

Ancestries of a Recombining Diploid Population

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Part I is joint work with: James Briskie, Marie Hale, Melanie Massaro, Don Merton, Anthony Poole (NZ)

Part II is joint work with: Bhalchandra Thatte (Brasil) and Amandine Veber (France)

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Ecological History of Black Robins

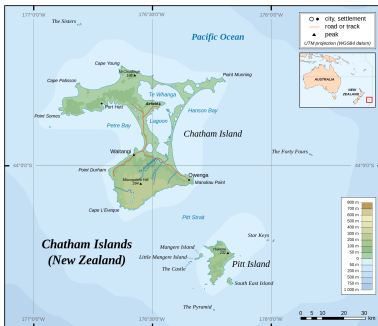
Likelihood of Population Pedigrees

Insights from the field

Ancestries of Recombining Diploid Populations

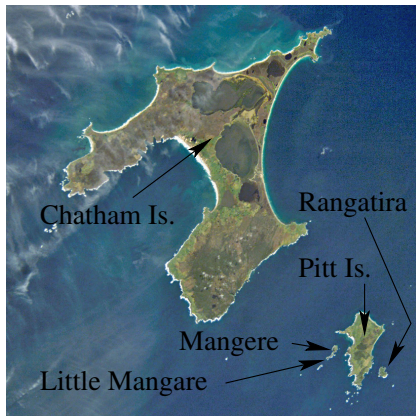
Part I

Map of Antarctica / Chatham Islands (New Zealand)



- ▶ The Chatham Islands lie 800 kms east of Christchurch.
- ▶ Two main islands – Chatham Island and Pitt Island

Chatham Islands (New Zealand)



- ▶ Many smaller islands – including Little Mangere, Mangere and Rangatira
- ▶ The islands have only emerged above sea level in the last 4 million years and are part of the Chathams rise connected below ocean to NZ.
- ▶ The climate is cool and wet with salt-laden winds all year round.

Chatham Islands (New Zealand)

Rangatira Island

- ▶ is the third largest island in the Chatham Islands
- ▶ covers an area of 218 hectares (539 acres)
- ▶ is a gazetted nature reserve since 1953
- ▶ is now home to many endemic species
- ▶ is **home to black robins** — saved from near extinction by team led by Don Merton in the 1980s

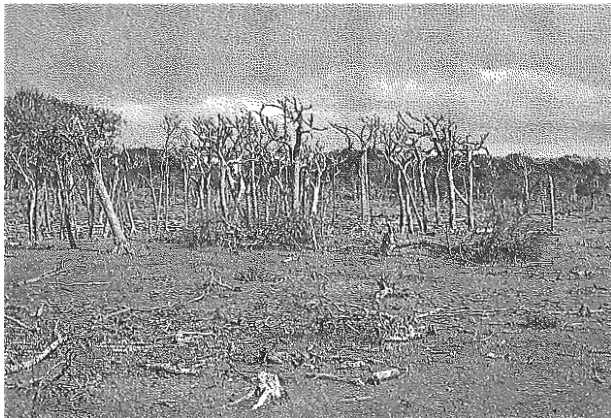


A Chatham island Black Robin in Rangatira today



Decimation and Conservation

Whaling (< 1964), Sealing (< 1926) & Farming destroyed Ecosystems



Decimation and Conservation

By 1938 black robins were wiped off from all the Chatham islands except for a few pairs on Little Mangare (a rocky outcrop of 15ha of bush)



Decimation and Conservation

Crown buys Rangatira and Magere Islands



Decimation and Conservation

A Massive Restoration Ecological Effort



Decimation and Conservation

Ecological Engineering of Native Flora and Predator-Proofing



Decimation and Conservation

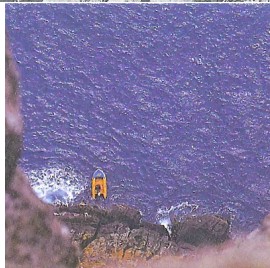
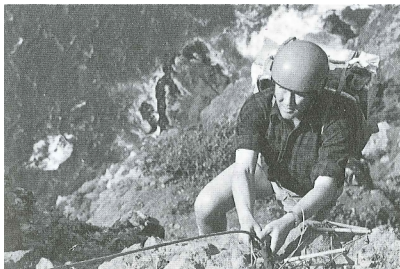
Native fauna (sea-birds) start returning



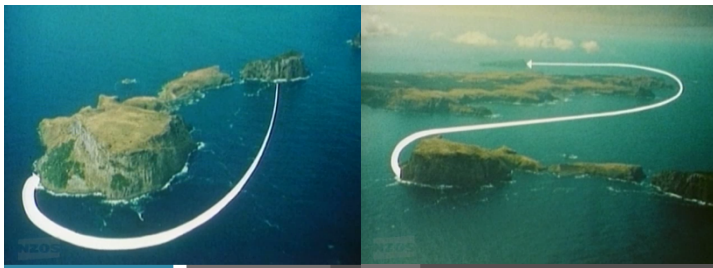
Early Studies and Relocation in 1980s

Little Mangare Island

- ▶ Studies in 1970s by Douglas Flack on Little Mangare (15ha) tracked a handful of breeding pairs and
- ▶ recommended translocation to nearby Mangere (113ha) and Rangatira islands (218ha)



Species Recovery Program in 1980s



Last 7 robins were moved.

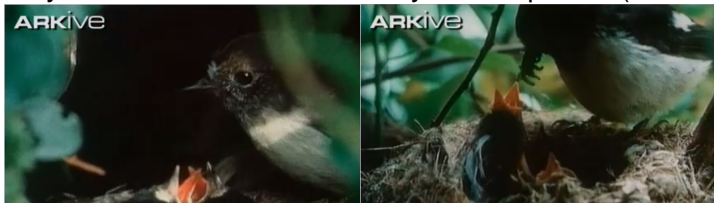


Species Recovery Program in 1980s

Eggs were removed after being laid to encourage egg-laying



They were hatched and raised by foster species (tomtits)



Species Recovery Program in 1980s

the foster-cared chicks were transferred to black robin nests for sexual imprinting by its own species



