A Discussion of Theories Relating to Population Dynamics of Passenger Pigeon Populations:

Abundance and Extinction

By: Samantha Cassista*

* Samantha Cassista is a 3rd Year Undergraduate Student studying Biological Anthropology and Global Health at the University of Toronto.

Abstract

The passenger pigeon was an extremely abundant species in the 16th-19th century that suffered a rapid extinction by the turn of the 20th century. Historical accounts place the population of the species at 3 to 5 billion by the 18th century, and extinct by the early 20th century. [The accepted reasons for this extinction include a drastic increase in the logging of deciduous forests, an improvements in firearms, and an increase in professional hunters aided by the mobility afforded them with the introduction of the railroad.] This paper addresses the debate within the academic community as to whether the passenger pigeon is an example of an outbreak species or if it was consistently abundant for at least the last thousand years. An outbreak species can be defined as a species that became abundant over a brief period of time. These species are characterized by wildly erratic population sizes before and after the "outbreak" accompanied by massive disturbance of surrounding ecosystems. [I used archaeological, ethnographic, and ecological evidence to debate both arguments. The results were not conclusive, but point towards passenger pigeons as an outbreak species that arose with the expansion of deciduous forests and the reduction of predators and competitors for food.

Introduction

Earth is currently experiencing a population explosion of *Homo sapiens* that exceeds natural carrying capacity. Economists, biologists, and politicians have noted this trend as a principal issue of the new century. Population explosions are not a new phenomenon. While there are comparatively few animal cases of the magnitude of the current human situation, the population of the passenger pigeon (*Ectopistes migratorius*) is an interesting case study in population dynamics. This paper will discuss varying hypotheses on the population structure of the passenger pigeon for prehistoric and historic times using archaeological, ethnographic, and current ecological evidence.

Passenger pigeon Background

The passenger pigeon was a very agile and swift bird. It was longer than the common pigeon today with a larger wingspan than birds of comparable size. This made it more aerodynamic overall, as well as more successful in evading predators (Schorger, 1955). It was a highly migratory species, which ranged from the deciduous forests in eastern and central Canada and the United States of America, occasionally

reaching north to British Columbia and northern Canada and south to Mexico and Cuba (Schorger, 1955). The passenger pigeon's feeding habits, numbers, and voracious appetite drove the need for such a large range. Its breeding habitat was focused in the temperate forests of eastern North America. They began laying their eggs between March and September; between laying the egg, incubation, and feeding the newly hatched squabs took approximately one month. Within a few days after hatching, the parents would "abandon" their helpless, undeveloped young to learn to fly and care for themselves. Neumann (1985) identifies this as the most vulnerable period in a passenger pigeon's life.

Passenger pigeons were very thin skinned and had short feathers. They had an extremely high metabolism, accounting for their reportedly large appetite. An adult passenger pigeon's daily mast consumption in the wild was between 118-237cm^3 or 30 acorns a day. Besides acorns, their diet consisted of small chestnuts, beechnuts, and all kinds of fruit, as well as insects and grains. Due to their flying skills and their breeding and nesting habits, the foraging pattern for a passenger pigeon would typically take it more than 80 km from the nesting site, as local food sources would become depleted. Adult birds would forage long distances [in this way] for themselves and their young, which would be fed a regurgitated milk curd (Schorger, 1955).

The most remarkable feature of the passenger pigeon was not its large range or appetite. It was the sheer abundance documented by historical witnesses overwhelmed by their massive flocks. These flocks could extend for days, and be a kilometer in width. Contemporary estimates place the population as 3 to 5 billion birds in the 18th century. By the mid to late 19th century, however, their numbers were noticeably depleted, and Schorger (1955) places extinction in the wild at 1900.

Aboriginal Background

Estimates on aboriginal human populations come from many sources, but primarily from a combination of oral tradition, written accounts at the time of contact, and archaeological evidence. Aboriginal populations were constrained by many natural variables, including limited access to food before the development of maize agriculture. Maize agriculture created a surplus of a food staple, and resulted in a population explosion in 1000 CE (Sadler and Savage, 2003). By 1450-1500, a major decline in the populations of the agricultural Mississippian culture that had occupied much of eastern North America for over 600 years occurred, particularly in the lower Mississippi valley and part of the Ohio River. The loss of Aboriginals is as high as 90% or more. Speculations for the cause of this drastic decrease include climate change (the "Little Ice Age" that lasted from 1400-1850), disease and war from interactions with European settlers (the "Great Dying"), or both (Neumann, 1985). Stephan Williams asserts that the growth of passenger pigeon bones in the archaeological record coincides with the decrease in aboriginal populations in the pigeon's nesting range. It is also hypothesized that the documented climate change of the "Little Ice Age" was responsible for a rapid transformation of abandoned agricultural land into the hardwood forests inhabited by passenger pigeons (Blockstein, 2003).

