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A Survey of the Literature Associated with the Bisexual Galton-Watson Branching Process

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1. Introduction

The proceedings of a symposium held at the Wistar Institute of Anatomy and Biology in April, 1966 were published under the title "Mathematical Challenges to the Neo-Darwinian Interpretation of Evolution". As a participant in this symposium, S.M. Ulam (1967) made the following observation in his presentation:

> How to Formulate Mathematically Problems of Rate of Evolution? "... there is a very nice and simple mathematical technique for describing processes starting with a single object, which then duplicates and gives 0, 2, or 3 or more descendants. It is called the theory of branching processes. It deals with asexual reproduction and gives methods to calculate the number of existing particles, of various kinds, in future generations, and other questions of this sort. I would like to stress that a corresponding theory for branching with *sex*, where particles get together, say at random and then produce offspring, i.e., a combination of a binary process of mating and reproduction, is mathematically much more difficult and no exact theory exists as yet."

S.M. Ulam held a position of respect and authority as a patriarch in the development of *branching process theory*. When he spoke, those of us committed to the application of branching processes listened. The above quotation is a prime motivation for the author in writing this paper.

Since 1966, fifteen authors have contributed twenty-nine papers in fifteen journals which deal directly with the *bisexual Galton-Watson branching pro-*

cess (bGWbp). This is a branching process in the spirit and style of Galton, Watson, Erlang, Haldane, and Steffensen where Ulam's requirement of sexual mating before reproduction can take place. This paper is intended to be a survey and summary of the development of bGWbp theory. In the absence of a published book on this model (such as Harris' classic text on processes where reproduction is asexual), the theory associated with the process appears in fragmented form in the previously mentioned fifteen journals. The author intends to summarize these fragments, draw together the various threads in the development of bisexual theory, and to make some suggestions for the directions of future research. While there is an abundant literature on two-sex population models in general and an increasing appreciation of the application of other branching processes to the development of bGWbp theory (such as the use of controlled branching processes and population size dependent processes), it is our purpose to focus solely on the literature which emphatically states its adherence to the bGWbp.

In addition to the introductory Section 1, this paper contains two additional sections. Section 2 will present the bGWbp with its assumptions, parameters, terminology, and symbolism. Section 3 will attempt to synthesize the literature and offer suggestions for the directions of future research.

2. The bisexual Galton-Watson branching process

The purpose of this section is to introduce the basic nomenclature and assumptions associated with the bGWbp. Compared to the standard Galton-Watson process (where individuals are all of the same type and reproduction is done asexually), the bisexual process requires more terminology and follows a more complicated scenario.

D.J. Daley (1968a) introduced the bGWbp – two years after the Wistar symposium. Dr. Daley has stated (via personal correspondence) that there was no connection between his work and the quotation from Ulam in Section 1. He was not aware of the symposium while preparing the initial paper on the bisexual process.

The bGWbp assumes that the population of the species under consideration consists of two disjoint classes (sexes), male and female. Reproduction can be accomplished only by mating units. A mating unit consists of one male and one female from the same generation who come together for the purpose of procreation.

Any realization or application of the bGWbp will require the continuing repetition of the following three-step process. It is assumed that there will be Z_0 mating units in the initial or zeroth generation.

1. The initial mating units produce offspring, independently of one another, as specified by a given probability distribution $\{p_k\}_{k=0}^{\infty}$ (i.e. The probability that a mating unit produces k offspring is p_k.)
2. An individual offspring will be female with probability α and male with probability $1-\alpha$. These sex designations are made independently among the offspring of any mating unit. If a mating unit produces k offspring, the number of females in this brood will have a binomial distribution with parameters k and α. (An alternative approach to steps one and two is to use an offspring probability distribution of the form $\{p_{jk}\}_{j,k=0,1,\ldots}$, where j is the number of females and k is the number of males generated by a mating unit. The independence of sex type among the offspring of a mating unit can be assumed here. Poisson distributions are appropriate when using this approach.)
3. Let X_{0i} and Y_{0i} be the number of females and males respectively, generated by the ith mating unit of the initial Z_0 mating units. The next (first) generation will have $Z_1 = \zeta(x, y)$ mating units where ζ is the mating unit of the process with

$$x = \sum_{i=1}^{Z_0} X_{0i} \quad \text{and} \quad y = \sum_{i=1}^{Z_0} Y_{0i}. \tag{1}$$

   ζ will specify the number of mating units in any generation. Specifically, ζ is a two-place function with inputs, the number of females and the number of males in that generation. Z_n will designate the number of mating units in the nth generation. A value for Z_n is found by inputing two sums similar to (1) where the 0 subscripts are replaced by $n-1$.

   Daley placed three obvious conditions on the mating function:

   (1) ζ is non-negative and integer-valued,
   (2) ζ is non-decreasing in both of its inputs (i.e. increasing the number of males or females in a generation will not decrease the number of mating units in that generation), and
   (3) $\zeta(x, 0) = \zeta(0, y) = 0$ for all non-negative integers x and y. (A generation without males or without females will not be able to form mating units.)

It is assumed that this three-step sequence (production of offspring, sex designation, and the formation of mating units) may continue indefinitely. $\{p_k\}_{k=0}^{\infty}$, ζ, α and Z_0 are the four parameters of the process. That is, these values must be specified in any realization of the process.

The sequence $\{Z_n\}_{n=0}^{\infty}$ is a discrete-time Markov chain with the non-negative integers as the state space. State zero is absorbing, while all other states are transient. *Population extinction* will occur iff $Z_n = 0$ for some positive integer n. (If there are no mating units formed in a particular generation, it is impossible to generate offspring to form the next generation.)

