Population pedigree process of the Chatham island black robin: A case of human-assisted spread of a maladaptive behavior in a critically endangered bird

Raazesh Sainudiin[†]

[†] School of Mathematics and Statistics, University of Canterbury,
Christchurch, New Zealand
Parts are Joint work with: James Briskie, Marie Hale, Melanie Massaro, Don Merton, Anthony Poole

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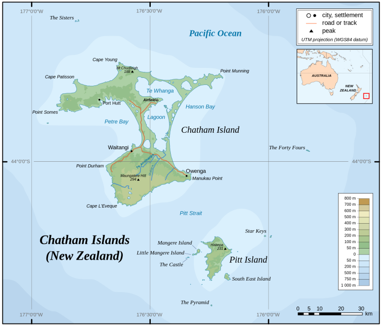
Ecological History of Black Robins

Likelihood of Population Pedigrees

Current & Future Plans

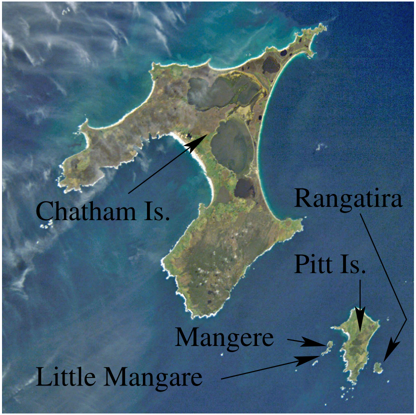
Part I

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)

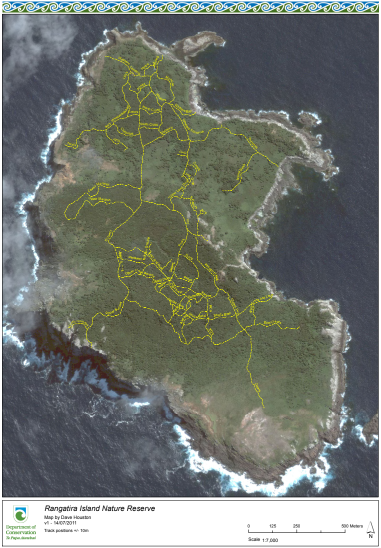


- Many smaller islands – including Little Mangere, Mangere and Rangatira
- The islands have only emerged above sea level in the last 4 million years and are part of the Chathams rise connected below ocean to NZ.
- The climate is cool and wet with salt-laden winds all year round.

Chatham Islands (New Zealand)

Rangatira Island

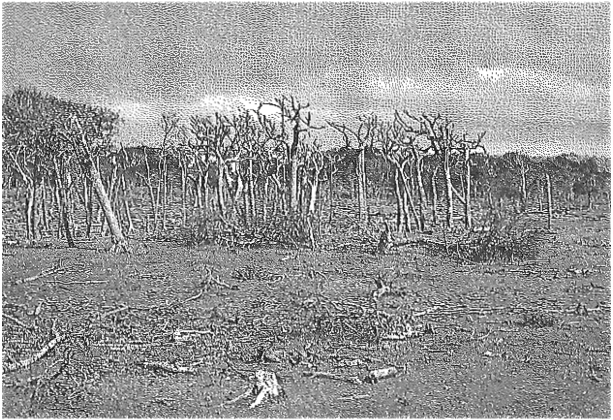
- is the third largest island in the Chatham Islands
- covers an area of 218 hectares (539 acres)
- is a gazetted nature reserve since 1953
- is now home to many endemic species
- is home to black robins – saved from near extinction by team led by Don Merton in the 1980s



A Chatham island Black Robin in Rangatira today

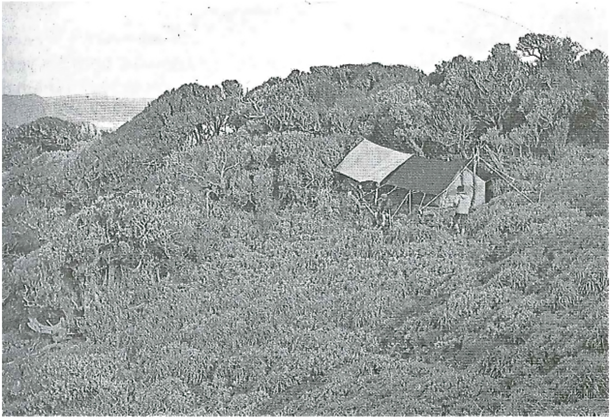
Decimation and Conservation

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 transloaction 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

