Open Access and Extinction of the Passenger Pigeon in North America

by

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Abstract

An open access model is formulated where X is a renewable resource and E is the level of effort devoted to harvest. Net growth is assumed to exhibit critical depensation and the open access system is described by two nonlinear differential equations $\dot{X} = rX(X/K_1 - 1)(1 - X/K_2) - qXE$ and $\dot{E} = \alpha[(p - s)qXE - cE]$, where $r > 0$ is the intrinsic growth rate, K_1 is the minimum viable population level, K_2 is the environmental carrying capacity $(K_2 > K_1 > 0)$, $q > 0$ is the catchability coefficient, $\alpha > 0$ is an adjustment coefficient, $(p - s) > 0$ is the market price net of shipping cost, and $c > 0$ is the unit cost of effort at the harvest site. It is shown that the $\dot{E} = 0$ isocline is a vertical line at $X_\infty = c/[(p - s)q]$ and that the open access system passes through a supercritical Hopf bifurcation as X_∞ moves from a level above $(K_1 + K_2)/2$ to a level below $(K_1 + K_2)/2$. For X_∞ above $(K_1 + K_2)/2$ the open access equilibrium is locally stable. For X_∞ below $(K_1 + K_2)/2$ the open access equilibrium will be locally unstable. At $X_\infty = (K_1 + K_2)/2$ the system has a stable limit cycle. This analysis is useful in interpreting the economic history of the passenger pigeon. The limited empirical evidence would suggest that $X_\infty = c/[(p - s)q]$ declined below $(K_1 + K_2)/2$ during the last half of the 19^{th} century as a result of improved rail transport and communications (the telegraph). It is thought that the passenger pigeon was extinct in the wild by 1901. The last passenger pigeon died in captivity at the Cincinnati Zoological Gardens on September 1^{st}, 1914.

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I. Introduction

> In the autumn of 1813, I left my house at Henderson, on the banks of the Ohio, on my way to Louisville. In passing over the Barrens a few miles beyond Hardensburgh, I observed the pigeons flying from northeast to southwest, in greater numbers than I thought I had ever seen them before, and feeling an inclination to count the flocks that might pass within the reach of my eye in one hour, I dismounted, seated myself on an eminence and began to mark with my pencil, making a dot for every flock that passed. In a short time, finding the task which I had undertaken impracticable, as the birds poured in in countless multitudes, I rose, and counting the dots then put down, found that one hundred and sixty-three had been made in twenty-one minutes. I traveled on, and still met more the further I proceeded. The air was literally filled with pigeons; the light of noonday was obscured as by an eclipse; the dung fell in spots, not unlike melting flakes of snow; and the continued buzz of wings had a tendency to lull my senses to repose.
>
> John James Audubon, *Ornithological Biography*, I (1833)

Audubon subsequently estimated the size of this flock to exceed one billion birds. Schorger (1955, p.204) places the population of passenger pigeons, at the time of European discovery of North America, at between three and five billion birds. By migrating and nesting in such huge flocks, the passenger pigeon may have reduced the effectiveness of natural predators (various raptors, but especially the peregrine falcon) as well as the mortality of juveniles (a single chick might be fed by several nesting adults). After European colonization, the aggregation of passenger pigeons into large flocks would make them conspicuous and vulnerable to rent-seeking *homo economicus*. In less than 90 years after Audubon's journey from Henderson to Louisville, Kentucky, the passenger pigeon would be extinct in the wild.

This paper has two objectives. The first is to develop an open access model which includes extinction as a possible dynamic outcome. The traditional, continuous-time model of pure open access, based on logistic net growth, does not allow for extinction. See Clark (1990, pp. 189-190). A model where net growth exhibits critical depensation is formulated and a sufficient condition for the local *instability* of the open-access equilibrium is identified. The Bendixson – Du Lac Criterion can be used to rule out limit cycles above and below a critical value at $X = (K_1 + K_2)/2$. The relationship of the open access equilibrium stock, $X_\infty = c/[(p-s)q]$ to the critical value $X = (K_1 + K_2)/2$ determines the dynamic behavior of the system. Numerical analysis shows that the system undergoes a supercritical Hopf bifurcation as X_∞ passes from above $X = (K_1 + K_2)/2$ to a level below $X = (K_1 + K_2)/2$.

The second objective is to survey the literature describing the economic history of the passenger pigeon to determine if the condition for local instability was likely to have been met. Extension of the railroad system in the early 1850s allowed passenger pigeons, taken from nesting sites in the mid-west, to be expressed shipped to Boston, New York, and Philadelphia, where they were sold at market and often served as entrees in fine restaurants. The telegraph allowed "pigeoners" to learn about the location of large flocks. These cost-reducing, market-expanding innovations, in combination with the biology of the passenger pigeon and the open access nature of the industry, led to unprecedented harvests between 1850 and 1885, and extinction, in the wild, by 1901.

The remainder of this paper is organized as follows. In the next section the literature on open access is reviewed and a model incorporating critical depensation is analyzed. A sufficient condition for the local instability of the open access equilibrium is identified and the Bendixson Du – Lac Criterion is used to rule out limit cycles in two regions of the phase plane. For $X_\infty = c/[(p-s)q] > (K_1 + K_2)/2$ the open access equilibrium will be locally stable. For $X_\infty = c/[(p-s)q] < (K_1 + K_2)/2$ the open access equilibrium is locally unstable and the resource is harvested to extinction. Numerical analysis reveals a stable (but empirically unlikely) limit cycle when $X_\infty = c/[(p-s)q] = (K_1 + K_2)/2$.

Section III discusses the biology and economics of the passenger pigeon. Attention is focused on the value of parameters that affect local stability of the open access equilibrium. The paper concludes in Section IV.