Species Recovery Program in 1980s

Managements ceased when the population reached about 100

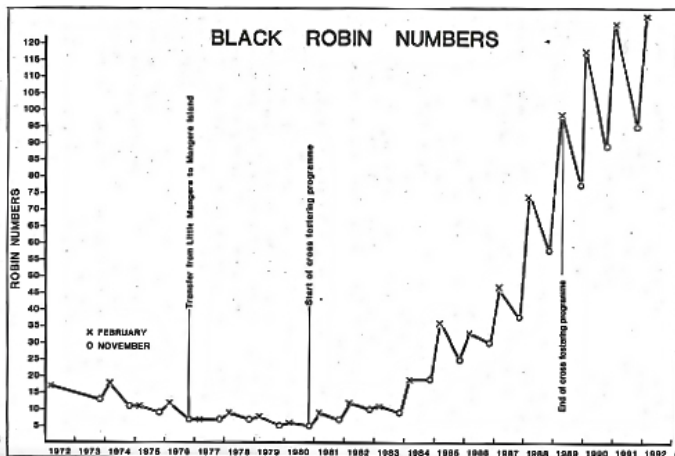


Fig. 22. Black robin numbers

Species Recovery Program in 1980s

Well-laid Eggs

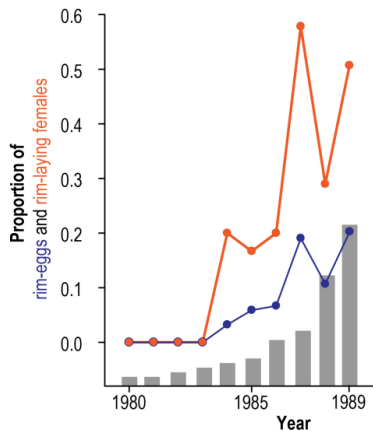


Rim-laid Egg



Unfortunately, a maladaptive behavioural trait of “rim-laying” also increased with the population

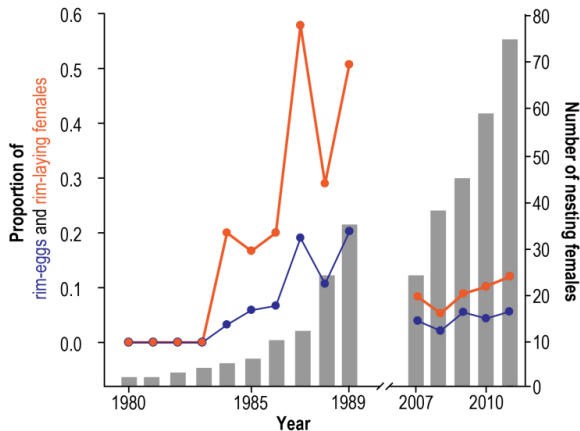
The Conservation Dilemma



Rim-laying increases in 1980s

- ▶ **Conservation Dilemma**
 - when to cease management?
- ▶ Need managed pop. size to ↑
- ▶ But rim-laying trait also ↑
- ▶ Don Merton's team ceased management when 50% of females were rim-layers by 1989
- ▶ **Our Question:** Is rim-laying a heritable trait?

The Conservation Dilemma



Rim-laying increases in 1980s

but between 2007 and 2011 (unmanaged phase) rim-laying is lower

The Conservation Dilemma

Fitness	Normal-laying	Rim-laying	Statistics			
Measure	Females (\pm std. err.)	Females (\pm std. err.)	<i>n</i>	χ^2	df	p-value
Clutch size	2.02 (\pm 0.03)	1.12 (\pm 0.11)	281	10.98	1	0.0009
Hatching success	1.48 (\pm 0.05)	0.61 (\pm 0.12)	260	29.48	1	<0.001
Fledgling success	1.03 (\pm 0.06)	0.50 (\pm 0.13)	242	9.41	1	0.0021

Data from 2007–11 (during which rim eggs were not repositioned) shows that females that laid rim eggs had a significantly reduced clutch size (i.e. number of eggs laid inside nests that were incubated), and decreased hatching and breeding success compared to normal-laying females. We obtain p-values from likelihood ratio tests with generalized linear mixed models of data with sample size *n*.

doi:10.1371/journal.pone.0079066.t001

Rim-laying females have reduced

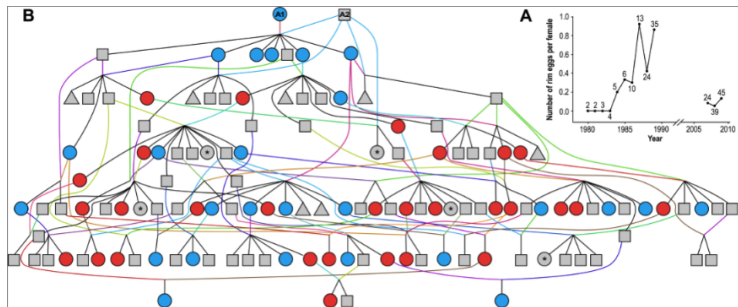
- ▶ clutch size
- ▶ hatching success
- ▶ fledgling success

during 2007-2011 (unmanaged phase)

Our Hypothesis: If rim-laying is heritable then natural selection would purge it from the population during unmanaged phase.

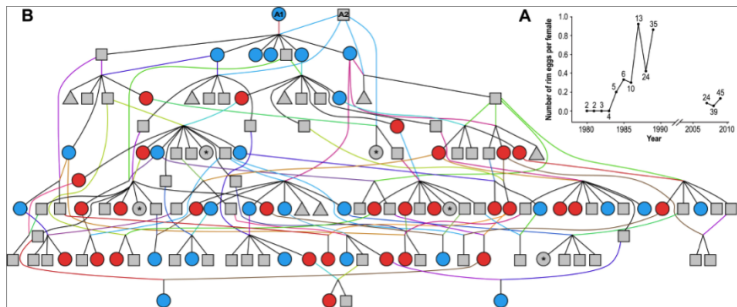
Need to show: rim-laying is heritable

Highly Looped Black Robin Pedigree in 1980s



cicle = female, square = male, traingle = unknown sex,
 red circle = rim-layer, blue circle = non-rim-layer

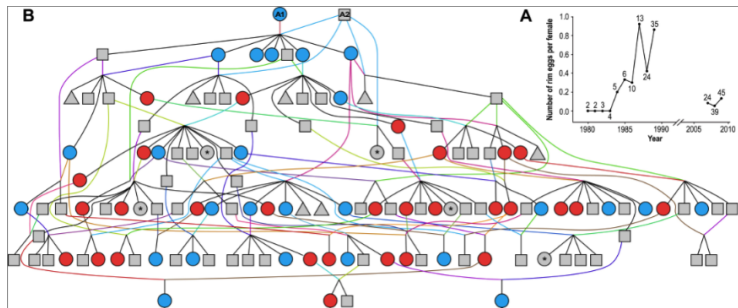
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Want: The likelihood of the observed rim-laying phenotypes on this population pedigree.

