates, following Pike (2011).

Figure 2: Sites where measurements were taken, with locality names and number of specimens measured at the site.

Results

Overall, the bow-net was the most successful trap for capture. In total 199 live and preserved specimens were measured. Of physical traits measured, tail length, bill length, bill depth, and tarsus length showed no statistical differences between sampling sites (Table 2). By contrast, body mass, head length and wing chord were all significantly correlated with latitude, with larger traits (i.e. heavier body masses, longer head lengths and longer wing chords) observed in northern sites (Table 2). Grouse length tends to increase with latitude, however this result is close to, but not statistically significant ($p = 0.056$, Table 2).

Uncommon phenotypes. At the Key West collection site, I observed two rare phenotypes among feral birds: the "crested" (a short, curving crest behind the head) and "split eye" (black spots on the iris). These individuals were unbanded and, other than these mutations, appeared to be feral, making it unlikely that they are escaped, domestic individuals. I also observed a third possible mutation, known as "green eye", however, its validity is questionable due to other factors such as age that can cause a similar appearance. Several free-living domestic birds were also found, but only one was observed behaving in a manner that would suggest possible interbreeding with the true feral population (an apparent pair bond).

Domestic escapes. Several escaped domestic, color-banded individuals were encountered and their breeds identified. The breeds and numbers of each breed encountered were: three racing homers, one Canadian tippler, one utility Strasser, and one Birmingham roller.

Table 2. Summary of regression analyses for all feral Rock Pigeon traits measured. Bold font indicates traits that differed significantly or near significantly at the 0.05 threshold.

Trait	#Individuals measured	Slope	SE	T-value	P-value	Adjusted p-value
Grouse length (mm)	162	0.108	0.056	1.929	0.056	0.074
Mass (g)	135	2.004	0.611	3.28	0.001	0.002
Tail length (mm)	171	0.13	0.135	0.963	0.337	0.317
Bill length (mm)	195	-0.009	0.011	-0.815	0.416	0.317
Tarsus length (mm)	195	-0.018	0.023	-0.804	0.422	0.317
Wing chord (mm)	181	0.365	0.098	3.736	0.0003	0.0008
Head length (mm)	196	0.137	0.025	5.584	<0.0001	<0.0001
Bill depth (mm)	192	0.0002	0.006	0.036	0.971	0.637

Discussion

The phenotypic traits that varied significantly between feral Rock Pigeon populations include body mass, wing chord, and head length. Grouse lengths trended higher in more northern populations, but was statistically insignificant. While these differences could be due to genetic drift alone, this is unlikely the case. The short time in which these differences must have emerged is not consistent with typical patterns of genetic drift, as well as the large population sizes present (Masel, 2016). It is possible, however, that genetic drift could have occurred in the early days of colonization, when feral populations were presumably smaller than they are today. Sexual selection is also a possible driver for these differences, but this possibility has not yet been investigated, and there is limited knowledge of the sexual selection methods of pigeons in the case of non-behavioral phenotypes. Below, I detail possible explanations for the geographic patterns in phenotypes observed across localities.

Traits that scaled positively with latitude

Body mass, head size and wind chord are all positively correlated with latitude (Figure 3). This pattern is consistent with Bergmann's Rule, which states that within a species of endotherms, individuals from populations in warmer climates will be smaller, while those in colder climates will be larger (Ashton, 2002). Bergmann's Rule holds that larger-bodied animals can retain heat more efficiently, while smaller animals can radiate heat more effectively. This pattern is manifested in about 72% of bird species (Meriri, 2003), and is most common in non-migratory species like Rock Pigeons (Meiri, 2003). True wild Rock Pigeon subspecies follow this pattern, while body weight is extremely variable in domestic breeds (Johnston, 1992).

Another trait showing positive variation was grouse length, the length of leg feathers found on the pigeons (Figure 4). The function of leg feathers in modern birds is varied and includes thermoregulation (Johnson, 1968), sexual display (Schuchmann, 1979), locomotion (Hohn, 1977), and other unknown functions. In Columbiformes, tarsi that are at least partially feathered are represented in green (Treron), mountain (Gymnophaps), topknot (Lopholaimus), New Zealand (Hemiphaga), imperial (Ducula), blue (Alectroenas), fruit (Ptilinopus), brown (Phapitreron), and olive pigeons (Columba). The function of these feathers (often found on tropical, tree-dwelling species) is unknown (Levi, 1996). In pigeons, it seems that thermoregulation is a possible selection pressure favoring leg feathering, as Rock Pigeons are known to lose significant heat through