II. Open Access

Open access might be defined as a situation where a common property resource is harvested by competitive, rent-seeking individuals, with no regulation on entry, exit, or the level of harvest.[1] The first static economic analysis of open access, in the context of a common-property fishery, was the classic article by Gordon (1954). Smith (1969) provided a general analysis of open access dynamics using two, non-linear, differential equations, again within the context of a common-property fishery. The first empirical study may have been Wilen (1976) who estimated two first-order difference equations from data on the commercial harvest of the North Pacific fur seal. A phase-plane plot of the seal population and the number of sealing vessels from 1882 to 1900 revealed the start of a convergent spiral to a stable, non-extinction equilibrium. Bjørndal and Conrad (1987) estimate a similar model for the North Sea herring fishery which was closed to fishing in 1977 when the stock was believed to have fallen to about seven percent of its historical maximum. More recently, Brander and Taylor (1998) use an open access model to speculate on the evolution of the human population and the resource base on Easter Island.

The traditional specification of the open access model employs a logistic net growth function and might be written as

$$\begin{aligned} \dot{X} &= rX(1 - X/K) - qXE \\ \dot{E} &= \alpha[pqXE - cE] \end{aligned} \tag{1}$$

where X is the resource stock and E is the level of effort (an aggregate measure of labor and capital) devoted to harvesting the resource. The first term on the right-hand-side (RHS) of the differential equation describing the change in the resource stock is the logistic net growth function, $F(X) = rX(1 - X/K)$, where $r > 0$ is the intrinsic growth rate and $K > 0$ is the environmental carrying capacity. The second term in this differential equation is the level of harvest, $Y = qXE$, where $q > 0$ is called the catchability coefficient. This term can be regarded as a special case of the Cobb-Douglas production function with unitary output elasticities for the resource stock and effort. If net growth is positive and greater than harvest, the stock increases ($\dot{X} > 0$). If harvest is greater than net growth the stock decreases ($\dot{X} < 0$).

The second equation in Specification (1) assumes that effort responds to the sign and size of net revenue. On the RHS of the second differential equation, $p > 0$ is assumed to be the constant unit price for the harvested resource so that $pqXE$ is the revenue from harvest at instant t. The cost of harvest is assumed to be linear in effort, where $c > 0$ is the unit cost of effort. Thus, $[pqXE - cE]$ is instantaneous net revenue, or what Gordon (1954) referred to as "rent." The parameter $\alpha > 0$ is an adjustment parameter reflecting the responsiveness of effort to positive or negative net revenue. If net revenue is positive, effort expands $(\dot{E}>0)$. If net revenue is negative, effort contracts $(\dot{E}<0)$.

This system has two isoclines (nullclines). Along the negatively sloping line $E=(r/q)(1-X/K)$, $\dot{X}=0$. Along the vertical line $X_\infty=c/(pq)$, $\dot{E}=0$. If $K > c/(pq) > 0$, there will be a unique, locally stable, open-access equilibrium at (X_∞,E_∞), where $E_\infty = r(pqK - c)/(pq^2K) > 0$. See Figure 1. Clark (1990, p.190) shows that the eigenvalues of the linearized system are given by

$$\lambda_i = -\frac{rX_\infty}{2K} \pm \sqrt{\frac{r^2X_\infty^2}{4K^2} - \alpha pq^2 X_\infty E_\infty}, \quad i = 1,2 \tag{2}$$

The first term on the RHS of (2) is negative and, depending on the sign of the discriminant, (X_∞,E_∞) will be a locally stable node or the focus of a stable spiral (a sink). Clark then uses the Bendixson Du – Lac Criterion to rule out limit cycles. Thus, for $K > c/pq > 0$, Specification (1) does not admit open-access extinction and would not be an appropriate specification for modeling the dynamics of the passenger pigeon.[2]

Consider now a specification where net growth exhibits critical depensation, as described in Clark (1990, pp. 20-21). The net growth function is a cubic and may be written as $F(X) = rX(X/K_1 - 1)(1 - X/K_2)$, where $r > 0$ is the intrinsic growth rate when X is slightly greater than K_1. This function has roots (zeros) at $X = 0$, $X = K_1$, and $X = K_2$, where K_1 is referred to as the minimum viable population level and K_2 is the environmental carrying capacity ($K_2 > K_1 > 0$). See Figure 2.

The differential equation for effort is modified so that (p - s) is market price, p, net of transport cost, s, from the harvest site. The open access system becomes

$$\begin{aligned} \dot{X} &= rX(X/K_1 - 1)(1 - X/K_2) - qXE \\ \dot{E} &= \alpha[(p - s)qXE - cE] \end{aligned} \tag{3}$$

Analysis of Specification (3) proceeds as follows. Along the curve $E = (r/q)(X/K_1 - 1)(1 - X/K_2)$, $\dot{X} = 0$. Along the vertical line $X_\infty = c/[(p - s)q]$, $\dot{E} = 0$. The $\dot{X} = 0$ isocline has two roots at $X = K_1$ and $X = K_2$. The maximum of the $\dot{X} = 0$ isocline occurs at $X = (K_1 + K_2)/2$. This turns out to be a critical value *vis-à-vis* the $\dot{E} = 0$ isocline where $X_\infty = c/[(p - s)q]$. If $c/[(p - s)q] < (K_1 + K_2)/2$, the open access equilibrium will be locally unstable. If $c/[(p - s)q] > (K_1 + K_2)/2$ the open access equilibrium will be locally stable. As $X_\infty = c/[(p - s)q]$ moves from a level above $(K_1 + K_2)/2$ to a level below $(K_1 + K_2)/2$ the open access system goes through a supercritical Hopf bifurcation. In the event that $X_\infty = c/[(p - s)q] = (K_1 + K_2)/2$ there is a stable limit cycle where the system, [X(t),E(t)], evolves in counter-clockwise motion along a closed orbit. The resource and the industry go through a perpetual "boom-bust" cycle, but the resource is never driven to extinction. A sufficient condition for the local *instability* of (X_∞, E_∞) is

$$c/[(p-s)q] < (K_1 + K_2)/2 \tag{4}$$

This condition is formally derived in the Appendix. Also in the Appendix, the Bendixson – Du Lac Criterion is used to show that a limit cycle will not exist if X is confined to the region $0 \le X < (K_1 + K_2)/2$ or if it is confined to the region $K_2 \ge X > (K_1 + K_2)/2$. A phase plane diagram for this system is drawn in Figure 3. Figure 4 shows numerical simulations of the system for three cases. In all three cases $r=0.2$, $K_1=0.1$, $K_2=1$, (so $(K_1 + K_2)/2 = 0.55$) $q=1$, $p=2$, $s=1$, $\alpha=0.5$, $X(0)=0.95$, and $E(0)=0.1$. In Figure 4a, $c=0.6$ so that $X_\infty = 0.6 > (K_1 + K_2)/2 = 0.55$ and the open access equilibrium is the focus of a stable spiral. In Figure 4b, $c=0.55$ so that $X_\infty = 0.55 = (K_1 + K_2)/2$ and the open access equilibrium is the focus of a stable limit cycle. In Figure 4c, $c=0.5$ so that $X_\infty = 0.5 < (K_1 + K_2)/2 = 0.55$ and the resource is driven to extinction.