3. The bisexual Galton-Watson branching process literature

We will consider the bisexual literature in the following categories; (1) extinction probabilities, (2) convergence results, (3) multitype processes, (4) statistical applications and (5) new bisexual Galton-Watson branching processes developed from the bGWbp. Each of these topics will have a specific sub-section. The format will be to focus on the development of that topic, summarize the present level of knowledge, and finally offer some suggestions for the directions of future research.

3.1. The probability of extinction in a bisexual Galton-Watson branching process

3.1.1. The development of the theory. Daley's initial paper (1968a) on the bGWbp formalized the definitions of the two most relevant mating functions for animal groupings and human societies. He then presented necessary and sufficient conditions for bisexual processes governed by these functions to undergo certain extinction.

Daley's two mating functions were given the titles; *completely promiscuous mating* and *polygamous mating with perfect fidelity*. Completely promiscuous mating assumes that a single *champion* male (possessing an infinite reproduction capacity) will emerge in each generation and then will mate with every female member of that generation. All other males of this generation are excluded from the mating process. This mating function has the form $\zeta(x, y) = x \min\{1, y\}$, where x and y are the numbers of females and males respectively in the given generation. Daley showed that a process with this mating function will become extinct with probability one for all positive integer values of Z_0 iff the mean number of females generated by a mating unit is less than or equal to one when $p_0 + p_1 + p_2 < 1$.

Polygamous mating with perfect fidelity is a mating function with a double standard. The females practice *perfect fidelity* (They are allowed to have at most one mate.), while the males (or at least some males) practice polygamy. A male may have up to d wives if enough females are available. d (a positive integer) is another parameter to be specified. Specifically, the mating function is $\zeta(x,y) = \min\{x, dy\}$. The special case, $d = 1$, is called the *perfect fidelity mating function.* Daley proved that extinction is certain in a process with this mating function for all possible values of Z_0 iff the minimum of the mean number of females and d times the mean number of males generated by a mating unit is less than or equal to one. (A process with $d = 1$ and $p_0 + p_1 + p_2 + p_3 = 1$ must be excluded from consideration here.)

Karlin and Kaplan (1973) published the second paper on the bGWbp. The bGWbp is just one of several models considered here. In their work on the bGWbp, they consider only those processes governed by Daley's two special functions. Basically, they duplicate Daley's results. However, their proofs are entirely probabilistic (with references to supermartingales) in content. (Daley made extensive use of the analytic iteration of functions and Cauchy's Integral Formula.)

It would be nine years before a third paper on the bGWbp would be published. Hull (1982) made the first attempt to employ mating functions in a bGWbp other than Daley's two functions. In particular, this paper sets forth the premise that the relevant mating functions (used in the literature on two-sex population models) are superadditive. A mating function ζ is said to be *superadditive* if for any pairs (x_1, y_1) and (x_2, y_2) of non-negative integers, the inequality $\zeta(x_1 + x_2, y_1 + y_2) \geq \zeta(x_1, y_1) + \zeta(x_2, y_2)$ holds. All superadditive mating functions satisfy Daley's requirement of monotonicity in both arguments. Hence, this is a stronger condition for mating functions.

The main emphasis of this paper is a further pursuit of conditions associated with the certain extinction of the species under consideration. Hull considers the mean number of mating units that can be formed from offspring of a single mating unit, i.e say $m = E(Z_1 | Z_0 = 1)$ (rather than the mean number of males and females as employed by Daley), as it relates to extinction probabilities. (A similar approach is employed in the classic consideration of extinction in the standard Galton-Watson branching process.) Let Q_k denote the probability of extinction in a bGWbp if there are k mating units in the initial generation. Using a branching process where only full siblings are allowed to mate, Hull shows that a process with a superadditive mating function and having $Q_j = 1$ for all positive integers j will imply that $m \leq 1$.

Unfortunately, the converse is not true. A counter-example is stated where a process has a superadditive mating function where both m and Q_1 are less than one.

At this point it was obvious that Hull's necessary condition for certain extinction in a bGWbp with a superadditive mating function should be upgraded to a condition that is both necessary and sufficient. This challenge provided an impetus to accelerate bGWbp publishing. Whereas only three papers relating directly to the bGWbp were published from 1968 to 1982, three papers appeared in the years 1984 to 1986, with the intent of pursuing that necessary and sufficient extinction condition.

Hull (1984) provided a necessary and sufficient condition by creating a hybrid of the bGWbp where mating was allowed only in certain well defined communities. This hybrid process then was considered in the format of standard multi-type processes as in Harris (1963). It was then possible to view this new process in the form of certain communities generating succeeding communities of various sizes.

Details of this approach as well as Hull's condition are omitted here. While the results of this paper are valid, it must be admitted that the approach taken here is quite unwieldy when attempting to determine if a species will experience certain extinction. A more efficient approach is presented in the next two papers. (This paper was used to construct an upper bound for a relevant extinction probability (Hull, 2001)).

F. Thomas Bruss (1984) proposed a more useful sufficient condition for certain extinction in a bGWbp. Earlier Daley (1968) made the conjecture that the extinction probability in a bGWbp will be one iff $E(Z_{n+1}|Z_n = j) \leq j$ for all sufficiently large positive integers j. Bruss' Theorem 1 formally proves that this condition is sufficient for certain extinction. Bruss also makes the helpful observation that Sevast'anov and Zubkov's (1974) work on controlled branching processes may be applied in developing theory for the bGWbp.