Highly Looped Black Robin Pedigree in 1980s



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Want: The likelihood of the observed rim-laying phenotypes on this population pedigree. **Trouble:** The likelihood via Peeling Algorithm (Cannings, Thompson & Skolnick 1978) in standard pedigree software runs out of RAM!

Likelihood of the Phenotypes on the Pedigree

For the likelihood we need:

1. simplest Model for Pedigree

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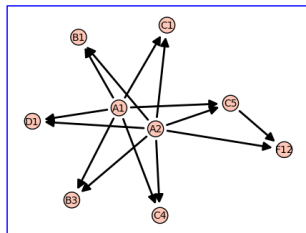
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Likelihood of the Phenotypes on the Pedigree

For the likelihood we need:

1. simplest Model for Pedigree
2. Phenotypes and Genotypes
3. Model for Mendelian Inheritance
4. Likelihood = the proportion of joint genotypic configurations that are compatible with the observed phenotypes under the model of inheritance on the observed pedigree

Simple Pedigree

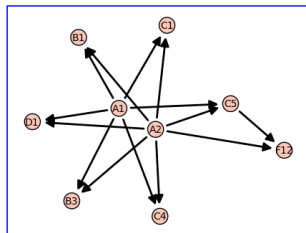


A pedigree is a directed acyclic graph $\mathcal{G} := (\mathbb{V}, \mathbb{E})$ in which \mathbb{V} partitions a set of individuals (males, females, unknown-sex):

$$\mathbb{V} = \mathbb{M} \cup \mathbb{F} \cup \mathbb{U}$$

and where each vertex either has no-incoming arc or two incoming arcs, with one from a vertex in \mathbb{M} and the other from a vertex in \mathbb{F} .

Simple Pedigree



Let the female and male founders be

$$\mathbb{A} := \{A1, A2\}$$

For an individual

$$u \in \mathbb{V} \setminus \mathbb{A}, \text{ let } M_u \text{ and } F_u$$

denote its mother and father, respectively.

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$$\text{for every } u \in \mathbb{L}, \quad \phi(u) = \begin{cases} 1 & \text{if } u \text{ lays rim eggs} \\ 0 & \text{if } u \text{ lays normal eggs} \end{cases} \quad (1)$$

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$$\mathbb{U} := \{u_1, \dots, u_m\}$$

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$$\phi(\mathbb{U}) := \{\phi(u) : u \in \mathbb{U}\} = \{\phi(u_1), \dots, \phi(u_m)\}$$

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So, with ~ 100 individuals in 1980-89: $|\Gamma^{\mathbb{V}}| = 4^{|\mathbb{V}|} > 10^{60}$

Mendelian Inheritance – Prob. of Genotype

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$$\Pr(\gamma(u) \mid \gamma(M_u), \gamma(F_u), \mathcal{M}_h^c)$$

$$= \begin{cases} \frac{1}{4} & \text{if } c = \alpha, \gamma_m(u) \in \{\gamma_m(M_u), \gamma_f(M_u)\}, \\ & \gamma_f(u) \in \{\gamma_m(F_u), \gamma_f(F_u)\} \\ \frac{1}{2} & \text{if } c = z, \gamma_m(u) = \gamma_f(M_u), \\ & \gamma_f(u) \in \{\gamma_m(F_u), \gamma_f(F_u)\}, u \in \mathbb{M} \\ \frac{1}{2} & \text{if } c = z, \gamma_m(u) = \gamma_m(M_u), \\ & \gamma_f(u) \in \{\gamma_m(F_u), \gamma_f(F_u)\}, u \in \mathbb{F} \\ 0 & \text{otherwise.} \end{cases} \quad (2)$$

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Finally the probability of $\phi(u)$, the phenotype for an individual u , given its genotype $\gamma(u)$ and the model of inheritance \mathcal{M}_h^c is the following:

Mendelian Inheritance – Prob. of Phenotype

Finally the probability of $\phi(u)$, the phenotype for an individual u , given its genotype $\gamma(u)$ and the model of inheritance \mathcal{M}_h^c is the following:

$$\Pr(\phi(u) \mid \gamma(u), \mathcal{M}_h^c) = \begin{cases} 1 & \text{if } \phi(u) = 1, \gamma(u) \in \Gamma \setminus \{(a, a)\}, h = D, u \in \mathbb{L} \\ 1 & \text{if } \phi(u) = 0, \gamma(u) \in \{(a, a)\}, h = D, u \in \mathbb{L} \\ 1 & \text{if } \phi(u) = 0, \gamma(u) \in \Gamma \setminus \{(a, a)\}, h = R, u \in \mathbb{L} \\ 1 & \text{if } \phi(u) = 1, \gamma(u) \in \{(a, a)\}, h = R, u \in \mathbb{L} \\ 1 & \text{if } u \notin \mathbb{L} \\ 0 & \text{otherwise.} \end{cases} \quad (3)$$

Likelihood, Prior and Posterior

We want probability of the inheritance model \mathcal{M}_h^c

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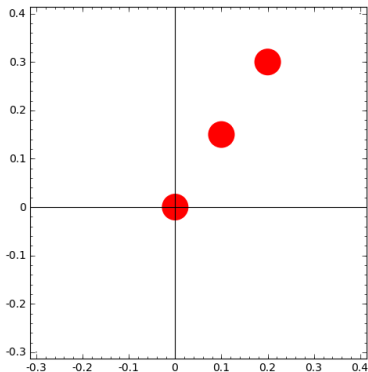
We assume a uniform prior probability $\Pr(\mathcal{M}_h^c, \gamma(\mathbb{A})) = \frac{1}{64}$ over the $2 \times 2 \times 4^2 = 64$ models in the family:

$$\{(\mathcal{M}_h^c, \gamma(\mathbb{A})) : c \in \{a, z\}, h \in \{D, R\}, \gamma(\mathbb{A}) \in \Gamma^{\mathbb{A}}\} .$$

Likelihood Computation - A Pedagogical Example

Sequential Monte Carlo (SMC) Algorithm for Rare Event Simulation

(Johansen, Del Moral & Doucet, 2006)



What is Prob. of Hitting First Red dot and then Second Red Dot?

Likelihood Computation - A Pedagogical Example

Sequential Monte Carlo (SMC) Algorithm for Rare Event Simulation

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Estim. Prob. Hitting First Red dot = $1/9$

Likelihood Computation - A Pedagogical Example

Sequential Monte Carlo (SMC) Algorithm for Rare Event Simulation

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Estim. Prob. Hitting First and Second Red Dots = $1/9 \times 1/9 = 1/81$

Likelihood Computation - Adapting SMC to Pedigrees

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$\Pr(\phi(\mathbb{V}) \mid \mathcal{G}, \mathcal{M}_h^c, \gamma(\mathbb{A}))$, the likelihood in (4), is computed using a sequential Monte Carlo Algorithm.