We now turn to the economic history of the passenger pigeon to see how $X_\infty = c/[(p-s)q]$ might have changed during the last half of the 19^{th} century.

III. The Biology and Economics of the Passenger Pigeon

The passenger pigeon (*Ectopistes migratorius*), with its small head and neck, powerful wings, and long tail feathers, was built for speed. Based on "date and time" observations of the same flock at two different locations, it was estimated that the passenger pigeon could reach a sustained speed of 60 miles per hour during its spring and fall migrations. The male of the species reached a length of 16.5 inches. The blue or bluish gray feathers on its back and wings provided an "elegant" contrast to the reddish-brown breast feathers, which faded to a white lower belly. The female of the species was an inch shorter in length and less vivid in color.

In pre-colonial North America, the passenger pigeon ranged from the eastern seaboard to the plains west of the Mississippi river. Pigeons would over-winter as far south as the Gulf of Mexico and their northward migration in spring would take them into present-day Manitoba, Ontario, Quebec, and the Canadian Maritimes. The spring migration would begin in late February or early March depending on weather and snow cover. The pigeons principal sources of food were the beechnuts and acorns found in the vast hardwood forests which still covered much of New York, Pennsylvania, Ohio, Indiana, Michigan and Wisconsin in the early 19th century.

Archaeological excavations at Native American encampments indicate that the passenger pigeon was an important seasonal food source. European colonists also harvested the passenger pigeon, especially at the nesting sites where millions of birds would congregate to build stick, platform-like, nests. Several nesting sites in New York State in the early- and mid-19th century were estimated to have been 30 miles long and three to six miles wide. The nests were often packed so close together that as the young pigeons (called squabs) grew, their combined weight would cause large branches to break, hurtling thousands of squabs to the forest floor.

It was at the nest sites that both adults and squabs were especially susceptible to predation. The adults would take turns tending the nest, with the male foraging for food and water in the morning, then returning to the nest to allow the female to forage from late morning into the early afternoon. The beechnuts and acorns ingested by the adults were transformed into a high-protein, high-fat "milk" or curd and later regurgitated to feed the fast-growing squabs. Well-fed squabs would weigh more than adults and were often the favored food of both Native Americans and colonists.[3]

Squabs were easily harvested by simply knocking the nests apart with a pole or branch. Adults were shot or netted. Mortality of nesting adults was likely to induce mortality in squabs. The clearing of beech and oak forests undoubtedly reduced the principal natural food sources of the passenger pigeon, but it was probably the practice of indiscriminant harvesting of squabs that lead to the rapid decline in the abundance of the passenger pigeon in the mid- and late- 19th century.

During this period two significant developments took place in transportation and communication. First, railroad tracks were extended into the mid-west allowing pigeons and squabs taken in Ohio, Indiana, Michigan, and Wisconsin to be packed in ice and shipped to New York, Boston, and Philadelphia in less than a week. (Pigeons and squabs were sold wholesale to restaurants and retail to individuals.) Second, the telegraph allowed "pigeoners" and buyers to communicate about the location of nesting sites and the market prices they might expect to receive on the east coast.

Professional pigeoners, who followed the flocks from nesting site to nesting site, were joined by local farmers and game hunters. In an open area near the nesting site a patch of ground was cleared, watered down, and covered with a mixture of corn kernels and salt. (Passenger pigeons seemed to crave salt.) The site was chosen so that saplings on the perimeter of the patch could be bent and used to spring the nets when pigeons had been attracted to the bait. To bring the baited patch to the attention of flocks flying to and from the nesting site, a "stool pigeon" was tethered to a perch in the middle of the patch. As a flock passed overhead, the perch was pulled from beneath the stool pigeon (by a cord running from the pigeoner's blind) causing it to flutter to the ground as if landing for food. If the stool pigeon was successful in attracting the flock, the pigeoner would wait until the baited patch was thick with feeding pigeons and then pull a second cord which would spring the nets. Depending on the size of the nets and the density of feeding pigeons it was not uncommon to trap 200 - 600 pigeons. In a nesting near Frankfort, Michigan in 1874, one pigeoner secured nearly 1,300 pigeons in a single set [Schorger (1955, p. 184)].

The sufficient condition for local instability of (X_∞, E_∞) in Specification (3), was $c/[(p-s)q] < (K_1 + K_2)/2$. Consider, first, the ratio on the left-hand-side. The parameter $c > 0$ would be the opportunity cost of professional pigeoners, local netters and game hunters. A plausible measure for the opportunity cost for these individuals might be the *daily farm wage*, since many local netters were engaged in agriculture.

A time-series for the daily farm wage, c, from 1857 to 1885, is given in Table 1. This time-series, along with the shipping cost index, I, were extracted from Adams (1943). Shipping charges were \$6-\$12 per barrel [Schorger (1955 p.146)]. A barrel would contain about 300 birds. E. Osborn, a professional pigeoner, kept detailed business records during the years he spent netting and shooting passenger pigeons. Mershon (1907, p.111) reproduces a letter from Osborn to H. T. Phillips, a game-dealer in Detroit, in which Osborn recalls that in 1862, the shipping cost from Monroe, Wisconsin was \$7-\$9 per barrel. Rescaling the Adams shipping index so 1862 = 1.00 and assuming a shipping cost of \$8 for 300 birds implies s=\$0.32 per dozen birds in 1862. Multiplying the re-scaled shipping index by \$0.32/dozen yields the shipping cost time-series, s, in the fourth column in Table 1.