Objective

The objective of this paper is to discuss multiple theories relating to the population size of passenger pigeons before and after European contact. This context is crucial for both arguments because the introduction of European explorers and settlers irreparably changed the lives of aboriginals as well as the land. It is also through the writings of the contemporary Europeans that passenger pigeon population sizes can be estimated. The first theory states that passenger pigeons were roughly as abundant in both before and after the arrival of Europeans. The second theory states that passenger pigeons were an outbreak species that thrived due to a changed ecology of the land. Specifically it is theorized that the depletion of aboriginal populations, which were both the passenger pigeon's main predators and competitors for tree mast, led to unstable population growth of the passenger pigeons. This paper is a meant to amass, analyze and attempt to resolve the debate of passenger pigeon population size discussed by researchers over the last 30 years.

Methods

Archaeological

Fossil records are very incomplete in regards to the small, fragile bones of passenger pigeons. However frail they may be, fossil records do extend back 100,000 years. Sadler and Savage (2003) report many sites from 500 B.C.E. – 1200 C.E. with passenger pigeon bones among other fossils. "It is notable that elements from this species [passenger pigeons] increased dramatically…from almost nil in 1540 A.D. to a peak about the mid-17th century" (Sadler and Savage, 2003:10). This poor representation in the archaeological record could be due to the frailty of the bones, although, less robust bones of frogs and other small birds are more commonly found than those of passenger pigeons. The poor representation could also be due to the greater ease of catching and butchering squabs, which were essentially fat passenger pigeon juveniles with little bone development, and therefore would be less common in the archaeological record. Another contributing factor is that passenger pigeon bones are found farther west of their marked migratory range (Sadler and Savage, 2003). This could indicate that their populations expanded when the cold climate allowed for larger stretches of deciduous forest. If so, then a large assortment of passenger pigeon bones might remain undiscovered, although they are most common in archaeological sites located within their historical breeding range.

Ethnographic

All ethnographic research comes from the historic time period; a time that scholars agree was marked by an abundance of passenger pigeons. Through an analysis of ethnographic material presented by Schorger (1955), Neumann (1985), and Blockstein (2002), it is clear that passenger pigeons were an inconsistent presence in settlers' lives, though dramatically devouring agriculture when they came. The earliest account is that of Jacques Cartier on July 1, 1534, and these "wood pigeons" as he called them were already abundant. Following Cartier, Alphonse of Xanctoigne reported an abundance of many types of birds, in which "turtle doves" appeared in 1542 (Schorger, 1955). As expected, no explorers or settlers remarked on seeing very few birds until the

end of the 19th century when it was an unexplained anomaly, and hindsight shows us this was the time the birds were heading towards extinction. This means that the ethnographic evidence is somewhat unrepresentative of the presence of these birds as either a constant or intermittent occurrence. Observations merely give us a rough framework for passenger pigeon population size after 1534. We can use this evidence to compare the reports over different centuries. Unfortunately, there is a limit to the usefulness of these reports, due to an absence of comparable accounts from before European exploration and settlement.

An alternative to written testimonies is the less appreciated practice of oral tradition carried through Native populations into historical and present time periods. It is unclear just how important the passenger pigeon's role was to aboriginal populations over the past five hundred plus years. However, there are some accounts of Aboriginal traditions regarding passenger pigeons. Sadler and Savage (2003) report that "While these birds are hatching their young, or while the latter are not yet able to fly, the savages or Indians in North America are in the habit of never shooting or killing them, nor allowing others to do so, pretending that it would be a pity on there young, which would in that case have to starve to death," (p. 3). They also note that the Huron "believed pigeons were human souls flown free from a cemetery after the great Feast of the Dead" (Sadler and Savage, 2003:3). Ethnographers and archaeologists generally feel that a natural entity has to be important to a group of people if they are to attribute religious interpretations or symbolism to it, and while these examples came from the 18th century, it is arguable that passenger pigeons had always played a major role in the native cultures. On the other hand, it can also be argued that the passenger pigeon population explosion made the birds more noteworthy, causing the aboriginals or the settlers to write about them and thereby incidentally expand their perceived relevance in the records.