The most comprehensive paper (to date) on the bGWbp was written by Daley, Hull, and Taylor (1986). Section 2 of this paper lists seven monotonicity properties associated with the bGWbp.

Property 1. Recall that $\{Z_n\}_{n=0}^{\infty}$ is a Markov chain. Since the mating function is non-decreasing in both arguments, it then follows that $\{Z_n\}_{n=0}^{\infty}$ is a stochastically monotone Markov chain as defined by Daley (1968b).

Property 2. Since $\{Z_n\}_{n=0}^{\infty}$ is stochastically monotone, $Q_j \geq Q_{j+1}$ for all non-negative integers j. (It is possible to show that there is strict inequality if $Q_j < 1$.)

The next four properties deal with the comparison of two processes which differ in just one parameter.

PROPERTY 3. Suppose that $\{Z'_n\}_{n=0}^{\infty}$ and $\{Z''_n\}_{n=0}^{\infty}$ are the sequences of mating units associated with two bisexual processes which differ only in the number of mating units in the initial generation. (The offspring probability distribution, the mating function, and the α-value are the same for both processes.) If Z'_0 is stochastically smaller than Z''_0, written as $Z'_0 \leq^d Z''_0$ (This means that $\Pr(Z'_0 \leq k) \geq \Pr(Z''_0 \leq k)$ for all positive integers k), then $Z'_n \leq^d Z''_n$ for all positive integers n and so the probability of extinction in the Z' process is not smaller than the probability of extinction in the Z'' process.

PROPERTY 4. Suppose that $\{Z'_n\}_{n=0}^{\infty}$ and $\{Z''_n\}_{n=0}^{\infty}$ have mating functions ζ' and ζ'', respectively, where it is known that $\zeta'(x, y) \leq \zeta''(x, y)$ for all non-negative integers x and y (with the same other three parameters for both processes), then again $Z'_n \leq^d Z''_n$ for all non-negative integers n and the probability of extinction in the Z' process is not smaller than that in the Z'' process.

PROPERTY 5. Statements similar to those in Property 3 can be made if one offspring probability distribution is stochastically smaller.

PROPERTY 6. This is an alternative version of Property 5. Assume that X'_n and Y'_n are the numbers of females and males respectively, in the nth generation of the Z'_n process. Similar statements hold for X''_n and Y''_n in the Z'' process. We assume that these processes have the same initial generation probability distribution, α-value, and mating function. If it is known that $E(f(X'_n, Y'_n)) \leq E(f(X''_n, Y''_n))$ for all component-wise non-decreasing functions f, then it follows that the probability of extinction in the Z' process is not smaller than that in the Z'' process.

PROPERTY 7. This is a result needed for the paper's main statement on extinction probabilities in Section 3. Let $m(j) = j^{-1}E(Z_{n+1} | Z_n = j)$ (as in Bruss). The sequence $\{m(j)\}_{j=1}^{\infty}$ has a limit r. In particular, $r = \sup_{j>0} m(j)$ when the mating function is superadditive. We shall refer to the sequence $\{m(j)\}_{j=1}^{\infty}$ as the *sequence of mean growth rates* and r as the *asymptotic growth rate*.

Section 3 presents a necessary and sufficient condition for certain extinction. Recall that Hull stated a necessary condition for certain extinction based on the mean number of mating units that can be generated by a single mating unit when there is a superadditive mating function. Bruss stated a sufficient condition for certain extinction using mean growth rates. (Bruss did not assume superadditivity.) Theorem 3.1 in this paper states that if a bGWbp has a superadditive mating function, then $Q_j = 1$ for all positive integers j iff $r \leq 1$ (r as in Property 7 above). Superadditivity is the essential assumption that makes $r \leq 1$ the significant necessary and sufficient condition. However, superadditivity is an essential (or used) prerequisite only in the critical case. (Critical in the sense that $r = 1$.)

The purpose of the final section (Section 4) is to establish upper and lower bounds for the extinction probability of a bGWbp. This is necessary since the generating function techniques used to find extinction probabilities in the standard process lose their simplicity in the bGWbp. Prior to developing the theory for such approximations it is noted that $Q_{i+j} \leq Q_i Q_j$ when the mating function is superadditive.

$q_i(k)$ is defined to be the probability that extinction occurs in the process before there are more than k mating units in any generation when $Z_0 = i$. It is obvious that as k increases, $q_i(k)$ approached Q_i and that each $q_i(k)$ is a lower bound for Q_i. Proposition 4.4 states a formula for constructing sequences of upper and lower bounds converging to Q_i.

Since Daley, Hull, and Taylor (1986) published their paper, five other papers dealing with extinction probabilities have appeared. These five papers apply theory from the 1986 paper or are expository works on issues that Daley, Hull, and Taylor raise.

M. González and M. Molina have published several papers on the bGWbp over the past decade. They are to be commended for their significant contributions to the development of bGWbp theory. González and Molina's first paper (1992) establishes a useful relation among certain generating functions associated with the bisexual process. It is assumed that the mating function is superadditive and that there is one mating unit in the initial generation. Let f be the generating function for the number of mating units that can be formed from the offspring of a single mating unit. Let f_n be the generating function for the number of mating units in the nth generation. It then follows that $f_n(s) \leq f_{n-1}(f(s))$ for s in the closed interval $[0, 1]$. Two main conclusions are drawn from this inequality. First, $E(Z_n) \geq (E(Z_1))^n$ for $n = 1, 2, \ldots$. Second, if $Q_1 = 1$, it then follows that the mean number of mating units generated by a single mating unit is less than or equal to one. This is Hull's (1982) necessary condition for certain extinction. However, this paper gives a compact and elegant proof of this result.