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The strategy involves sequentially growing the pedigree as a nested and increasing family of sub-graphs via a breadth-first expansion from the founders A1 and A2.

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Let $\mathcal{G}[\mathbb{V}_t]$ denote the sub-pedigree of \mathcal{G} induced by vertices \mathbb{V}_t .

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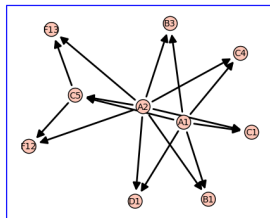
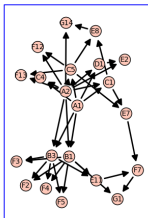
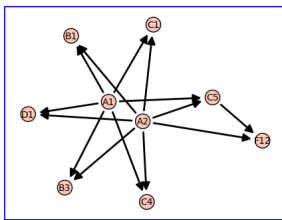
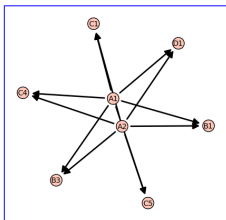
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Let $\mathbb{A} = \mathbb{V}_0 \subset \mathbb{V}_1 \subset \dots \subset \mathbb{V}_T = \mathbb{V}$ denote the increasing sequence of vertices in \mathcal{G} obtained by a breadth-first expansion from \mathbb{V}_0

Sequential Monte Carlo on Nested Combinatorial Structures



Sequential Monte Carlo on Nested Combinatorial Structures

- ▶ At $t = 0$, initialize all particles at the founder nodes
 - FOR $i = 1, \dots, N$; DO:
 - ▶ $\gamma_0^{(i)}(u) \leftarrow \gamma(u)$, for each founder $u \in \mathbb{V}_0 = \mathbb{A}$
 - ▶ $W_0^{(i)} \leftarrow \prod_{u \in \mathbb{V}_0} \Pr(\phi(u) \mid \gamma_0^{(i)}(u), \mathcal{M}_h^c)$
- ▶ FOR $t = 1, \dots, T$; DO:
 - ▶ Resample to obtain $\left\{ \frac{1}{N}, \left(\hat{\gamma}_{t-1}^{(i)}(u) : u \in \mathbb{V}_{t-1} \right) \right\}_{i=1}^N$
 - ▶ FOR $i = 1, \dots, N$; DO:
 - ▶ Extend $\left\{ \hat{\gamma}_{t-1}^{(i)}(u) : u \in \mathbb{V}_{t-1} \right\}$ to $\left\{ \gamma_t^{(i)}(u) : u \in \mathbb{V}_t \right\}$ by proposing genotypes for each new offspring node in $\mathbb{V}_t \setminus \mathbb{V}_{t-1}$ according to \mathcal{M}_h^c and the genotypes of its parent nodes in \mathbb{V}_{t-1} specified by the sub-pedigree $\mathcal{G}[\mathbb{V}_t]$.
 - ▶ $W_t^{(i)} \leftarrow \prod_{u \in \mathbb{V}_t \setminus \mathbb{V}_{t-1}} \Pr(\phi(u) \mid \gamma_t^{(i)}(u), \mathcal{M}_h^c)$
- ▶ Estimate $\Pr(\mathcal{G}, \phi(\mathbb{V}) \mid \mathcal{M}_j^c, \gamma(\mathbb{A}))$ by $\prod_{t=0}^T \hat{Z}_t$, $\hat{Z}_t = \frac{1}{N} \sum_{i=1}^N W_t^{(i)}$.

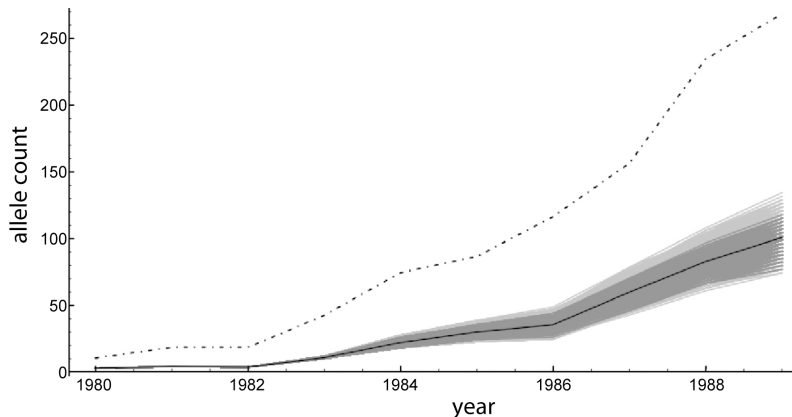
Model Selection – Results

Model	Founder Genotype	Mendelian	Chromosomal	$-2 \times \log$	Posterior
Number	Female \times Male	Inheritance	Location	likelihood	Probability
1	Aa \times AA	Recessive	Autosome	92.250	0.0013
2	AA \times Aa	Recessive	Autosome	92.428	0.0012
3	Aa \times Aa	Recessive	Autosome	87.486	0.0142
4	aa \times Aa	Dominant	Autosome	79.006	0.9832
5	aa \times Aa	Dominant	Z	96.988	0.0001

Log likelihood and posterior probability of the phenotypes conditional on the pedigree, founder genotypes and model of inheritance. Z is a sex chromosome. The prior probability of each model is uniformly distributed and all other models considered (see text) have zero likelihood.
doi:10.1371/journal.pone.0079066.t002

The best model (Model 4) is the simple autosomal dominant model with homozygous founding female (aa) and heterozygous founding male (Aa).

Allele Trajectory – Results



Inferred trajectories of allele A under Model 4 between 1980 and 1989. The mean trajectory (black); 50% and 95% confidence sets (dark & light grey); $2N$ (dash-dotted).

Phenotype Permutation Test of Heritability

- ▶ Under Null Hyp.: Environmental (non-genetic) Basis to Rim-Laying
- ▶ Permuting female phenotypes would leave the null likelihood unchanged
- ▶ Use likelihood under Model 4 as the test statistic
- ▶ p-value = fraction of 10000 phenotype permutations have a likelihood greater than the observed likelihood
- ▶ Result: p-value = 0.03

Conclusions - Part I

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- ▶ Merton suspected rim-laying was heritable (persn. commn. to Massaro)

Conclusions - Part I contd...