Ecological Research

Current scientific research can be related in a theoretical application to the passenger pigeons' population as well as to the birds' rapid extinction. Their extinction is an important focus in a discussion on population. The extinction of the passenger pigeon can be an honest portrayal of the unsteady nature of this species' population size including the contestable rate at which it grew, or it can be used to show how human interaction can affect such a prolific species.

Multiple criteria were analyzed to determine the potential requirements for an outbreak species to thrive, as well as research on the importance of genetic fraternity with other species for adaptability. Modern methods, such as the measurement of tree rings and the analysis of pollen from sediment, were also considered. These tools can describe forest composition more accurately than most ethnographic literature on the subject. One final premise that can be applied to the study of the population history of passenger pigeons is the theory known as the "Allee Effect". The Allee Effect impacts gregarious species such as the passenger pigeon, and is a positive feedback loop that can lead to extinction. In essence, social species that depend on high population numbers have a certain critical point below which their numbers cannot drop without it affecting their long-term success. After that point, it becomes harder to defend against predators, find mates, protect their young, etc

(Halliday, 1980). It is plausible that passenger pigeons were indeed such a species that could be impacted by the Allee Effect. Large social numbers were necessary for breeding, protection of nesting sites, and for travel, so reduced numbers made survival highly tenuous.

Results and Discussion

Archaeology

The archaeological data is insightful, albeit inconclusive. The paucity of faunal evidence for passenger pigeons before 1540 could easily be explained by the fragility of the birds, and the ease both aboriginals and settlers had with catching squabs rather than adults. These young pigeons leave very little archaeological proof of their existence, as they do not have gizzard stones or fully formed and fused bones. However, passenger pigeons are far more numerous, even in recent archaeological work, in sites after 1540 and in their historical breeding range (Sadler and Savage, 2003; Neumann, 1985, Blockstein, 2003). None of this distinctly provides evidence for either the argument that passenger pigeons were always abundant or the argument that they are an example of an outbreak species. The deposits in which passenger pigeon bones can be found are surprisingly scarce of resources for maintaining fossils. Sadler and Savage (2003: 19) state that the acidic soil in Ontario negatively impacts preservation of bones. This faster rate of decomposition could be a reason why passenger pigeon bones are found less often in pre-contact archaeological sites.

Some other interesting archaeological evidence was brought to light. First of all, the range of passenger pigeons was very likely larger before contact, which could explain why fewer bones are found (Sadler and Savage, 2003). A larger range, with an increasing expanse of deciduous forest, would certainly mean that there was an abundance of mast.

Archaeological evidence can also be useful in discussing the likelihood of passenger pigeons being important to prehistoric human populations. Sadler and Savage (2003) state that many intertwined elements led to the significance and therefore the representation of birds on prehistoric sites. "Perhaps the most distinctive aspect of the archaeological bone samples is that they do not represent a cross section of the species available but that the sample is selective. It was deposited due to human activity and reflects the requirements of the site's inhabitants" (Sadler and Savage, 2003:19). On the whole, an important quality reflected in the fauna is the quality of meat gathered at the expense of effort and materials. Although passenger pigeon adults ate avidly, they were constantly flying, and therefore had little fat on their bodies. They are termed "light meat", by Sadler and Savage (2003). Neumann (1985) felt that the expenditure of energy was not worth the meat gathered by hunting adults. This ignores the ease with which settlers and aboriginals hunted squabs. Neumann (1985) feels that hunting passenger pigeons was only efficient with the development of guns, but both Aboriginals and settlers had success trapping squabs by setting fires to the underbrush below their nests after the adults went out to forage or to migrate. The frightened squabs would teeter to the edge of their nests, and within minutes, there would be a veritable feast ready for the hunters. However, it is clear that the technology of guns

and ammunition were a decisive blow to adult populations in the 18th and 19th centuries.