The wholesale prices of passenger pigeons in New York City, p, were calculated as the sample mean of wholesale prices in the months of April, May, and June for each year, 1857-1885, as reported in the *New York Daily Tribune*. The price was for a dozen pigeons and the market reporter would occasionally comment on the quantity, quality, and origin of pigeons reaching the market. There would be considerable variation in prices within a year based not only on the quantity supplied, but also on the quality or "freshness" of the "wild" pigeons. Warm weather might result in barrels of spoiled pigeons being confiscated and destroyed by the New York City Department of Health, with the buyer/shipper in the mid-west incurring a loss for what was paid to the pigeoner as well as the shipping cost.

During the period 1857-1885, the average wholesale price was \$1.55/doz., the average shipping cost was \$0.36/doz., and the average farm wage was \$1.09/day. The remaining parameter needed to calculate X_∞, is the catchability coefficient, q. In Specifications (1) or (3), the production function takes the form Y=qXE. Solving for q yields q=Y/(XE), where Y is the number of birds harvested from a nesting site, X is the number of birds at the nesting site, and E is the number of "netter days," the product of the estimated number of netters and the number of days spent harvesting pigeons at a particular nest site. The catchability coefficient has the dimension 1/days. Reports and descriptions of the netting of pigeons at two large nest sites in 1874 and 1878 will be used to calibrate the parameter q.

In Shelby, Michigan in 1874, H.T. Philips, the game dealer from Detroit, estimates that 1,075,000 pigeons were shipped over a 30 day period from a large nest site worked by 600 professional netters [Schorger (1955 pp.146-149)]. If the nesting population was 5 million pigeons, then $q = 1{,}075{,}000/(5{,}000{,}000 \times 600 \times 30) = 1.19 \times 10^{-5}$.

There were conflicting reports on the harvest from a large nest site at Petoskey, Michigan in 1878. E. T. Martin was a buyer and shipper with offices in Chicago. Professor H. B. Roney was an early proponent of conservation and laws to limit the netting of adults and the harvest of squabs. Roney (1879) estimates that a grand total of *one billion* pigeons were killed, including those that were harvested and shipped and those killed but never shipped. Martin (1879) regards Roney's estimate as inflated and, based on his records, estimates the total number of birds shipped to be about 1,107,866. The first shipments from Petoskey started on March 22nd and ended on August 12th. Assuming a six day week (or about 120 working days) and 500 netters, this would imply E = 60,000 netter days. The nest site at Petoskey was estimated to have been 40 miles long and three to 10 miles in width. If we adopt Martin's estimate of harvest and put the nesting population at 1 billion birds the catchability coefficient would be

$q = 1{,}107{,}866/[(1.0 \times 10^{9}) \times (60{,}000)] = 1.85 \times 10^{-8}$.

In Table 2 we convert the average wholesale price and shipping cost to a per pigeon basis and then use the estimates of q from Shelby, Michigan in 1874 and from

Petoskey, Michigan in 1878 to calculate X_∞, the open access equilibrium stock. With the price per pigeon now $p = \$0.13$, shipping cost $s = \$0.03$ per pigeon, and the cost per netter day of $c = \$1.09$, the average open access equilibrium stock, X_∞, would be $X_\infty = 915{,}966$ pigeons based on the q-value from Shelby, Michigan in 1874, or $X_\infty = 589{,}189{,}189$ pigeons, based on the q-value from Petoskey in 1878. For a comparison with $(K_1 + K_2)/2$, it is useful to express these values in units of 10^9 pigeons. The Shelby value is rounded up to one million, and the Petoskey value is rounded up to 600 million. It is hypothesized that $0.6x10^9 \geq X_\infty \geq 0.001x10^9$.

Remember that if $X_\infty=c/[(p-s)q]$ is less than $(K_1 + K_2)/2$, the open-access equilibrium will be locally unstable The pre-colonial estimate of K_2 was between $3x10^9$ and $5x10^9$ pigeons. During the 19th century the clearing of beech and oak forests undoubtedly reduced the value of K_2. Offsetting this reduction in the pigeons' natural food supply was the increase in the cultivation of corn and wheat, which the pigeons, to a farmer's distress, would also consume. If, by the mid-19th century, the value of K_2 had declined to $2.0x10^9$ and if the value of K_1 were small but positive, the average, $(K_1 + K_2)/2 \approx 1.0x10^9 > X_\infty \approx 0.6x10^9$, and (X_∞,E_∞) would be locally unstable. While the available empirical evidence is limited, and far from conclusive, it would seem to suggest that the railroad, telegraph, and open access nature of the industry satisfied Inequality (4) and led to the ultimate extinction of the passenger pigeon.

IV. Conclusions and Caveats

Based on the available data and accounts of the commercial exploitation of the passenger pigeon in North America, there appears to be evidence supporting an open-access model leading to extinction. This was likely to have occurred because $X_\infty = c/[(p-s)q] < (K_1 + K_2)/2$ and the population was less than $(K_1 + K_2)/2$ during the last half of the 19^{th} century. It was not possible to obtain time-series data that would allow a precise estimate of q, the catchability coefficient. The estimates of q from accounts at the Shelby, Michigan nest site in 1874 and the Petoskey, Michigan site in 1878 yielded estimates of X_∞ between $0.001x10^9$ and $0.6x10^9$ pigeons.

The carrying capacity, K_2, and the minimum viable population, K_1, were speculative. We know with certainty that $K_1 \geq 1$, and that K_2 was likely to have declined from the pre-colonial estimate of $3x10^9$ to $5x10^9$ pigeons. The remaining forest, in the mid-1800s, plus the production of corn and wheat would probably have supported a pigeon population of $1x10^9$ to $2x10^9$ birds. Thus, even with the decline in carrying capacity it would seem that given the prevailing market price for pigeons, shipping costs from the mid-west, and the opportunity cost of netters, that X_∞ was less than $(K_1 + K_2)/2$.