- ▶ Our research group at Canterbury (with Briskie, Hale, Massaro and Poole) have developed tests to establish that rim-laying during 1980s is likely to be a heritable trait

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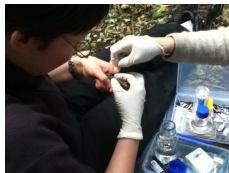
Conclusions - Part I contd...

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- ▶ To appreciate the intensity of field operations and limitations of biomathematical models read: *The black robin: saving the world's most endangered bird*, David Butler and Don Merton, Oxford University Press, 1994.

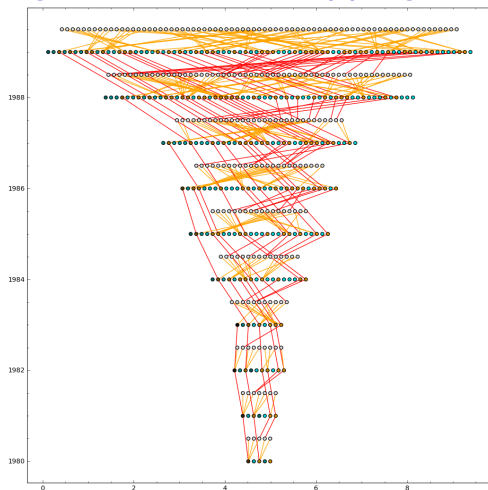
Insights from field work in November 2011



A Chatham island Black Robin in Rangatira today

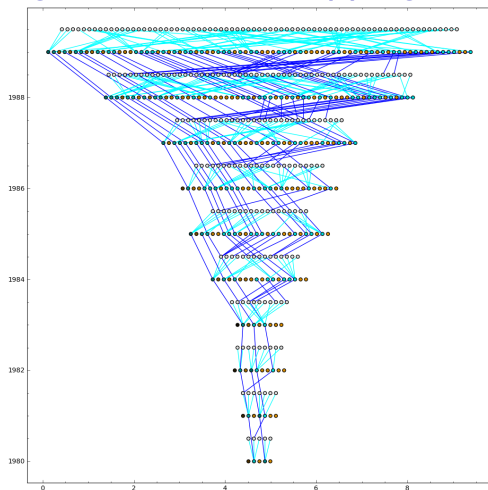


Temporal Pedigrees with Overlapping Generations



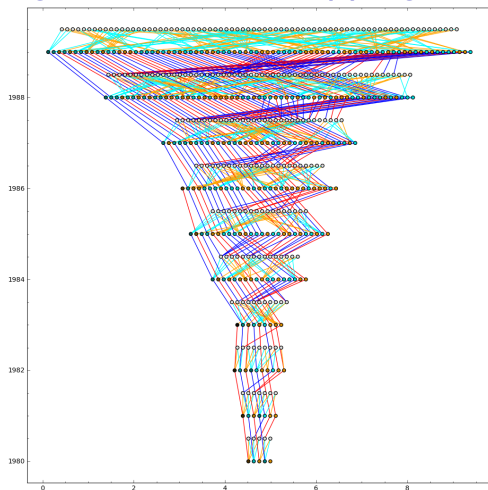
Female Population Tree during Field Conservation in 1980s

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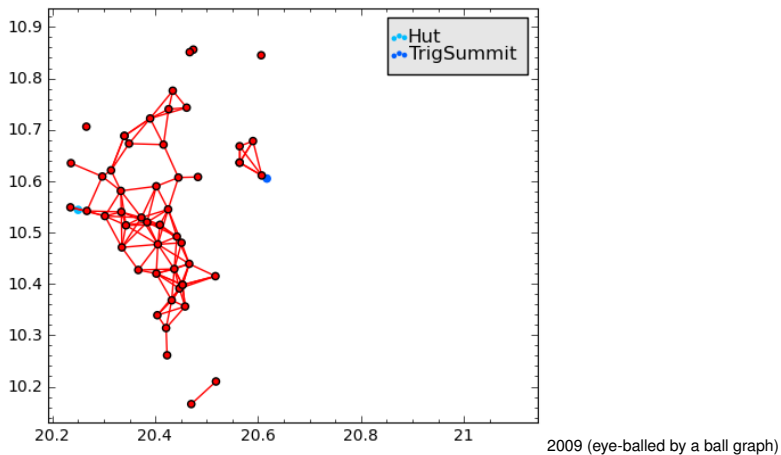


Population Pedigree during Field Conservation in 1980s

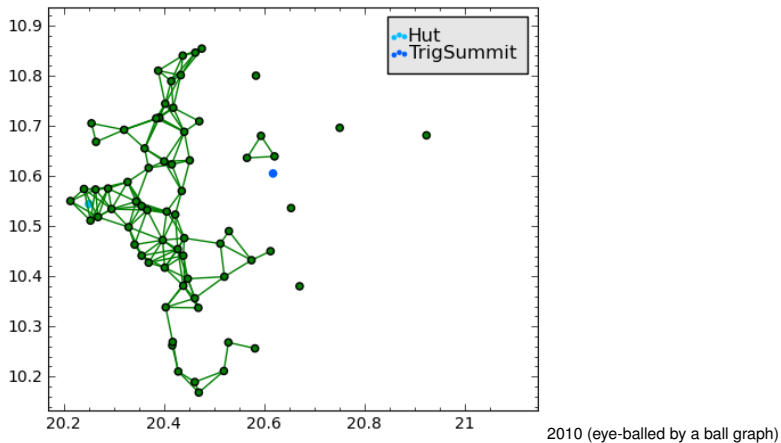
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Coalescent Sub-Pedigree of the 1989 population \implies Part ARDP

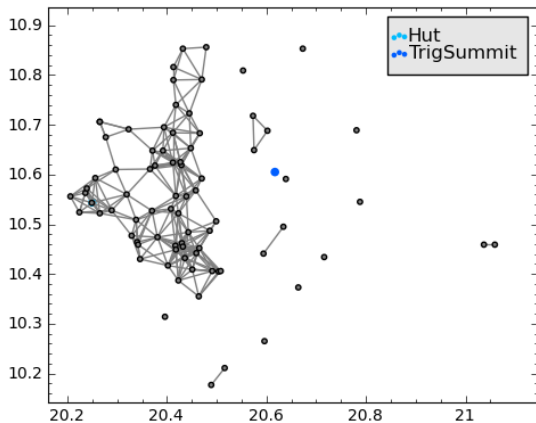
Male Territory Graphs by year



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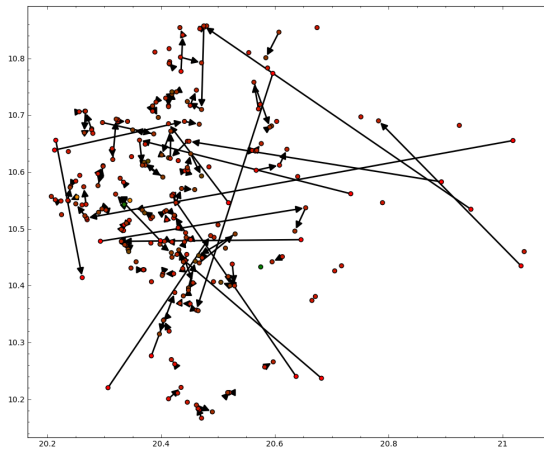