Sadler and Savage (2003) also note that spirituality and religion were tied in with animal and bird use. From archaeological evidence gathered, it does not appear that passenger pigeons played a particularly large part of any culture. However, as cited above, the Huron had religious attachment to passenger pigeons. It is clear some cultures valued passenger pigeons - for example, the species is cited by Engelbrecht (2003:14) as "a major resource for the Iroquois".

Ethnography

The ethnographic accounts do not give categorical evidence for either argument. Accounts show that passenger pigeons population rates were fluctuating. This could be a side effect of a rapidly growing outbreak species giving way to oscillations under the strain of resource depletion or habitat/breeding range being at capacity (Neumann, 1985). Conversely, it could be a sign that this highly migratory bird had many routes and ranges, so as to maximize the availability of their resources. The ethnographic evidence does show interesting human-wildlife interactions. Aboriginals could likely have impacted passenger pigeon carrying capacity by other, less direct, methods than hunting. For instance, humans, as well as a select few species, gathered the products of masting trees – trees that erupt seeds annually. Deer, raccoons, turkeys, gray squirrels and fox squirrels are mast – or tree nut predators. The human population increased passenger pigeons' proportion by hunting these groups of animals in both the prehistoric and the historic past, thereby reducing some of the passenger pigeon's most avid competitors for [mast]. "Thus, between 68-74% of the terrestrial fauna remains from prehistoric sites in the eastern United States are remains of those five species," (Neumann, 1985:402). As Native populations disappeared, settler populations continued the practice of hunting these species, especially deer, raccoons, and turkeys. However, these settlers used firearms, and could successfully kill more of the passenger pigeons' competition. The settlers also continued and expanded agriculture, which gave passenger pigeons more dietary options on their travels if the forest's mast was depleted. While this minor growth in agriculture would not have hurt passenger pigeons much, because they were highly mobile and generalist eaters, it easily could have impacted the success of other [mast eating] populations who were less mobile and larger, and therefore needed more sustenance than agricultural fields could provide.

Ecological Research

Scientific research continues, and perhaps the future will shed more light on the stories of extinct species like the passenger pigeon. Some new theories relating to the extinction have been debated, though several have been ignored. For instance, causes for how passenger pigeons' numbers could have swelled so rapidly have never been firmly stated or scientifically critiqued. Mark Peck (2008), a scientist in the ornithology department of the Royal Ontario Museum, stated that there had to be some climate change or resource abundance change to allow passenger pigeon populations to grow exponentially between approximately 1400 and 1600. As discussed above, there was indeed a climate change known as the Little Ice Age that lasted from 1400 to 1850. This led to an expansion of pine forests, and is a potential cause for the migration southwards of the depleted populations of Aboriginals. Passenger pigeons also have a

high metabolism and Schorger (1955) reports that they could withstand cold wind and temperatures, as long as snow did not accumulate and hide their greatest nutritional resource, deciduous tree forest mast.

Dr. Peck also says that passenger pigeons were a highly specialized bird. In eating habits, they were generalists, but their large flock sizes and nesting strategies are evolved traits that made them unique. This ties in with Austin Hughes' (2004) statistical research on monotypic vs. polytypic bird extinction. Hughes (2004) states that birds with a single species in their genus (monotypic) have a higher extinction rate from human interaction as compared to those with more filial species kin groups (polytypic). Some other species of birds that fall into this category are the Great Auk, Ivy Billed Woodpecker, and many flightless birds. These species diverge away from and out-compete closely related species (Pers. comm. 2008). Though Hughes did not give any real analysis as to why this is the case, it can be hypothesized that this successful strategy does not offer a species any real adaptability if the environment changes. They have no closely related kin to interbreed with and create diverse phenotypes that could thrive in a new situation. These monotypic genera are limited because they are less able to adapt quickly.

Forest composition is also a key factor in the discussion of passenger pigeon extinction. Ellsworth and McComb (2003) used pollen analysis to reconstruct the eastern hardwood forests in conjunction with passenger pigeon population size as well as the physical effects of the large numbers of this species on the forest. The nesting sites of passenger pigeons are a particularly poignant example of the destructive force of this species on the environment. Passenger pigeons bred in large colonies that tended to be long and narrow. Schorger (1955) stated that the average nesting sites were 16 km long and 5 km wide, but reports cite nesting sites reaching 64 km and even 160 km in length. This intensive population pressure caused damage to the temperate forests in the breeding range. The forest canopy was opened by limb destruction. This affected the forests, allowing small shrubs and plants to grow, as well as increasing the potential for fire. More importantly, the passenger pigeons' extremely high levels of excrement disturbed the chemical composition of the forest soil. An ecosystem inundated with bird guano can create "a decreasing ratio of carbon to nitrogen through the influx of nitrates…and can also detrimentally affect vegetation through a change in osmotic balance due to salt accumulation" (Ellsworth and McComb, 2003:1553).