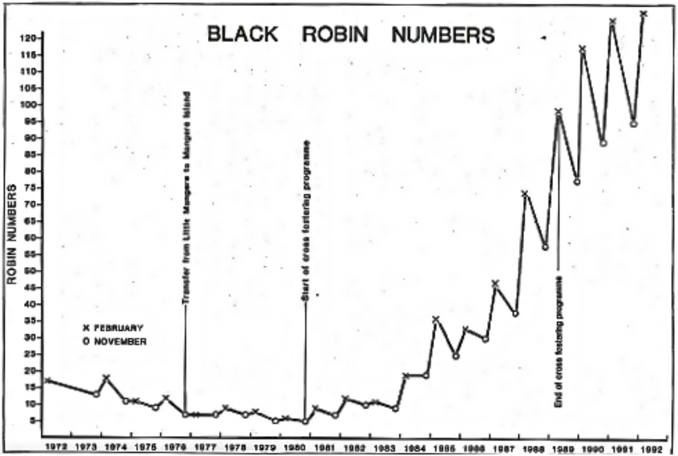


Fig. 22. Black robin numbers

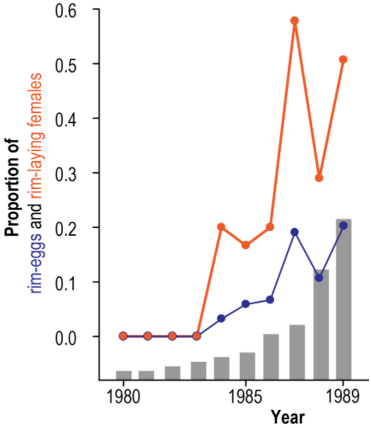
Species Recovery Program in 1980s

Well-laid Eggs

Rim-laid Egg

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

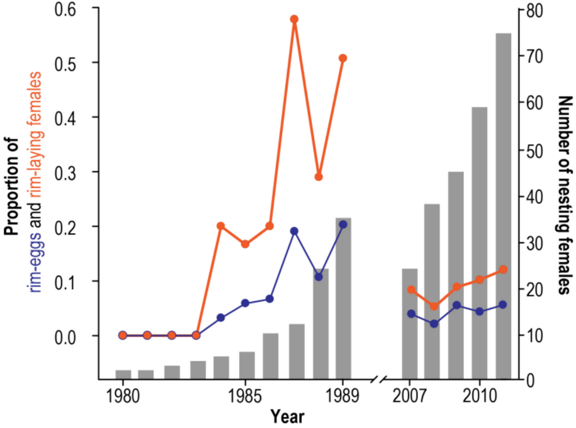
The Conservation Dilemma



Rim-laying increases in 1980s

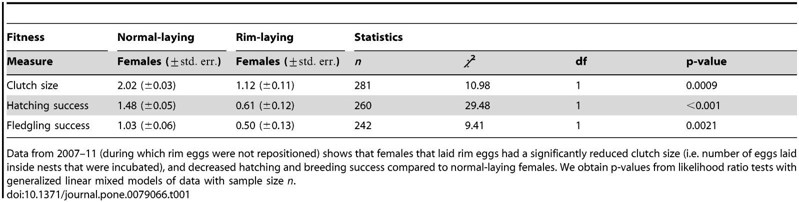
- Conservation Dilemma – when to cease management?
- Need managed pop. size to ↑
- But rim-laying trait also ↑
- Don Merton’s team ceased management when 50% of females were rim-layers by 1989
- Our Question: Is rim-laying a heritable trait?

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 (±std. err.)**	**Females (±std. err.)**	n	χ^2	**df**	**p-value**
Clutch size	2.02 (±0.03)	1.12 (±0.11)	281	10.98	1	0.0009
Hatching success	1.48 (±0.05)	0.61 (±0.12)	260	29.48	1	<0.001
Fledgling success	1.03 (±0.06)	0.50 (±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*.