Recall that Daley (1968a) and Daley et al. (1986) state conditions where extinction is certain in a bGWbp for all possible values of Z_0. If these conditions do not hold, the next question is, "How large a value of Z_0 will move the process away from certain extinction?". Hull's paper (1993), "How many mating units are needed to have a positive probabilty of survival?", is an attempt to answer this question. Example 1 describes a case where $Q_1 = 1$. But, when Z_0 is increased to 2 (with the other three parameters fixed), $Q_2 < 1$. (It should be noted that a similar situation will not occur in the standard Galton-Watson branching process. The independence assumption associated with the production of offspring implies that if extinction is certain when there is one individual in the initial generation, extinction will also be certain if there are $n > 1$ individuals initially.)

One definition is needed before proceeding to the main result of the paper. Hull states that in addition to superadditivity, two other reasonable conditions can be imposed on mating functions.

Condition 1. $\zeta(1,1) = 1$. If a generation has just one male and one female, they will mate.

Condition 2. $\zeta(x,y) \leq \min\{xy, x+y\}$. There will never be more mating units than the number of individuals in any generation.

Any superadditive mating function which satisfies these conditions is said to be *population bounded*, i.e. spb.

Theorem 2 states that if the mating function is spb with $r > 1$ (r as in Daley et al. (1986)), then $Q_j < 1$ iff $P(Z_{n+1} > j \mid Z_n = j) > 0$. Two counter-examples are given to show that if either of the spb conditions do not hold, the conclusion of Theorem 2 is no longer valid.

A paper by Alsmeyer and Rösler (1996) was written as a response to a passing statement in the conclusion of Daley, Hull and Taylor (1986, page 599). When comparing extinction probabilities in two processes, one governed by completely promiscuous mating and the second process by the mating function $\zeta(x,y) = x$ (with the other three parameters equal), Daley et al. note that the ratio of the extinction probabilities of these two processes tends to a particular limit as the common value Z_0 increases. However, they state that they have no theoretical justification for the value of this constant. Alsmeyer and Rösler provide that theoretical justification. Their effort is so thorough – that this is the longest paper published solely on the bGWbp.

The main project in this paper is to provide upper and lower bounds for the sequence formed by the quotients $q(j)/q^j$ where the numerator represents the extinction probability in the completely promiscuous process and the denominator represents the extinction probability in the second process (when $Z_0 = j$). Alsmeyer and Rösler make two other significant contributions to bGWbp theory in this paper. First, they establish a linkage to standard Galton-Watson theory by comparing the completely promiscuous process to a standard process based on female lines of descent where extinction can also occur due to a *catastrophe* (i.e. there are no males in that generation). Second, Alsmeyer and Rösler actually produced an equation, which when solved provides the extinction probability for a completely promiscuous process. (This is the approach used in finding the extinction probability in a standard Galton-Watson process.) It had been thought that such an approach is difficult, if not impossible in a bGWbp. Alsmeyer and Rösler have shown that this is not the case – at least for the completely promiscuous mating function.

Alsmeyer and Rösler (2002) pursue their consideration of the sequence of ratios $q(j)/q^j$ in a second paper. Here they identify these ratios as a certain functional of a subcritical standard Galton-Watson branching process. Considering such functionals, a distinction is made between the convergence of these ratios and a second case where these ratios do not actually converge, but rather oscillate very slowly. It is pointed out that a similar phenomenon occurs for certain supercritical standard processes. The authors specify certain parameters which enable one to ascertain whether the sequence of such ratios from a given bisexual process will converge or oscillate.

It is generally recognized that Alfred Lotka (1931a, 1931b) made the first application of standard Galton-Watson branching process theory to calculate an extinction probability in a specific population assuming asexual reproduction. (Specifically, Lotka's calculations were based on data from the 1920 United States census.) Hull (2001) used bisexual Galton-Watson theory along with Lotka's parameters and then found a somewhat higher extinction probability. Hull's approach was to generate a sequence of lower bounds as in Daley, et al. (1986) and a sequence of upper bounds based on his 1984 paper, both of which converged to the bisexual extinction probability.

3.1.2. A summary of the theory developed on extinction probabilities. Much of the research associated with the bGWbp has concentrated on extinction probabilities. Significant and rewarding progress has been made on this topic. Daley's necessary and sufficient conditions for certain extinction for the two most relevant mating functions are intuitive and can be easily applied. We do have a necessary and sufficient condition for certain extinction in a process where the mating function is superadditive. Finally, when an extinction probability is known to be less than one, there are procedures to estimate that probability to any desired degree of accuracy. (This is done by constructing a finite number of terms from a sequence of lower bounds and from a sequence of upper bounds, both of which converge to the extinction probability.)

3.1.3. Suggestions for further research. The bGwbp can be applied to controversies associated with theories of evolution. Here the main concern may not be whether or not extinction occurs, but rather *time to extinction*. The topic time to extinction has been discussed in just one paper so far. Specifically, Daley, et al. (1986) considered this topic in processes using the perfect fidelity mating function. Their treatment of this topic in such a restricted case is far from complete. This important topic is in need of a more comprehensive and thorough investigation.

The bGwbp assumes that each couple has the same offspring distribution and alpha value. So far, no one has considered the prospects of extinction in the bisexual model if there is some variance in these two parameters among the mating units in a generation.