"Researchers recognize the impact of passenger pigeons' roosting and nesting on forests at a local level [limb breakage and soil composition]…but there has been little discussion of the potential of their impact on broader forest landscapes in eastern North America" (Ellsworth and McComb, 2003:1549). At the height of their population expansion, passenger pigeons were a destructive force on the ecosystem. Their heavy predation on acorns of Red Oak during the spring breeding season of the passenger pigeon may explain the dominance of White Oak, which masts in the fall after the pigeons have left. There has subsequently been an increase and expansion of Red Oak, which is likely a result of the passenger pigeon's extinction. In this one example, passenger pigeons may have played a pivotal role in their ecosystem (Ellsworth and McComb, 2003). This opposes the idea that passenger pigeons were always as abundant as they were in the 18th and 19th century because constant population levels would manifest themselves as a more consistent forest composition.

Conclusion

Archaeological evidence is inconclusive. It is widely understood in the discipline of archaeology that very few irrefutable statements can be made. Currently the archaeological record would indicate that passenger pigeons became more abundant after 1500. Some large discoveries of passenger pigeon bones have been found that predate the 16th century. However, there is some confusion in the record, including why passenger pigeon bones were found outside of their historical range (Neumann, 1985: 391-392), demonstrating that there is still more to learn about passenger pigeons from archaeology. The ethnographic evidence is less helpful, being highly subjective and open to interpretation for either theory. Current ecological evidence can provide useful, although primarily hypothetical, insights. For example, current populations of certain species of birds, such as the Double Breasted Cormorants and Snow Geese, have been growing exponentially within the last twenty years. With evidence that bird populations can change visibly within comparably short time frames, it is possible that those historical authors who were writing about abundant "doves" and "fowl" could have been early witnesses to a population explosion, even as early as the 1540s. In conclusion, I can only add to the hypothesis already circulating on the passenger pigeon. The majority of researchers on this topic feel that passenger pigeons were only impacted by human overkill. The evidence, while inconclusive, demonstrates that passenger pigeons could be an early example of an opportunistic outbreak species that thrived and plummeted within a span of 400 years. Certainly, some of the archaeological evidence as well as scientific theories of today supports this contention.

Acknowledgments

I thank Professor Jock McAndrews for his assistance in helping research archaeological remains of passenger pigeons as well as his unwavering guidance and input at each step of the way. I also thank Mr. Mark Peck for his professional opinion on the subject and generosity with his time.

References Cited

Blockstein, D. E. 2003. Passenger Pigeon. In: *Encyclopedia of World Environmental History.* Pages 6-8. Routledge, London.

Ellsworth, J.W. and B.C. McComb. 2003. Potential Effects of Passenger Pigeon Flocks on the Structure and Composition of Presettlement Forests of Eastern North America. Conservation Biology 17(6):1548-1558.

Engelbrecht, W. 2003. Iroquoia: The Developments of a Native World. Syracuse University Press, Syracuse, NY.

Halliday, T.R. 1980. The Extinction of the Passenger Pigeon *Ectopistes migratorius* and its relevance to contemporary conservation. Biological Conservation 17:157-162

Hughes, A. L. 2004. A Statistical Analysis of Factors Associated with Historical Extinction and Current Endangerment of Non-passerine Birds. The Wilson Bulletin 116(4):330-336.

Neumann, T.W. 1985. Human-wildlife competition and the passenger pigeon: Population growth from system destabilization. Human Ecology 13(4): 389-410

Peck, M. March 28, 2008. Phone Interview.

Sadler, D. C. and H. G. Savage. 2003. Birds from the Ground: The Record of Archaeology in Ontario. Department of Anthropology, Trent University, ON.

Schorger, A. W. 1955. The Passenger Pigeon. University of Wisconsin Press, Madison WI.

Undergraduate Journal of Anthropology, Volume 1, 2009. pp. 141-149.
http://jps.library.utoronto.ca/index.php/uja/index