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Rim-laying females have reduced

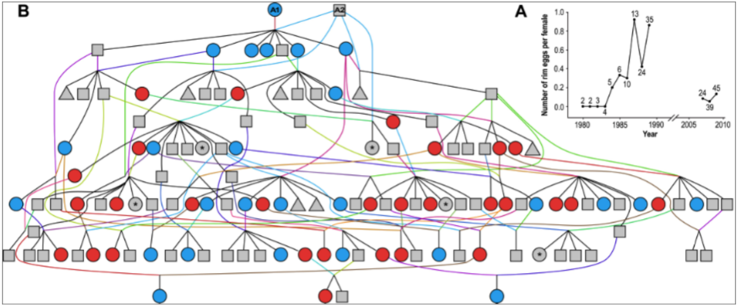
- clutch size
- hatching success
- fledgling success

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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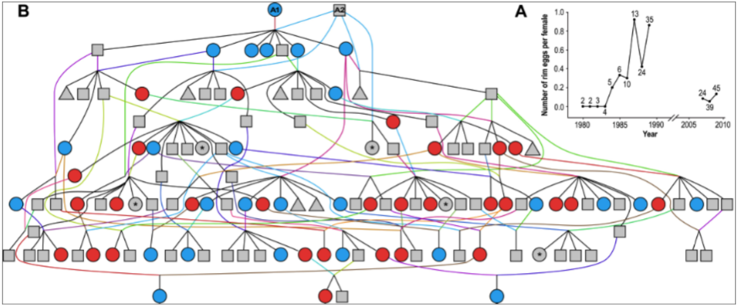

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Want: The likelihood of the observed rim-laying phenotypes on this population pedigree.

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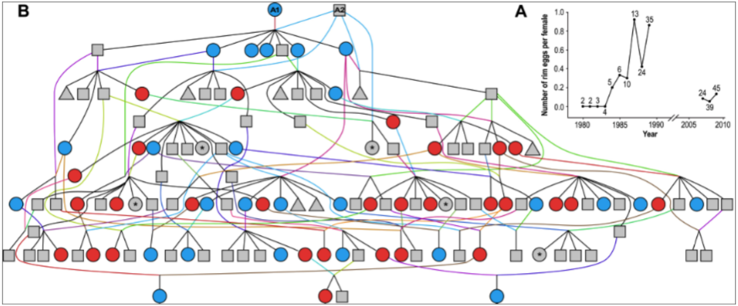

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Want: The likelihood of the observed rim-laying phenotypes on this population pedigree. Trouble: The likelihood via Peeling Algorithm (Cannings,Thompson & Skolnick 1978) in standard pedigree software runs out of RAM!

Likelihood of the Phenotypes on the Pedigree

For the likelihood we need:

1. simplest Model for Pedigree

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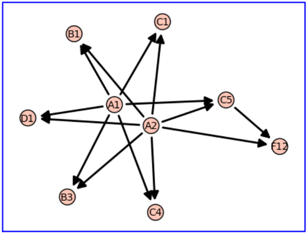
4. Likelihood = the proportion of joint genotypic configurations that are compatible with the observed phenotypes under the model of inheritance on the observed pedigree

Simple Pedigree

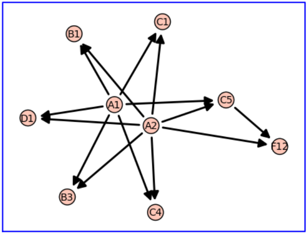


A pedigree is a directed acyclic graph $\mathcal{G} := (\mathbb{V}, \mathbb{E})$ in which $\mathbb{V}$ partitions a set of individuals (males,females,unknown-sex):

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

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

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

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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Let $\phi : \mathbb{L} \to \{0, 1\}$ denote a binary phenotype map:

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

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Let the phenotypes of a set of individuals