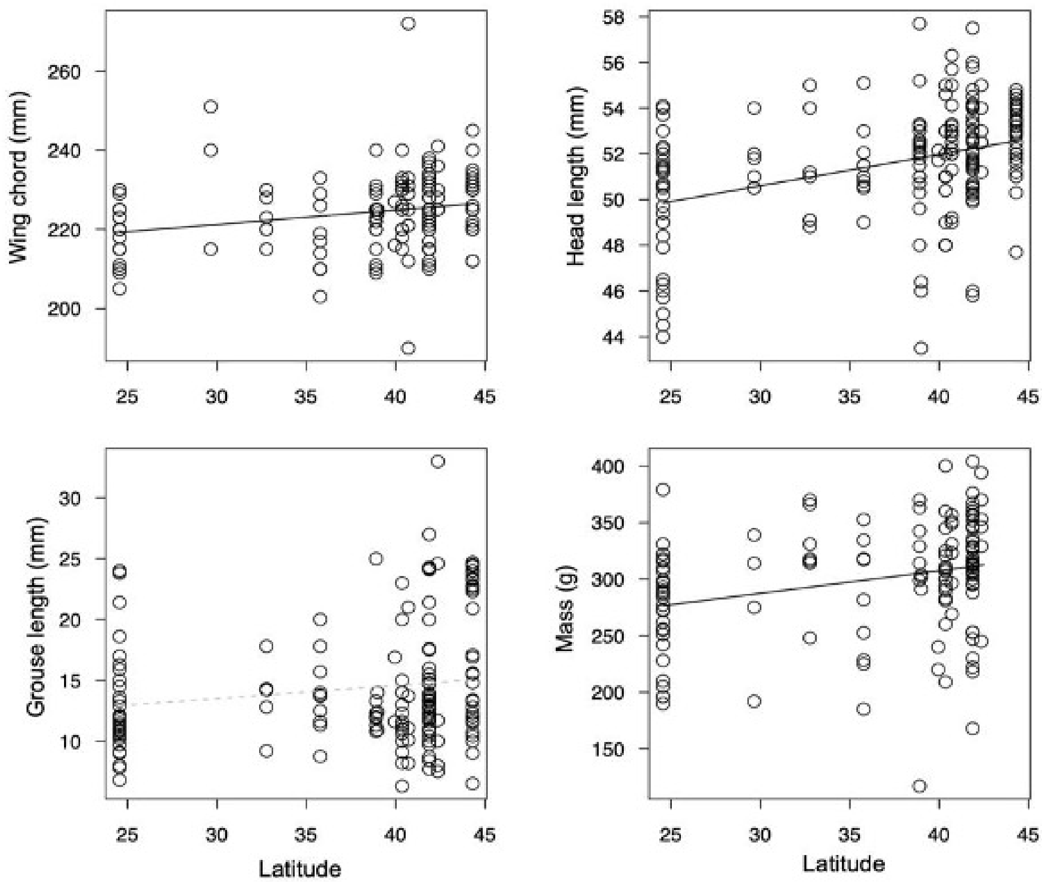

Figure 3. Regression plots of significant characters.

Figure 4. Variation in grouse length of feral pigeons

their legs (Martineau, 1988), suggesting that individuals in cold, northern climates might benefit by increased leg feathering.

Of the traits that showed no patterns with latitude (tail length, bill depth, bill length, and tarsus), some of these findings were surprising (Figure 5). For example, tarsus length and other linear traits often scale with body size and thus would have been expected to increase with heavier body mass at northern sites. Similarly, bill length might have been expected to increase in ways similar to head length. There are a number of explanations for why some traits but not others might vary with latitude. Traits that do not vary with latitude may not be important for coping with different environmental conditions, may be optimized for other functions (i.e., sexual display, which does not vary geographically), or may not have sufficient variation to respond to geographic variation in environmental conditions.