The extinction probability in a standard Galton-Watson branching process can be found by solving a single equation defined by the generating function of the offspring probability distribution. Several papers have suggested that the simplicity of such an approach is lost in the bGWbp. However, this approach should be investigated further. Alsmeyer and Rösler have shown that this approach is practical with completely promiscuous mating. Can this approach be applied to other mating functions?

3.2. Convergence properties in the bGWbp

3.2.1. The development of the theory. If the mean number of offspring per individual, call it m, exceeds one in the standard Galton-Watson branching process, then the species can survive indefinitely. Let X_n denote the number of individuals in the nth generation and $W_n = m^{-n} X_n$. The classic convergence theorem is

Theorem. *If $m > 1$ and $E(X_1^2)$ is finite, then the sequence of random variables $\{W_n\}_{n=0}^{\infty}$ converges with probability one (in distribution and* *in mean square) to a random variable* W *with* $E(W) = 1$ *and* $Var(W) = Var(X_1)/(m^2 - m) > 0$.

The distribution of W is then used to study the distribution of X_n for large n. Some effort has been made to develop an analogous theory for the bGWbp.

J.H. Bagley (1986b) published the first paper dealing with similar convergence properties in the bGWbp. This paper was written to establish one significant result, which is stated in Theorem 1.

THEOREM 1. *Assume that a bGWbp has the perfect fidelity mating function. Let* m *be the minimum of the mean number of males and the mean number of females that are generated by a single mating unit,* M_n *is the number of males in the nth generation, and* F_n *is the number of females in that generation. Assume that there is one mating unit in the initial generation. If* $m > 1$, *there exists a random variable* W *such that as* n *approaches infinity* $m^{-n}M_n$ *approaches* W *almost surely and* $m^{-n}F_n$ *approaches* $\alpha(1-\alpha)^{-1}W$ *almost surely.*

Bagley also develops an analogue of the familiar $X \log^+ X$ as used in the standard process. He shows that $E[M_1 \log^+ M_1] = \infty$ (or $E[F_1 \log^+ F_1] = \infty$) implies that $W = 0$ almost surely and that $E[M_1 \log^+ M_1] < \infty$ (or $E[F_1 \log^+ F_1] < \infty$) implies that $P(0 < W < \infty) = 1 - Q$. Suggestions are made as to how other properties of W may be developed (in a section labeled "Remarks"). Finally, Bagley (1986a) has published on the topic *controlled branching processes*. He makes the helpful remark that bisexual processes governed by Daley's two mating functions are actually special cases of controlled branching processes.

González and Molina (1996) extended Bagley's results to superadditive mating functions in general. Recall that Bagley assumed the use of the perfect fidelity mating function. Defining $W_n = r^{-n}Z_n$ (r as used in Daley, et al. (1986)), sufficient conditions are given for the sequence $\{W_n\}_{n=0}^{\infty}$ to converge a.s. to a non-negative and finite limit. Also, this sequence converges in L^1 to a non-negative and finite limit. These two limits are equal a.s. Similar results are obtained for the sequences $\{r^{-n}M_n\}_{n=0}^{\infty}$ and $\{r^{-n}F_n\}_{n=0}^{\infty}$. Finally, this paper begins a study of L^1 convergence under the classic $Z \log^+ Z$ condition (classic in the standard Galton-Watson branching process). Specifically, it is shown that if the perfect fidelity mating function governs a process, a finite value of $E[F \log^+ F]$ (F being the number of females generated by a single mating unit) will insure that the sequence $\{r^{-n}F_n\}_{n=0}^{\infty}$ converges in L^1 to a non-degenerate random variable. Some of the theory introduced in this paper is based upon the work of Klebaner on population-size dependent branching processes. Letting Y_n be the total number of mating units up to and including the nth generation, González and Molina (1997b) find a.s. limits for the sequences $\{Y_n\}_n^\infty$, $\{F_n\}_n^\infty$, and $\{M_n\}_n^\infty$.

González and Molina's next project (1997a) was to establish necessary and sufficient conditions for the L^2 convergence of $\{W_n\}_{n=0}^\infty$ to a nondegenerate limit. Assuming that the variance of the offspring distribution is finite, along with a superadditive mating function, Theorem 5.1 shows that the L^2 convergence of any one of the sequences $\{W_n\}_{n=0}^\infty$, $\{r^{-n}M_n\}_{n=0}^\infty$, and $\{r^{-n}F_n\}_{n=0}^\infty$ implies the L^2 convergence of the other two. Again, reference is made to the work of Klebaner (1984) and the connection between the bGWbp and population-size dependent branching processes.

González and Molina's 1998b paper extended their previous work (1996) on L^1 convergence under the classic $Z \log^+ Z$ condition from the perfect fidelity mating function to superadditive mating functions in general. The paper concludes with corollaries dealing with convergence on processes governed by Daley's two special mating functions.

3.2.2. A summary of the theory developed on convergence properties. Based mainly on the extensive work of González and Molina, there is a coherent theory for the L^1 and L^2 convergence of the three sequences $\{r^{-n}Z_n\}_{n=0}^\infty$, $\{r^{-n}M_n\}_{n=0}^\infty$ and $\{r^{-n}F_n\}_{n=0}^\infty$. If a two-sex species has a positive probability of survival, there are theoretical distributions to approximate the numbers of males, females, and mating units in the nth generation (for large values of n).

3.2.3. A suggestion for further research. So far, all we know is that the previously mentioned limiting distributions exist. Now, we need to focus on discovering the basic properties of these distributions. Bagley (1986) has made some suggestions on developing such properties in a section entitled "Remarks".