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

be

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

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

Mendelian Inheritance – Prob. of Genotype

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$$\Pr\left(\gamma(u) \mid \gamma(M_u), \gamma(F_u), \mathcal{M}_h^c\right) = \begin{cases} \frac{1}{4} & \text{if } c = \alpha, \gamma_m(u) \in \{\gamma_m(M_u), \gamma_f(M_u)\}, \\ & \quad \gamma_f(u) \in \{\gamma_m(F_u), \gamma_f(F_u)\} \\ \frac{1}{2} & \text{if } c = z, \gamma_m(u) = \gamma_f(M_u), \\ & \quad \gamma_f(u) \in \{\gamma_m(F_u), \gamma_f(F_u)\}, u \in \mathbb{M} \\ \frac{1}{2} & \text{if } c = z, \gamma_m(u) = \gamma_m(M_u), \\ & \quad \gamma_f(u) \in \{\gamma_m(F_u), \gamma_f(F_u)\}, u \in \mathbb{F} \\ 0 & \text{otherwise.} \end{cases} \qquad (2)$$

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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:

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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:

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

Likelihood, Prior and Posterior

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

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We want probability of the inheritance model $\mathcal{M}_h^c$ and the founder genotypes $\gamma(\mathbb{A})$ given $\mathcal{G}$, the observed pedigree, and $\phi(\mathbb{V})$, the observed phenotypes over the nodes in $\mathcal{G}$:

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$$\begin{aligned}&\Pr\left(\mathcal{M}_h^c, \gamma(\mathbb{A}) \mid \mathcal{G}, \phi(\mathbb{V})\right)\\ &\qquad = \frac{\Pr\left(\phi(\mathbb{V}) \mid \mathcal{G}, \mathcal{M}_h^c, \gamma(\mathbb{A})\right) \Pr\left(\mathcal{M}_h^c, \gamma(\mathbb{A})\right)}{\sum_{\substack{c \in \{a,z\} \\ h \in \{D,R\} \\ \gamma(\mathbb{A}) \in \Gamma^{\mathbb{A}}}} \Pr\left(\phi(\mathbb{V}) \mid \mathcal{G}, \mathcal{M}_h^c, \gamma(\mathbb{A})\right) \Pr\left(\mathcal{M}_h^c, \gamma(\mathbb{A})\right)} \qquad (4)\end{aligned}$$

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\end{aligned} \tag{4}$$

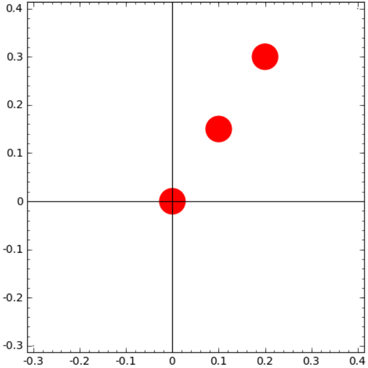
We assume a uniform prior probability $\Pr\left(\mathcal{M}_h^c, \gamma(\mathbb{A})\right) = \frac{1}{64}$ over the $2 \times 2 \times 4^2 = 64$ models in the family:

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

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?

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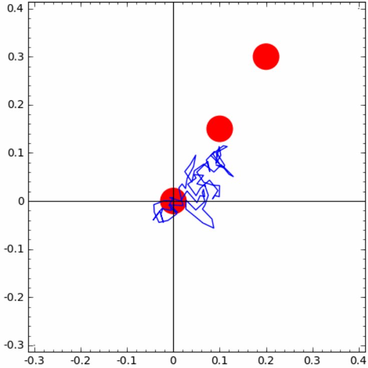

Estim. Prob. Hitting First Red dot $= 1/9$

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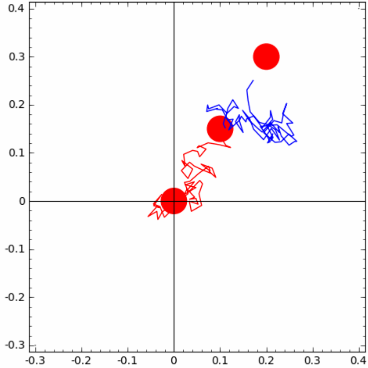

Estim. Prob. Hitting First and Second Red Dots $= 1/9 \times 1/9 = 1/81$

Likelihood Computation - Adapting SMC to Pedigrees

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$\Pr\left(\phi(\mathbb{V}) \mid \mathcal{G}, \mathcal{M}_h^c, \gamma(\mathbb{A})\right)$, 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 $\mathbb{V}_0 = \{\mathsf{A1}, \mathsf{A2}\}$ be the vertex set of the founding male and female.