Male Territory Graphs by year



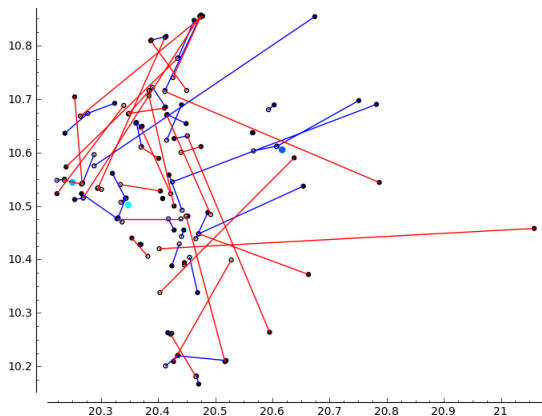
2011 (eye-balled by a ball graph)

Male Territorial Dynamics – yearly nest site relocation

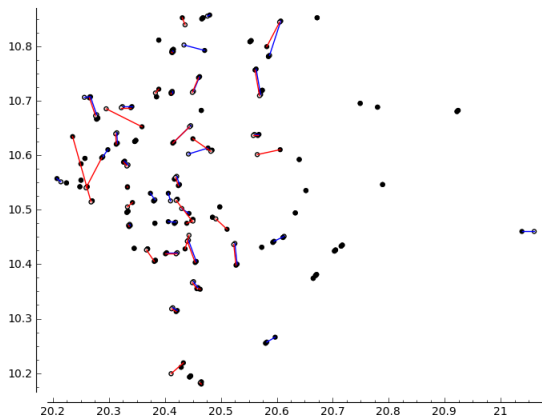


Male / Female yearly nest to nest distance

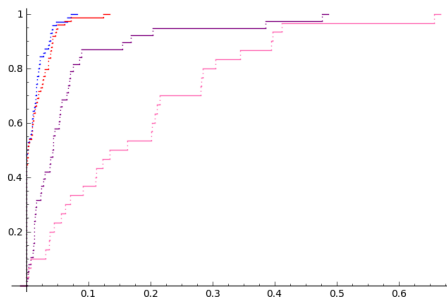
sex-specific distance between home nest and first nest



Male / Female yearly nest to nest distance

sex-specific distance between nest at age ≥ 1 and next nest

Male / Female yearly nest to nest distance

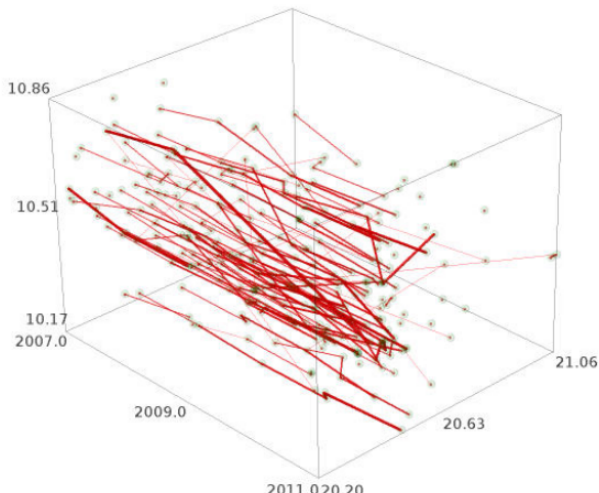


male / female distance from home nest to first nest

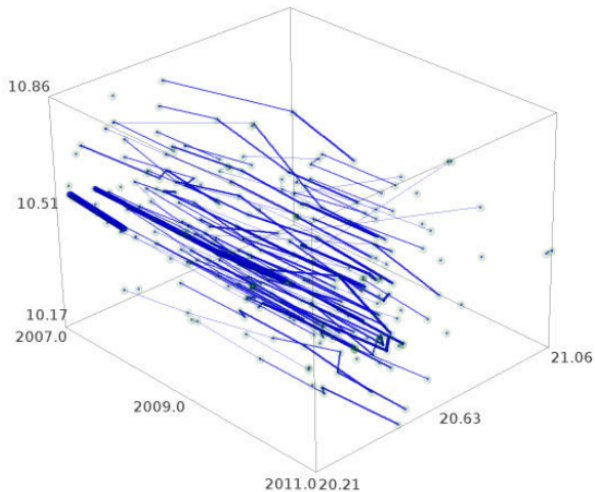
male / female distance from nest at age ≥ 1 to next nest

- ▶ Permutation Test to Reject H_0 : male dist = female dist (10⁵ MC samples)
- ▶ Strongly reject H_0 for home to first nest (pv = 0.00025)
- ▶ Fail to reject H_0 for nest at age ≥ 1 to next nest (pv = 0.14)

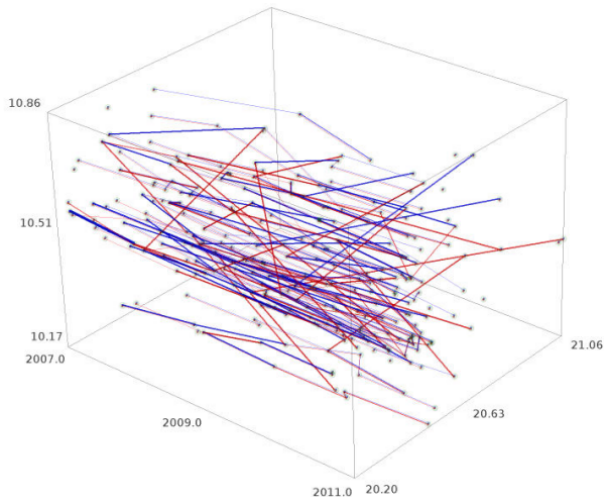
Need Models of Spatio-temporal Behavioural Population Pedigrees