3.3. Multitype processes

3.3.1. The development of the theory. Karlin and Kaplan (1973) introduced the concept of a multitype bGWbp. (This is multitype in the sense that individuals in the species under consideration are in certain categories independent of the two sex designations.) Their Theorem 3 considers a bGWbp with the completely promiscuous mating function with multiple types of males and females. Analogous to the approach used in asexually reproducing multitype process, a matrix of means (m_{ij}) is constructed where m_{ij} is the mean number of offspring of type j generated by a female of type i. The classic result then follows, extinction is certain iff the largest positive eigenvalue of the matrix of means does not exceed one. The only unfortunate feature of Theorem 3 is that the a female can reproduce only when there are males of every type in her generation. This would suggest that a female will give birth only after interaction with every type of male in her generation. This unrealistic situation is made more palatable when there is just one type of male with several types of females. This formulation can be useful in considering the evolution of certain traits or characteristics in a species which offspring receive solely from their mothers when the process is governed by the completely promiscuous mating function.

The only other paper which has considered a multitype version of the bGWbp was written by Hull (1998). The intent of this work is to consider Galton's classic problem (which furnished the original motivation for the development of branching process theory) regarding the extinction of family names of *men of note*. Galton's problem is approached using the bGWbp, rather than the traditional asexual reproduction assumption.

Here, a multitype process is defined based on some characteristic that each individual inherits solely from his or her father (such as a title or surname). Specifically, we assume that every member of a given species has a property (or characteristic) that can be partitioned into two disjoint categories (called traits) P and N. P will be the trait of primary concern (i.e., those who possess a specific surname). Each mating unit carries the male's trait designation. Offspring generated by the mating unit receive the unit's trait designation. P-extinction is said to occur if all members of some generation of the species all possess trait N or if the entire species become extinct. P-permeation is said to occur if all members of some generation all possess trait P.

The main modification in the bGWbp needed to consider Galton's problem involves the mating function. We need a mating function, say M, with domain W^4 and range W^2, (W is the set of whole numbers.) of the form $M(x_p, x_n, y_p, y_n) = (s, t)$ where x_p and x_n represent the number of females in a given generation which have traits P and N respectively. y_p and y_n have similar meanings for the males in that generation. s represents the number of P-mating units and t the number of N-mating units in that generation.

There are four obvious conditions that should be imposed on M. These conditions are analogs of the conditions Daley placed on mating functions in his initial paper on the bGWbp (1968a). Let $M^{(1)}$ and $M^{(2)}$ be the component functions of M, i.e. $M^{(1)}(x_p, x_n, y_p, y_n) = s$ and $M^{(2)}(x_p, x_n, y_p, y_n) = t$; then

(1) $M^{(1)}(x_p, x_n, 0, y_n) = 0$ (No P-type males means no P-type mating units.)

(2) $M^{(2)}(x_p, x_n, y_p, 0) = 0$ (No N-type males means no N-type mating units.)

(3) $M^{(1)}$ is non-decreasing in y_p, in x_p, and in x_n and is non-increasing in y_n

(4) $M^{(2)}$ is non-decreasing in y_n, in x_p, and in x_n and is non-increasing in y_p.

The states in this Markov chain can be partitioned into the following mutually disjoint classes: I. the absorbing state $(0, 0)$, II. the P-permeation states $(k, 0)$, III. the P-extinction states $(0, k)$, and IV. the states (i, j) where i, j, and k are positive integers. The possible movements among these classes are indicated in the following transition diagram;

$$\begin{tikzcd} & \mathrm{II} \arrow[dr] & \\ \mathrm{IV} \arrow[ur] \arrow[rr] \arrow[dr] & & \mathrm{I.} \\ & \mathrm{III} \arrow[ur] & \end{tikzcd}$$

Since perfect fidelity was the standard of Galton's time and culture, that was the only mating function considered in this paper. The next relevant question is "If there are more males than females, who has the priority to mate?". Four distinct approaches are suggested. M_I – P-priority mating, P-type males secure mates before any N-type males are able to seek spouses. M_{II} - cross breeding preferred, opposite types are mated first. Any left-over individuals are allowed to have spouses of the same type. M_{III} - in breeding preferred, same types are mated first. Any left-over individuals are allowed to have spouses of a different type. M_{IV} – N-priority mating. Since Galton was concerned about upper class males, M_I is given the main emphasis in this paper. (Specific formulas for all four of these functions are given on pages 109-110 of this paper.)

Let $q_{i,j}$ denote the probability of P-extinction when there are i P-type and j N-type mating units in the initial generation. It is shown that $q_{i,j} = 1$ for all non-negative integers i and j iff Daley's necessary and sufficient condition (1968a) for certain extinction in a process governed by the perfect fidelity mating function holds. The next question is "If this condition does not hold, for what values of i and j will there be a positive probability of P-survival?". Theorem 4 gives sufficient conditions for survival in a perfect fidelity process for given values of i and j. Theorem 5 extends this to superadditive mating functions in general. The validity of several intuitive inequalities among P-extinction probabilities are demonstrated. The paper closes with a comparison of P-extinction probabilities using this new version of the bGWbp with Alfred Lotka's (1931a,b) classic results from the 1920 U.S. census.

3.3.2. A summary of the theory developed on multitype processes. This will be very brief since this is a relatively untouched topic. We do have a necessary and sufficient condition for certain extinction for a species governed by the completely promiscuous mating function when there are several types of females, but only one kind of male. We also have a theory of extinction for a certain paternal trait in a species that employs the perfect fidelity mating function.