We also know, with certainty, that the passenger pigeon became extinct in the wild around 1900. The rapid decline in abundance from 1813 is an unfortunate testimony to the efficiency of rent-seeking by game hunters in the 19th century.

References

Adams, T. M. 1943. *Prices Paid by Vermont Farmers for Good and Services and Received by Them for Farm Products, 1790 - 1940*, Ph.D. Dissertation, Cornell University.

Audubon, J. J. 1831-39. *Ornithological Biography*, (5 Volumes) Edinburgh.

Bjorndal, T. and J. M. Conrad. 1987. "The Dynamics of an Open Access Fishery," *Canadian Journal of Economics*, 20(1):74-85.

Brander, J. A. and M. S. Taylor. 1998. "The Simple Economics of Easter Island: A Ricardo-Malthus Model of Renewable Resource Use," *American Economic Review*, 88(1):119-138.

Brooks, R., Murray, M., Salant, S., and J. C. Weise. 1999. "When is the Standard Analysis of Common Property Extraction under Free Access Correct? A Game-Theoretic Justification for Non-Game-Theoretic Analysis," *Journal of Political Economy*, 107(4):843-858.

Clark, C. W. 1990. *Mathematical Bioeconomics: The Optimal Management of Renewable Resources*, Wiley-Interscience, John Wiley & Sons, New York.

Conrad, J. M. 1999. *Resource Economics*, Cambridge University Press, New York.

Gordon, H. S. 1954. "The Economic Theory of a Common Property Resource: The Fishery," *Journal of Political Economy*, 62:124-42.

Homans, F. R. and J. E. Wilen. 1997. "A Model of Regulated Open Access Resource Use," *Journal of Environmental Economics and Management*, 32:1-21.

Mershon, W. B. 1907. *The Passenger Pigeon*, The Outing Publishing Company, New York.

New York Daily Tribune. 1857 - 1885. New York.

Pokagon, S. 1895. "The Wild Pigeon of North America," *The Chautauquan*, 22. (Reprinted in Mershon (1907) as Chapter V.)

Schorger, A. W. 1955. *The Passenger Pigeon: Its Natural History and Extinction*, The University of Wisconsin Press, Madison.

Smith, V. L. 1969. "On Models of Commercial Fishing," *Journal of Political Economy*, 77:181-198.

Wilen, J. E. 1976. "Common Property Resources and the Dynamics of Overexploitation: The Case of the North Pacific Fur Seal," Department of Economics, Programme in Natural Resource Economics, Paper No. 3, The University of British Columbia, Vancouver.

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Endnotes

[1]Homans and Wilen (1997) would refer to this situation as "pure" open access, and contrast it to a situation they call "regulated" open access, where a management authority sets a total allowable catch (TAC). Brooks *et al*. (1999) analyze pure open access using a game-theoretic approach and determine when the two approaches (continuous-time dynamical systems and game-theoretic) yield the same predictions.

[2]In discrete-time, the system

$$X_{t+1} - X_t = rX_t(1 - X_t/K) - qX_tE_t$$
$$E_{t+1} - E_t = \alpha[pqX_tE_t - cE_t]$$

is capable of more complex dynamics, including limit cycles and possibly deterministic chaos. See Conrad (1999).

[3]Simon Pokagon was a Pottawattomie chief. He was the author of the "Red Man's Greeting," and was regarded as the "poet, bard and Longfellow of his race" by many non-natives. His father, chief before him, sold the site of Chicago and surrounding lands to the U.S. Government in 1833. In an article on the wild (passenger) pigeon published in *The Chautauquan* in November, 1895, and reprinted in Mershon (1907), Pokagon notes "A pigeon nesting was always a great source of revenue to our people. Whole tribes would wigwam in the brooding places. They seldom killed old birds, but made great preparation to secure their young, out of which the squaws made squab butter and smoked and dried them by the thousands for future use. Yet, under our manner of securing them, they continued to increase."

Appendix

The Jacobian of the linearization of Specification (3), evaluated at (X_∞, E_∞), is given by

$$J = \begin{bmatrix} (-r/K_2)X_\infty(X_\infty/K_1 - 1) + (1 - X_\infty/K_2)r(2X_\infty/K_1 - 1) - qE_\infty & -qX_\infty \\ \alpha(p-s)qE_\infty & 0 \end{bmatrix} \quad \text{(A.1)}$$

Denote the eigenvalues (characteristic roots) of J by λ_1 and λ_2. It is well known that $\lambda_1 + \lambda_2 = \mathrm{Tr}(J)$ and that $\lambda_1 \bullet \lambda_2 = |J|$. For (X_∞, E_∞) to be stable the eigenvalues must both be negative if real or have a negative real part if complex conjugates. This *cannot* be the case if

$$(-r/K_2)X_\infty(X_\infty/K_1 - 1) + (1 - X_\infty/K_2)r(2X_\infty/K_1 - 1) - qE_\infty > 0 \quad \text{(A.2)}$$

(A.2) is a sufficient condition for the local instability of (X_∞, E_∞). If one substitutes $E_\infty = (r/q)(X_\infty/K_1 - 1)(1 - X_\infty/K_2)$ into (A.2), and does the algebra, it can be shown that (A.2) implies

$$\frac{c}{(p-s)q} < \frac{(K_1 + K_2)}{2} \quad \text{(A.3)}$$

as stated in Inequality (4) in the text.

If (X_∞, E_∞) is locally unstable there is a possibility that it might be the focus of a stable limit cycle. The Bendixson – Du Lac Criterion, if satisfied, rules out the existence of a limit cycle. The Bendixson – Du Lac Criterion says that if $\dot{X} = F(X, E)$ and $\dot{E} = G(X, E)$ are smooth functions in a given, simply-connected, region, D, and if $B(X,E)$ is also a smooth function in D, then *if* the expression

$$\frac{\partial(BF)}{\partial X}+\frac{\partial(BG)}{\partial E} \qquad (A.4)$$

does not change sign in D, the system $\dot{X}=F(X,E)$ and $\dot{E}=G(X,E)$ has no closed trajectories in D, and thus no limit cycles.