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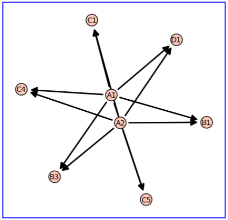
Let $\mathbb{A} = \mathbb{V}_0 \subset \mathbb{V}_1 \subset \cdots \subset \mathbb{V}_T = \mathbb{V}$ denote the increasing sequence of vertices in $\mathcal{G}$ obtained by a breadth-first expansion from $\mathbb{V}_0$

Sequential Monte Carlo on Nested Combinatorial Structures



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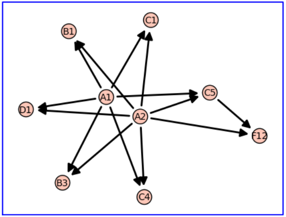
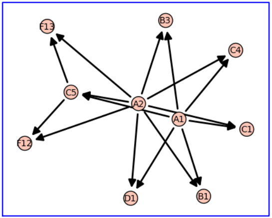
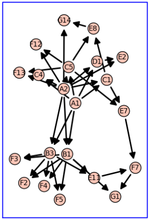


$\downarrow$



$\leftarrow \cdots$

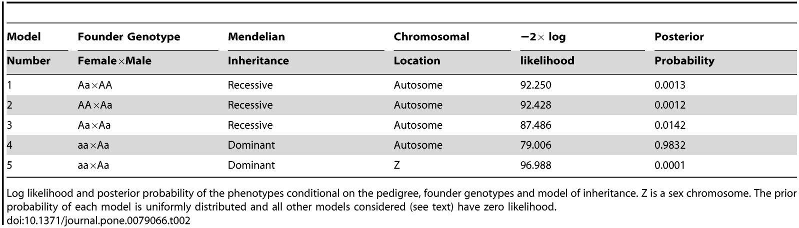


$\leftarrow \cdots$

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 $\Pr\left(\mathcal{G}, \phi(\mathbb{V}) \mid \mathcal{M}_j^c, \gamma(\mathbb{A}) \right)$ by $\prod_{t=0}^{T} \hat{Z}_t$, $\hat{Z}_t = \frac{1}{N} \sum_{i=1}^{N} W_t^{(i)}$.

Model Selection – Results



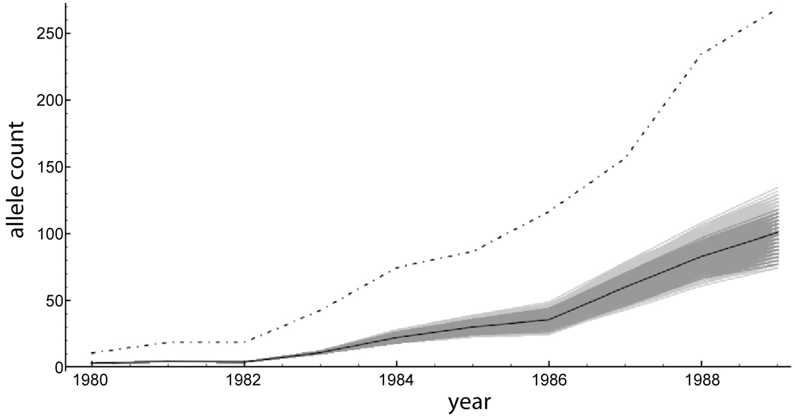
Model Number	Founder Genotype Female×Male	Mendelian Inheritance	Chromosomal Location	−2× log likelihood	Posterior Probability
1	Aa×AA	Recessive	Autosome	92.250	0.0013
2	AA×Aa	Recessive	Autosome	92.428	0.0012
3	Aa×Aa	Recessive	Autosome	87.486	0.0142
4	aa×Aa	Dominant	Autosome	79.006	0.9832
5	aa×Aa	Dominant	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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- In the case of black robins the managers seemed to have succeeded by stoppping management when half the population were rim-layers
- 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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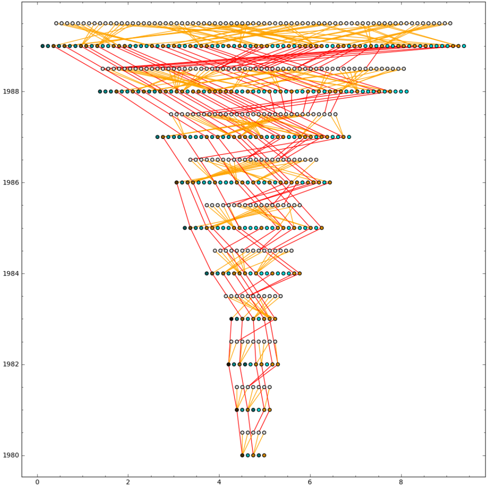
- To appreciate the intensity of field operations and limitations of biomathematical models read: *The black robin: saving the world's most endangered bird*, David Butler and Don Merton, Oxford University Press, 1994.