3.3.3. Suggestions for further research. Multitype processes will be the most relevant topic for future research associated with the bisexual process. We most develop an *extinction theory* for traits that are inherited from both parents (not just the Father, as in Hull's paper). We need to consider superadditive mating functions in general and how they might relate to Hull's M-notation (priority in mating). It has been said that the 20$^{\text{th}}$ century was the century of physics and the 21$^{\text{st}}$ century will be the age of biology. The bGWbp may be the most relevant model to use in questions associated with the human genome. But first, a multitype bGWbp needs to be developed to model classic Mendellian genetics.

3.4. A statistical approach to the bGWbp

3.4.1. The development of the theory. There are five papers that belong in this category. Instead of assuming that the bGWbp parameters are known, González and Perez-Abreu (1991) constructed maximum likelihood estimators for the mean number of females per mating unit, the mean number of males per mating unit, and the asymptotic growth rate r. Superadditivity is assumed throughout the paper. Also, the inequality $\zeta(x, y) \leq x$ is assumed. These estimators are shown to be consistent and efficient. Finally, certain products and differences associated with these estimators are shown to be asymptotically normal.

González (1995) developed ratio estimators of the offspring means (male and female), which are important in determining if extinction is certain. This paper recognizes and reviews maximum likelihood estimators of these means (as developed in the previous paper). However, González makes a strong argument for the use of his ratio estimators by stating several advantages associated with the use of these estimators when compared to the maximum likelihood estimators. In addition to these advantages, the paper presents three theorems which show that the ratio estimators are unbiased and consistent estimators of the offspring means, and there is convergence in distribution to a bivariate normal distribution.

González and Molina (1998a) assume that the number of males and females in the first n generations of a bisexual process have been observed. Nonparametric estimators for the mean and variance of the numbers of males and females generated by a mating unit are constructed and their moment properties are investigated.

Molina, González and Mota (1998) introduced a Bayesian approach for estimating parameters in a bGWbp. Two different models are considered. The first model (the parametric case) assumes that the offspring distribution belongs to a power series family of distributions having the form $p_{jk} = a_{jk}\Theta_1^j\Theta_2^k(A(\Theta_1,\Theta_2))^{-1}$ where j is the number of females and k, the number of males generated by a mating unit. (This is an exponential family which includes the bivariate Poisson, trinomial, and negative trinomial distributions.) The second model (the nonparametric case) has a finite set S as the support for the offspring probability distribution p_{jk}.

In both cases, Bayes estimators under weighted squared error loss are obtained for the means, variances, and the covariance of an offspring probability distribution. A Bayes estimator for the asymptotic growth rate r is formulated for those processes governed by superadditive mating functions.

González, Molina and Mota (2001a) obtain estimators for the offspring distribution and for the mean numbers of females and males generated by a mating unit in a nonparametric setting. That is, if p_{jk} is the probability that a mating unit produces j females and k males, the probability distribution $\{p_{jk}\}$ has its support S contained in the Cartesian Product of the set of nonnegative integers with itself.

Assuming the entire family tree of the species under consideration up to the current nth generation has been observed, it is shown that the maximum likelihood estimator of p_{jk} is the relative proportion of mating units (in the known history of the species) that has generated exactly j females and k males. Conditional moments given non-extinction, unconditional moments, asymptotic properties, and confidence intervals associated with this estimator are developed. This maximum likelihood estimator is shown to be a strongly consistent estimator of p_{jk} and certain expressions involving this estimator converge in probability to standard normal.

Estimation of the mean vector (i.e. the mean numbers of females and of males generated by a mating unit) is considered as three cases. Case 1: only the number of mating units in the $(n-1)$st generation and the numbers of males and females in the nth generation are known. A method of moments estimator is obtained. Case 2: a complete history of the species up to and including the nth generation is known (i.e the numbers of males and females in these generations are available and are used). A weighted average of estimators for the various generations (as used in Case 1) is developed. Case 3: a maximum likelihood estimator based on the entire species history up to the nth generation is presented. As before, moments, asymptotic properties, and confidence intervals associated with these estimators are developed. Again, the estimators are strongly consistent and certain expressions involving these estimators converge in probability to standard normal.

3.4.2. A SUMMARY OF THE THEORY DEVELOPED ON STATISTICAL APPROACHES. The previous mentioned five papers offer a substantial number of estimators having good properties for the estimation of offspring means and variances and for the asymptotic growth rate r. Classical and Bayesian approaches have been used. Both the parametric and non-parametric cases have been considered.

3.4.3. SUGGESTIONS FOR FURTHER RESEARCH. Section 3.5 will present some modifications to the bGWbp. Each of these new processes will require estimators for its offspring distribution and the asymptotic growth rate. Some thought has been given to the form of these estimators. Some effort will be needed to construct proofs of the desirable characteristics of these estimators.

If we have data for r generations, say Z_{n+j}, M_{n+j}, and F_{n+j}, $j = 1, 2, \ldots, r$, can we form estimators for n (the generation number) and for Z_0 (the number of individuals in the initial generation)? Also, given certain ordered pairs (i, j), we may need an estimate of the mating function value $\zeta(i, j)$.

3.5. SOME MODIFIED BISEXUAL GALTON-WATSON BRANCHING PROCESSES

3.5.1. THE DEVELOPMENT OF THE THEORY Recent modifications of the bGWbp can be placed in three categories; immigration (4 papers), population-size dependent mating (1 paper), and processes in varying environments (1 paper). We will consider these topics in the above order.