For Specification (3), define $B(X,E)\equiv(XE)^{-1}$. Then

$$\frac{\partial(BF)}{\partial X}+\frac{\partial(BG)}{\partial E}=\left[\frac{r}{EK_2K_1}\right](K_1+K_2-2X) \qquad (A.5)$$

This expression will not change sign if $X<(K_1+K_2)/2$ or if $X>(K_1+K_2)/2$. In the first instance we are in the region where if (A.3) is also satisfied, the open access equilibrium (X_∞,E_∞) is unstable. In the second instance, if $\frac{c}{(p-s)q}>\frac{(K_1+K_2)}{2}$, we are in the region where (X_∞,E_∞) will be the focus of a stable spiral. See Figure 3. In Figure 4b we numerically show the case where $X_\infty=c/[(p-s)q]=0.55=(K_1+K_2)/2$ and observe that the open access equilibrium is the focus of a stable limit cycle. This case does not violate the Bendixson – Du Lac Criterion because the limit cycle produces values of X(t) that oscillate above and below $(K_1+K_2)/2=0.55$. If by the mid – 19th century (A.3) was holding and the passenger pigeon population was *permanently* below $(K_2+K_1)/2$, then no limit cycles exist and the system would be on an irreversible course to extinction.

Table 1. The New York City Wholesale Price for Passenger Pigeons (p=$/doz.), A Shipping Index (I, 1862=1.00), Shipping Cost (s=$/doz.), and the Daily Farm Wage (c=$/day) for 1857 - 1885.

Year	p	I	s	c
1857	$1.70	1.03	$0.33	$0.92
1858	$1.13	1.03	$0.33	$0.87
1859	$1.63	1.00	$0.32	$0.91
1860	$1.15	1.00	$0.32	$0.89
1861	$0.75	1.03	$0.33	$0.82
1862	$0.72	1.00	$0.32	$0.85
1863	$1.33	1.07	$0.34	$1.00
1864	$2.10	1.03	$0.33	$1.40
1865	$3.28	1.27	$0.41	$1.29
1866	$1.46	1.24	$0.40	$1.36
1867	$1.73	1.27	$0.41	$1.47
1868	$1.58	1.27	$0.41	$1.48
1869	$2.00	1.27	$0.41	$1.40
1870	$1.60	1.24	$0.40	$1.14
1871	$1.50	1.21	$0.39	$1.15
1872	$1.63	1.21	$0.39	$1.17
1873	$1.31	1.24	$0.40	$1.26
1874	$1.39	1.24	$0.40	$1.24
1875	$1.33	1.27	$0.41	$1.26
1876	$1.05	1.27	$0.41	$0.93
1877	$1.83	1.24	$0.40	$0.76
1878	$0.79	1.24	$0.40	$0.81
1879	$1.50	1.10	$0.35	$0.81
1880	$1.00	1.10	$0.35	$0.83
1881	$2.16	1.07	$0.34	$0.88
1882	$1.61	1.07	$0.34	$1.16
1883	$1.42	1.03	$0.33	$1.17
1884	$2.51	1.03	$0.33	$1.29
1885	$1.75	0.93	$0.30	$1.09

Table 2. Estimates of q, the Catchability Coefficient, for Two Nesting Sites, Shelby, Michigan in 1874 and Petoskey, Michigan in 1878, and the Implied Values for X_∞=c/[(p-s)q].

Shelby, Michigan in 1874	Petoskey, Michigan in 1878
Y = 1,075,000 (pigeons)	Y = 1,107,866 (pigeons)
E = 18,0000 (netter days)	E = 60,000 (netter days)
X = $5x10^6$ (pigeons)	X = $1x10^9$ (pigeons)
q = $1.19x10^{-5}$	q = $1.85x10^{-8}$
p = 0.13 ($/pigeon)	p = 0.13 ($/pigeon)
s = 0.03 ($/pigeon)	s = 0.03 ($/pigeon)
c = 1.09 ($/day)	c = 1.09 ($/day)
X_∞ = 915,966 ≈ $0.001x10^9$ (pigeons)	X_∞ = 589,189,189 ≈ $0.6x10^9$ (pigeons)

Figure 1. The Phase-Plane Diagram for Specification (1)