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Part II

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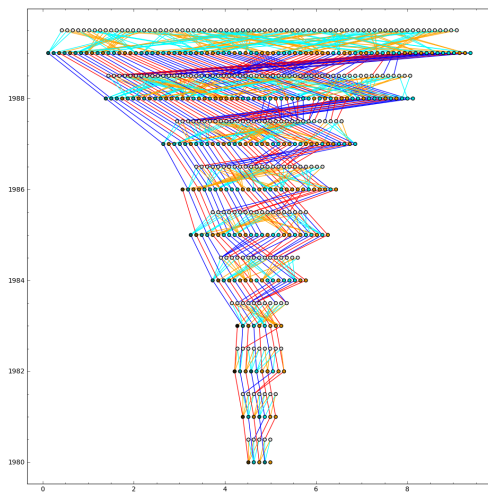
Ancestries of Recombining Diploid Populations

Raazesh Sainudiin, Bhalchandra Thatte, and Amandine Véber,

Journal of Mathematical Biology, 46 pages, 2015

Diploid Ancestries

└ Ancestries of Recombining Diploid Populations



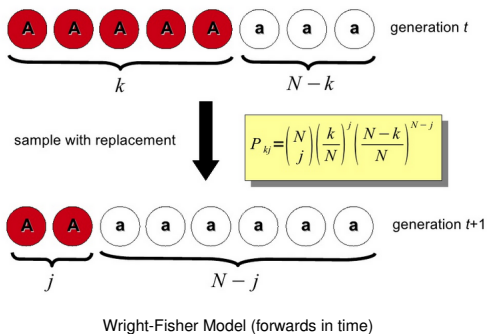
Motivation: Diploid Population Pedigree (forwards in time)

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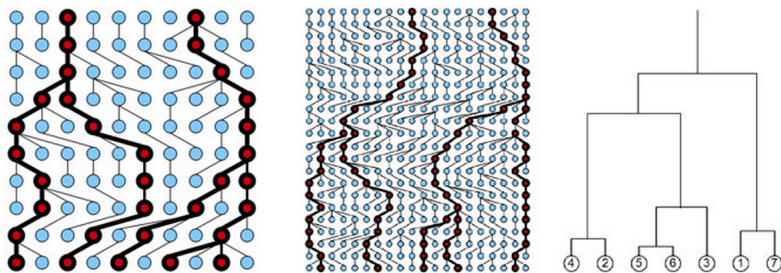
Coalescent Sub-Pedigree (backwards in time) “inheritance topology of diploid zygotes?”

Three Notions of Molecular continuums within W-F Population Pedigrees

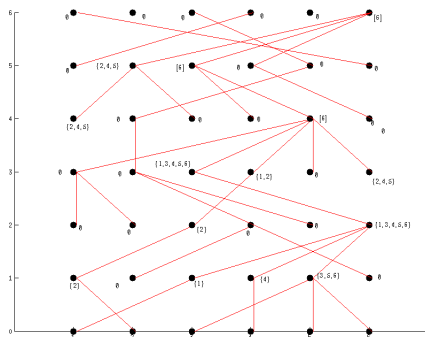
One r to rule them all!

where $r = 0$ is the probability of recombination per locus per meiotic generation

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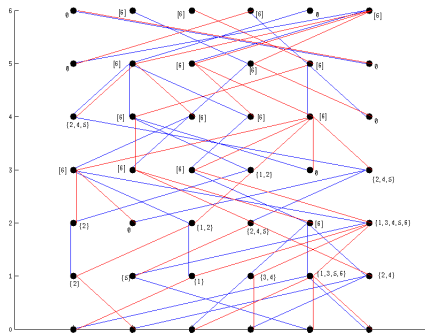
One r to rule them all!Wright-Fisher Genealogy with Large $N \implies$ Kingman's Coalescent Tree for small n (backwards in time)where r is the probability of recombination per locus per meiotic generation ($r = 0$ for Kingman's model)

Three Notions of Molecular continuums within W-F Population Pedigrees

One r to rule them all!(1) Kingman's Discrete Genealogy at a non-recombining locus with $r = 0$ (forwards in time)

Observe: Time to most recent ancestor (TMRC) = 4 (can you locate the MRCA?)

Three Notions of Molecular continuums within W-F Population Pedigrees

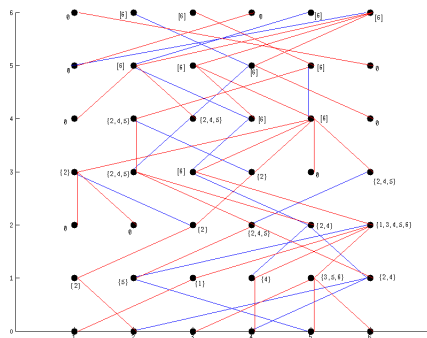
One r to rule them all!

(2) Chang's Discrete Pedigree as the Genealogy of an always-recombining locus with $r = 1$ (forwards in time)

Observe: Time to most recent ancestor (TMRCA) = 2 (can you locate the MRCA? how about other CAs?)

Observe: Time to be or not to be (TTBONTB) = 5 (can you say why?)

Three Notions of Molecular continuums within W-F Population Pedigrees

One r to rule them all!(3) Hudson-Griffiths Discrete Ancestral Recombination Graph at a recombining locus with $0 < r < 1$ (fwds in time)SIMPLEST UNIFICATION PROBLEM: What is TMRCA and TTBONTB for any r ?

Unifying these three notions of molecular ancestry

Consider the **ancestral graphs** of these three genealogical processes for a given sample taken today (backwards in time).

- ▶ Uni-parental Ancestry of sample : Kingman's Discrete Genealogy at a non-recombining locus (1982)
- ▶ Bi-parental Ancestry of sample : Chang's Discrete Pedigree (1999)
- ▶ Uni/Bi-parental Ancestry of sample: Hudson-Griffiths Discrete Ancestral Recombination Graph (1983-1989)

This unification was an open problem since 1983

This topologically consistent notion of diploid ancestry (RS, Thatte & Veber, 2015) in a common probability space is a pre-requisite for more realistic models of population pedigree processes, including:

- ▶ non-overlapping generations

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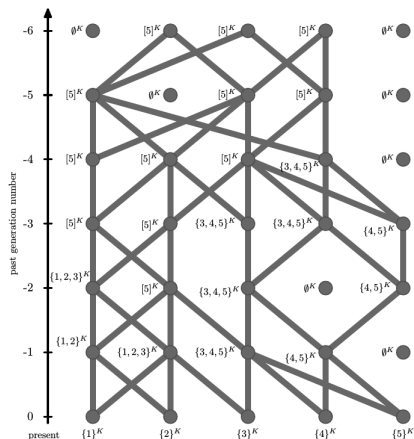
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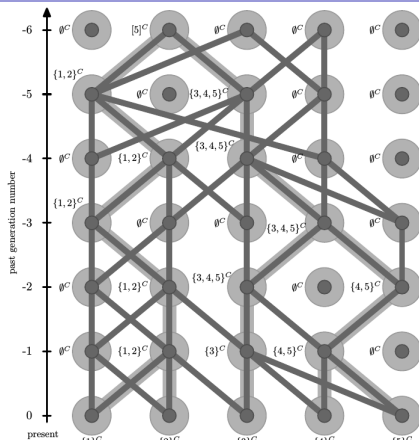
- ▶ non-overlapping generations
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- ▶ gender-specific behavioural effects on spatio-temporal pedigree through which genes flow under natural selection...
- ▶ etc. (think of Florida Scrub Jay, feral cat populations, heroms of Mujahidiin warlords post Soviet withdrawal in 1980s)



karyotic ancestral graph of a bi-parental Wright-Fisher population with five eukaryotic individuals

Can you find the MRC-karyotic-A (MRCKA)? TMRCKA? TT-karyotically-BONTB (TTkBONTB)?