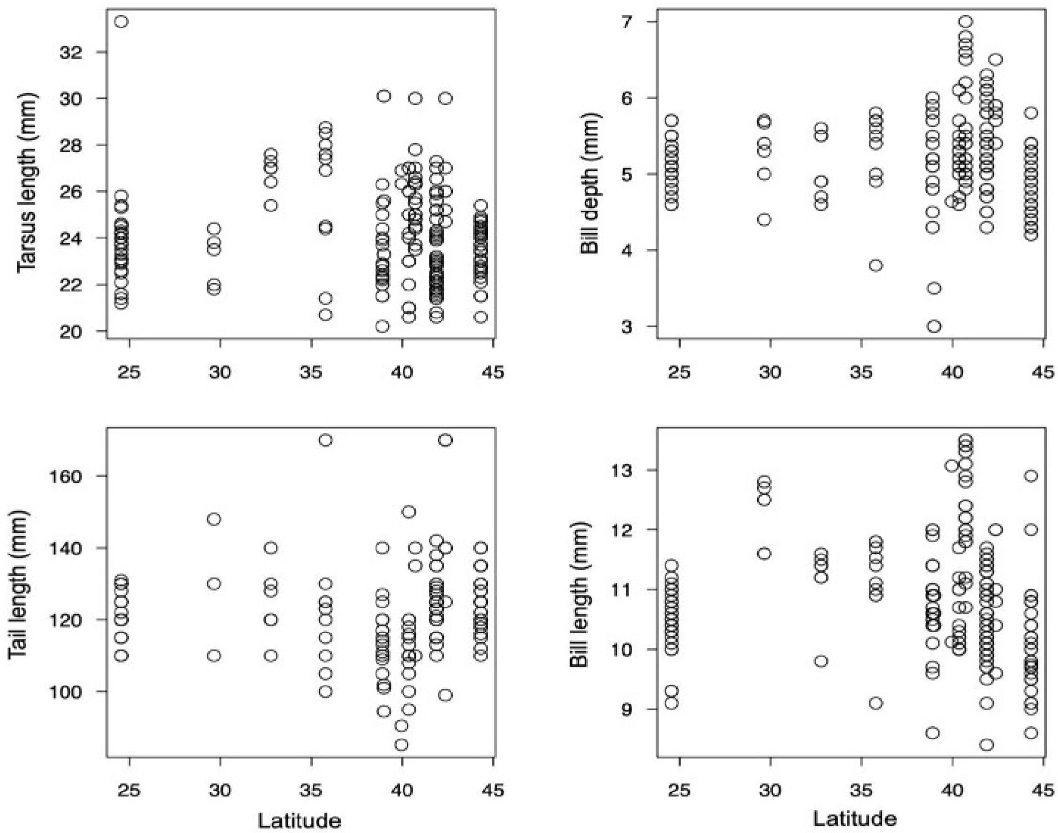

Figure 5. Regression plots of insignificant characters

Uncommon phenotypes

The two confirmed uncommon phenotypes "split eye" and "peak crest", were seen at the Key West trapping site (Figure 6). A third, unconfirmed phenotype "green eye" was also seen in Key West, but the validity of this trait as a mutation, rather than an unusually prominent but typical neotenic feature in a young pigeon, is uncertain. A heritable trait, "crest" is a common mutation seen in domestic pigeons caused by a point mutation of the EphB2 gene, where an arginine base is replaced by a cysteine base. This then causes feathers on the back of the head to grow in "backward" with tips pointing towards the bill rather than the tail producing a crest (Shapiro, 2013). Due to the sheer simplicity of the mutation needed to produce this phenotype, it is likely it could arise spontaneously within a population. Mutations of eye color are less well known. "Split eye" refers to the presence of patchy black in the iris, and is an uncommon but regular trait in many domestics. It has been postulated by pigeon keepers that split eye is a result of an improper migration of the typical colored pigment on the surface of the iris, exposing the dark lower layer. However, no studies have confirmed this, and nothing is known about the heritability of this trait (Muntaz, 2017). The "green eye" trait, defined as the presence of green in the iris, is rare among domestic birds. Only a handful of domestic breeds (such as the Syrian Tarbesh and Madrasi Highflier) have green eyes as a regular trait (Walker, 2011). In domestic racing pigeons, this mutation is very rare. In the United States, an otherwise undistinguished partially green-eyed bird was recorded as sold for 300 USD (CBS pigeon, 2020). Nearly nothing is known about the mechanisms of production or inheritance for this trait. The green-eyed individual captured for this study appeared to have this very rare trait; however, it was a hatch-year bird with its eye color not fully developed. While other hatch-year birds at the site lacked green eyes, the green seen on this bird might have been a juvenile trait that would fade with age.

Figure 6. Unusual phenotypes, left to right, crest, split eye and green eye.

Intrusion of domestic individuals

Of the domestic individuals found the Birmingham roller, identified by body shape and visible "rolling" aerial phenotype was the only domestic escape showing any potential breeding behaviors (such as allopreening and visiting potential nest sites). It is not known how long the Birmingham roller had been living feral or whether it has produced offspring. However, the bird appeared to be pair-bonded with a feral bird, suggesting the roller has been living among feral birds for at least three months (the minimum length of time for the formation of a pair-bond) (Wosegien, 1997). Another factor in determining the status of this bird was the condition of its toes. Part of one hallux was missing and one phalange was severely damaged, likely due to a condition called stringfoot, where a toe is tangled by hair or string and is then amputated due to a lack of circulation (Jiguet, 2019.) Birds in human care usually have objects tied around their feet removed, again pointing to this bird being outside of human care for some time. Other feral pigeons at this site also had apparent stringfoot injuries. Because no other pair-bonds were seen between feral and domestic birds, this does not appear to be a common phenomenon. Therefore, it is unlikely that the variation between populations of feral pigeons is heavily influenced by interbreeding with domestic pigeons.

Conclusion

Rock pigeons have been living in the US for about 400 years and, despite this relatively short time period, have a robust population and thrive throughout the continental US. This study revealed that introduced Rock Pigeons in the eastern United States show significant morphological variation between their populations. Pigeon traits change across latitude in ways consistent with Bergman's Rule, whereby populations in colder northern sites had traits indicative of larger individuals. The patterns in phenotypic variation I observed in feral pigeons are consistent with patterns observed in wild pigeons and in other species of birds. It is possible that the disparities in traits observed across pigeon populations will continue to widen, and further the Rock Pigeon's contemporary evolution.

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