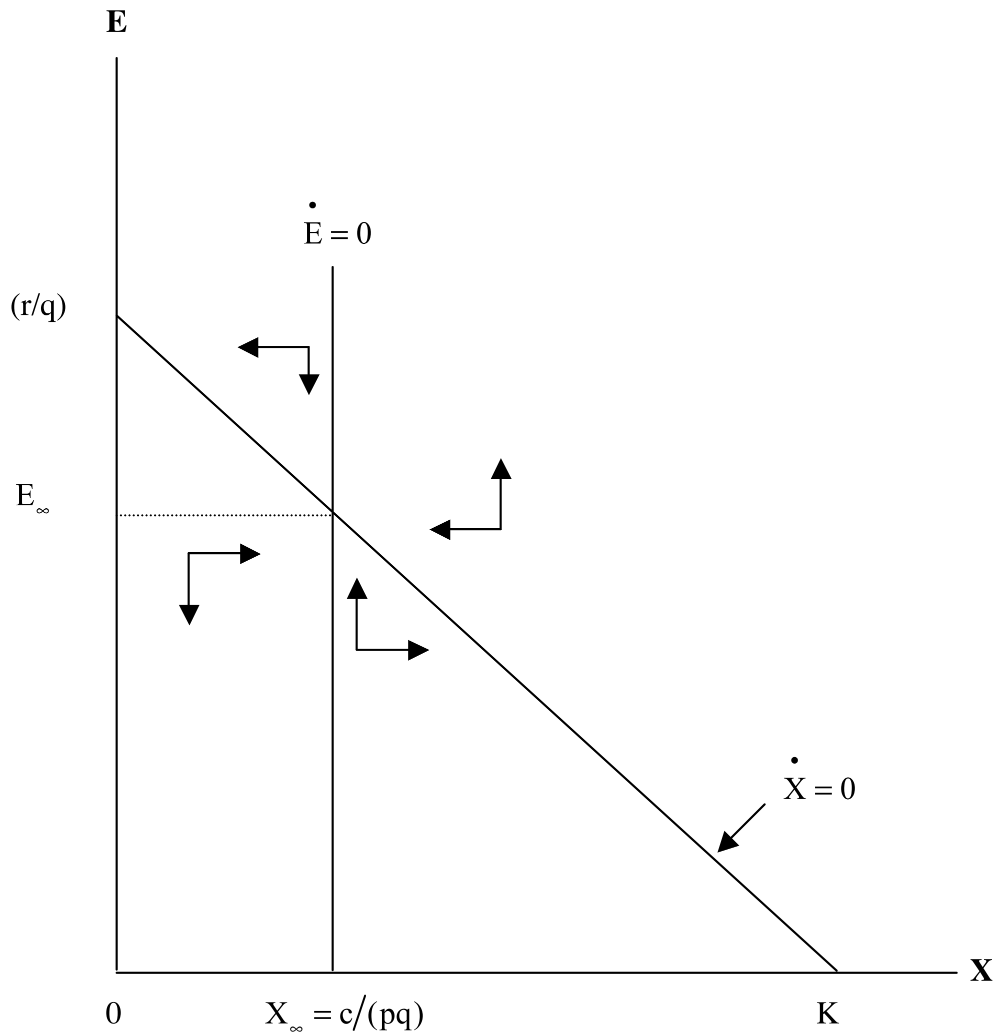

Figure 2. The Critically Depensatory Net Growth Function

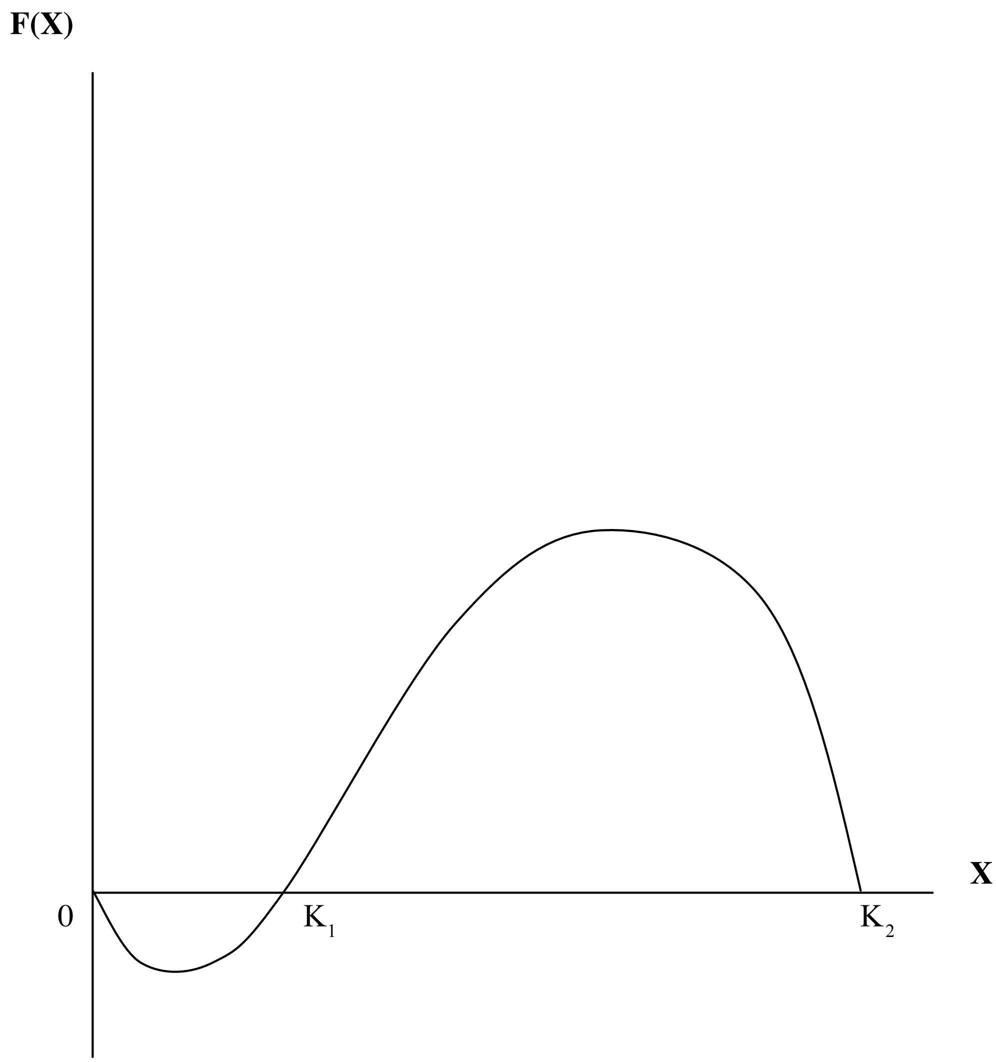

Figure 3. The Phase-Plane Diagram for Specification (3)