Chang's Main results say that TMRCKA and TTkBONTB $\sim O(\log_2(n))$, where n = population size

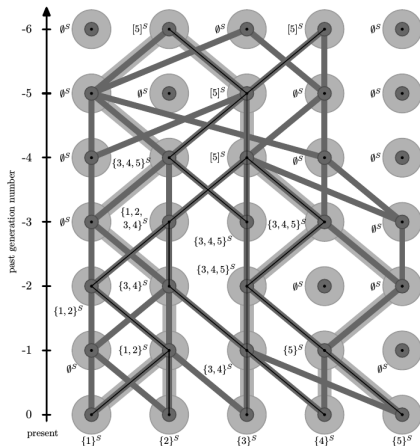


Zygotic pedigree containing the cytoplasmic tree (Kingman's discrete coalescent) and karyotic ancestral graph of a bi-parental Wright-Fisher population

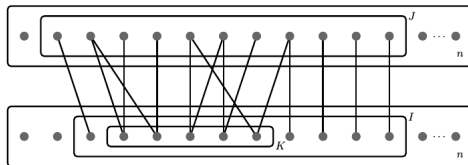
Can you find the MRC-cytoplasmic-A (MRCcA)? TMRCcA?

Kingman's Main results say that TMRCcA and TtCBONTB $\sim O(n)$, where $n =$ population size

so: $O(\log_2(n))$ versus $O(n)$ is a huge difference!



Putting it all together: Zygotic, cytoplasmic, karyotic and sub-karyotic ancestral graphs (discrete ARGs of Hudson and Griffiths) of a bi-parental Wright-Fisher population with five eukaryotic diploid individuals



Combinatorial Structure Diagram

Theorem 1 *The exact transition probabilities of the ancestral process $\{^{n,r}X(t)\}_{t \in \mathbb{Z}_-}$ are*

$$^{n,r}P_{i,j} = \begin{cases} \binom{n}{j} \sum_{k=(j-i)_+}^j \frac{\binom{i}{k} r^k (1-r)^{i-k}}{2^k n^{i-k} \binom{n}{2}^k} \sum_{m=0}^j (-1)^{j-m} \binom{j}{m} m^i (m-1)^k & \text{if } 1 < j \leq 2i, \\ \frac{(1-r)^i}{n^{i-1}} & \text{if } j = 1, \\ 0 & \text{otherwise.} \end{cases}$$

Kingman-Chang-Hudson-Griffiths Unified Ancestral Chain

Theorem 2 Let \mathcal{T}_n denote the number of generations, counting back in time from the present, to an MRCA of all present-day individuals. Then for every $\varepsilon > 0$,

$$\lim_{n \rightarrow \infty} \mathbb{P}\{(1 - \varepsilon)C(r) \ln n \leq \mathcal{T}_n \leq (1 + \varepsilon)C(r) \ln n\} = 1,$$

where

$$C(r) := \frac{1}{\ln(1+r)} - \frac{1}{\ln(1-r)}.$$

Time to MRCA for a possibly recombining locus with intra-locus recombination probability per non-overlapping meiotic generation in a population of n diploid individuals.

Theorem 3 Let \mathcal{U}_n denote the number of generations, counting back in time from the present, to a generation in which each individual is either a CA of all present-day individuals or an ancestor of no present-day individual. Let $\rho = \rho(r)$ be the unique solution in $(0, 1)$ to the equation $x = e^{-(1+r)(1-x)}$, and recall the definition of $C(r)$ given in the statement of [Theorem 2](#). Then for every $\varepsilon > 0$,

$$\lim_{n \rightarrow \infty} \mathbb{P} \left\{ (1 - \varepsilon) \left(C(r) - \frac{1}{\ln((1+r)\rho)} \right) \ln n \leq \mathcal{U}_n \leq (1 + \varepsilon) \left(C(r) - \frac{1}{\ln((1+r)\rho)} - \frac{1}{\ln(1-r)} \right) \ln n \right\} = 1.$$

Time to Be or Not to Be for a possibly recombining locus with intra-locus recombination probability per non-overlapping meiotic generation in a population of n diploid individuals.

Proof ideas

Sketches of the Proofs of Thms 1 & 2 is a 50 minute chalk talk.

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- ▶ For Thm 1: Just count the integers in the numerator and denominator of the rational probabilities
 - ▶ counting Wright-Fisher constrained bipartite graphs from the combinatorial diagram
- ▶ For Theorems 2 and 3:
 - ▶ carefully partitioning the time-axis into six distinct n -asymptotic regimes

$$\left[0, \oplus \frac{2 \log \log n}{\log(1+r)}, \oplus \frac{\log n}{\log(1+r)}, \oplus \log \log n, \oplus \log \log n, \oplus - \frac{\log n}{\log(1-r)}, \oplus \frac{-2 \log \log n}{\log(1-r)} \right]$$

and applying the right tools from below:

- ▶ \cong the $\#$ (descendants / non-descendants of individual l_i), binomial RVs, by a GW branching process with Poisson($1 + / - r$) offspring distribution (start/end)
- ▶ Bernstein \neq 's for the Binomial RVs away from start/end
- ▶ standard branching process results from Athreya & Ney

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A paradigm for "Population Structure From Behavior"

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A paradigm for "Population Structure From Behavior"
- ▶ PLAN: continue to work on Behavioural Population Pedigrees (Two-Sexes/Monogamy/Patrilocal)

Thank you!

Funds for Theory:

- ▶ School of Maths & Stats (solar panels for remote computing in 2011; Sabbatical grant 2014),
- ▶ Research Chaire in 2013 & 2016: Vieola Environment - French Natural History Museum - Ecole Polytechnique.