Part II

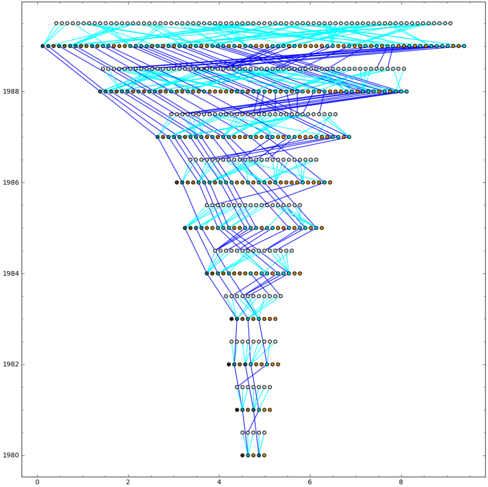
Insights from field work in November 2011

Temporal Pedigrees with Overlapping Generations



Female Population Tree during Field Conservation in 1980s

Temporal Pedigrees with Overlapping Generations



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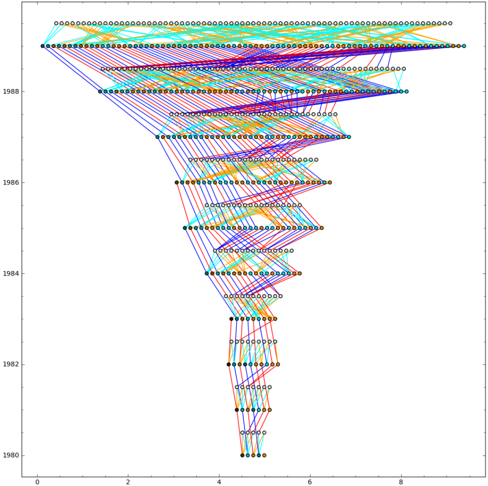

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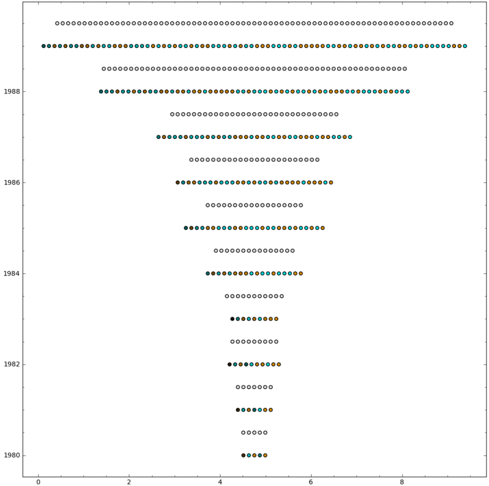
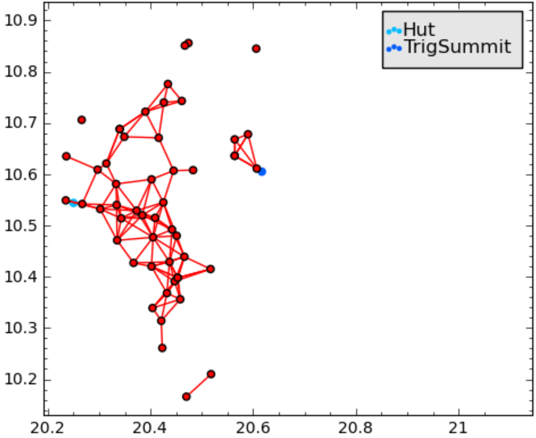


Coalescent Sub-Pedigree of the 1989 population

Male Territory Graphs by year



2009 (eye-balled by a ball graph)