González, Molina and Mota (1999) introduced the concept of immigration into the bGWbp. They considered two models; (1) the immigration of males and females into the general population and (2) the immigration of mating units. The following topics are considered in both models; communication classes of states in the underlying Markov chains, equations and inequalities relating the generating functions associated with births and immigration, and equations and inequalities relating reproduction means and covariance matrices with immigration means and covariance matrices. Estimators for the mean numbers of males and females by means of birth and immigration are developed in model one. These estimators are shown to be unbiased and strongly consistent. The authors note that many of their results are analogous to those obtained when immigration is applied in the standard (asexual reproduction) Galton-Watson branching process.

González, Molina and Mota (2000) considered the introduction of immigration into a subcritical bGWbp (subcritical in the sense that the growth rate limit $r < 1$). Using model 1 (as in their previous paper) with r_k the mean growth rate of the kth generation in the subcritical bGWbp and r_k^* the mean growth rate in the kth generation of the modified process where immigration may occur in certain generations, González et al. state sufficient conditions are given so that the sequence $\{r_k^*\}_{k=1}^{\infty}$ (as well as the sequence $\{r_k\}_{k=1}^{\infty}$) converges to r as n goes to infinity. A counter-example is given which shows that the convergence of the r_k^*-sequence to r does not occur in general. Since $r < 1$ (with a superadditive mating function), it is known that the sequence $\{Z_n\}_{n=0}^{\infty}$ converges in distribution to a non-degenerate random variable in 0 as n goes to infinity. Let $\{Z_n^*\}_{n=0}^{\infty}$ be the number of mating units in the nth generation of the modified process with immigration. Conditions are given so that the sequence $\{Z_n^*\}_{n=0}^{\infty}$ converges in distribution to a positive, finite, and non-degenerate random variable as n goes to infinity. A corollary which relates the mean numbers of males and females in the two processes then follows.

González, Molina and Mota (2001b) continue their development of a bGWbp theory with immigration included in the model. In particular, they develop convergence properties when the asymptotic growth rate r is greater than one, the mating function is superadditive, and mating units are allowed to immigrate into the population. The sequence $\{I_n\}_{n=1}^{\infty}$ is a sequence of i.i.d. non-negative integer-valued random variables representing the number of immigrating mating units in the various generations.

Z_n, M_n, and F_n are the numbers of mating units, males and females in the nth generation with immigrants entering the population in that generation included. The relevant sequences are $\{r^{-n}Z_n\}_{n=0}^{\infty}$, $\{r^{-n}M_n\}_{n=0}^{\infty}$ and $\{r^{-n}F_n\}_{n=0}^{\infty}$. Under appropriate conditions, these sequences converge almost surely and converge in L^1, to non-negative, finite random variables.

The above paper introduced immigration into a bGWbp of model 2 type as in González, Molina and Mota (1999). Their next paper (González, Molina and Mota, 2002) included immigration in a bGWbp of model 1 type. The mating function is assumed to be superadditive. Emphasis is placed on the case where $r > 1$. Under appropriate conditions the same three sequences defined in the previous paper are shown to converge a.s to finite, non-negative, and non-degenerate random variables.

Molina, Mota and Ramos (2002a) have introduced a bGWbp where the mating function depends on the population size in each generation. Here it is assumed that the process is governed by a sequence of mating functions. Each function in this sequence corresponds to a particular population value. Several equations and inequalities using the generating functions of the numbers of males and females in the nth generation, the number of mating units in the nth generation (n, a positive integer), and the numbers of males and females generated by a single mating unit are developed. These lead to equations and inequalities involving the means and variances of the numbers of mating units in succeeding generations and to a sufficient condition for the number of mating units in the nth generation either to go to zero or to go to infinity as n goes to infinity. Superadditivity is applied in this model in two forms. Necessary and sufficient conditions for a.s. extinction (using mean growth rates) are presented for both superadditivity forms.

A third type of variation in the bGWbp has been provided by Molina, Mota and Ramos (2002b). This paper considers a bGWbp where the offspring probability distribution varies among the generations. Probability generating functions are defined for the numbers of females and males generated by a mating unit in the nth generation (n, a positive integer), the total number of individuals generated by a mating unit in the nth generation, the numbers of females and males in the nth generation, the number of mating units in the nth generation, and the number of mating units generated by a mating units in the nth generation if only full siblings are allowed to mate. This paper presents numerous equations and inequalities using these generating functions. Mean growth rates per mating unit are defined in a manner in a manner similar to Daley et al. (1986). Necessary and sufficient conditions for a.s. extinction are developed in terms of these mean growth rates and certain fractional linear functions.

3.5.2. A SUMMARY OF THE THEORY DEVELOPED ON THE IMMIGRATION MODEL. We will comment only on the immigration model since each of the latter two models has only one published paper. González, Molina and Mota have introduced this model, specified the two types of immigration, and have laid a theoretical foundation with their expositions on generating functions, their initial development of relevant estimators, the use of the asymptotic growth rate as it relates to extinction, and some significant convergence properties.

3.5.3. SUGGESTIONS FOR FURTHER RESEARCH. Since the immigration model comes to us in an introductory phase, it is apparent that there is refinement and development needed for each of the topics mentioned in the preceding section. In particular, other estimators and their properties should be developed. Theoretical considerations associated with the comment "the r_k^* sequence does not generally converge to r" should be explored. Finally, given a sub-critical or critical process ($r < 1$), what immigration characteristics will create a positive probability of survival. Also, given a super-critical process ($r > 1$), what emigration characteristics will cause certain extinction.

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