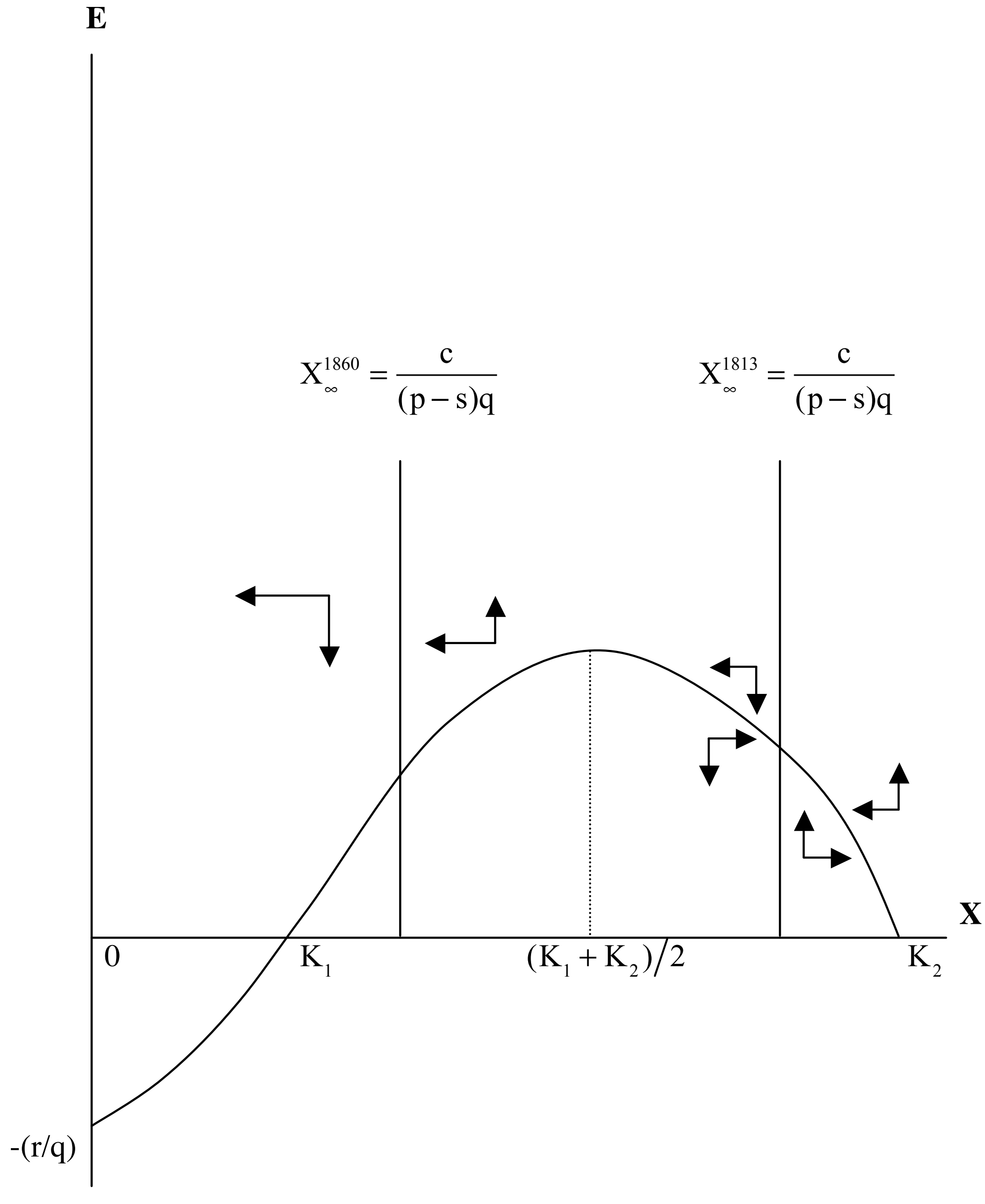

Figure 4a: $(K_1+K_2)/2=0.55$, $X_\infty=0.6$

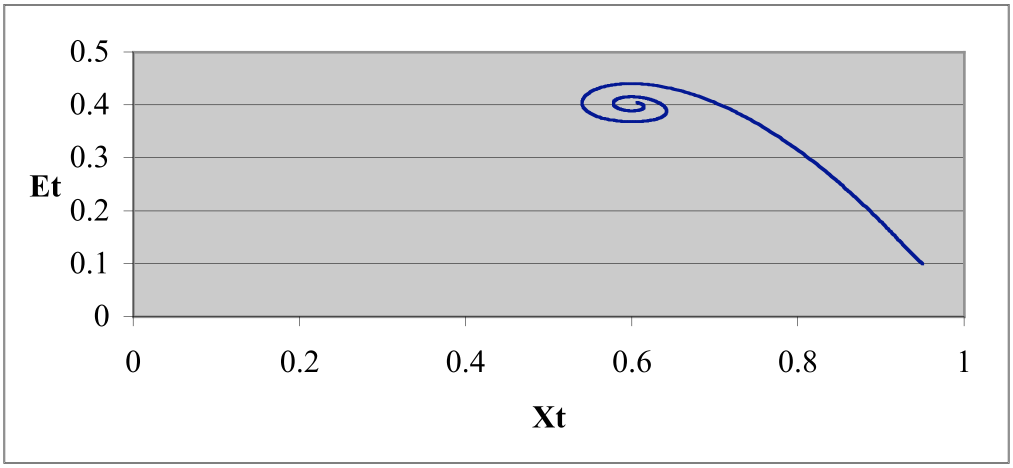

Figure 4b: $(K_1+K_2)/2=0.55$, $X_\infty=0.55$

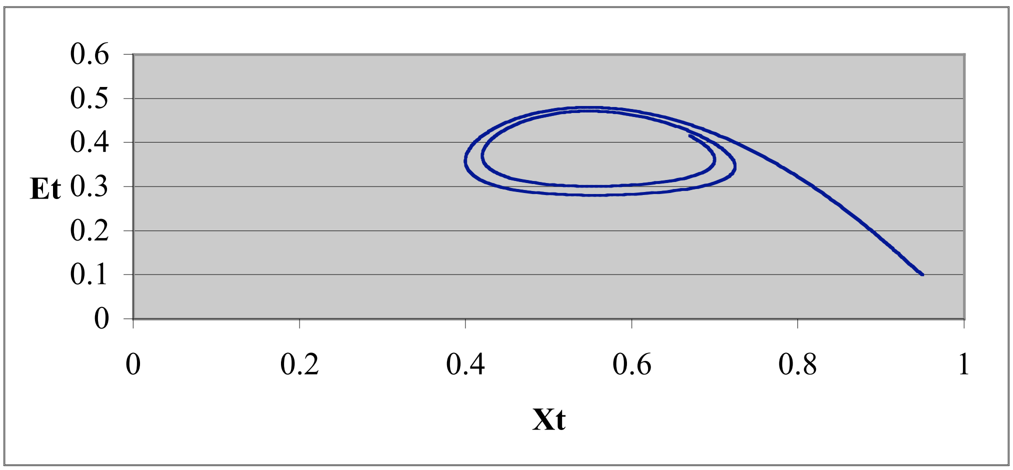

Figure 4c: $(K_1+K_2)/2=0.55$, $X_\infty=0.5$