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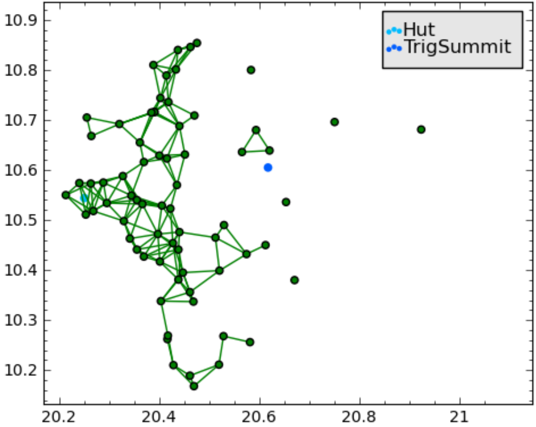

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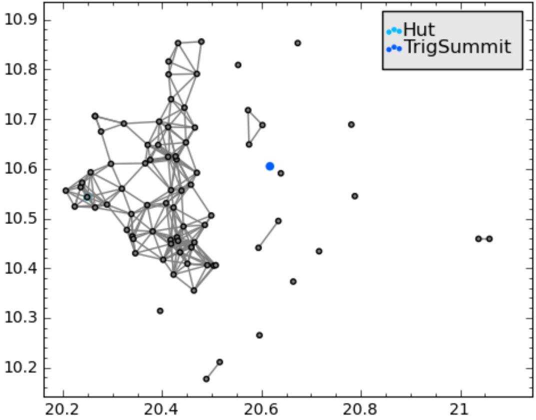
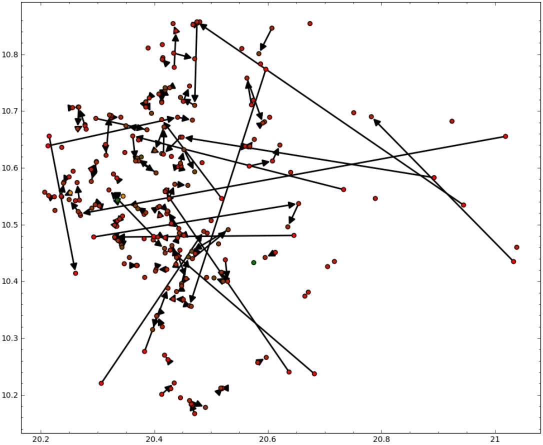


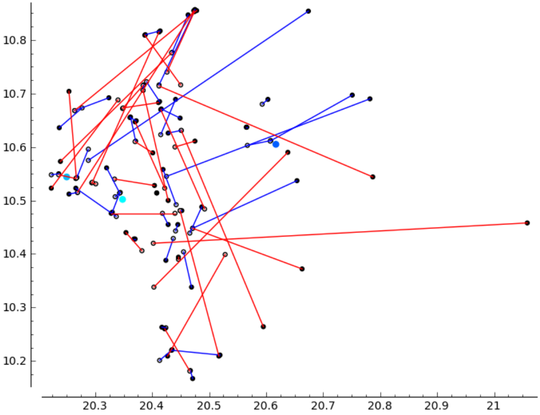
2011 (eye-balled by a ball graph)

Male Territorial Dynamics – yearly nest site relocation



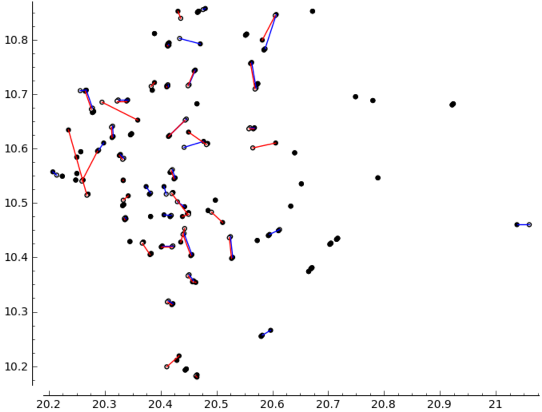
Male / Female yearly nest to nest distance

sex-specific distance between home nest and first nest



Male / Female yearly nest to nest distance

sex-specific distance between nest at age $\geq$ 1 and next nest



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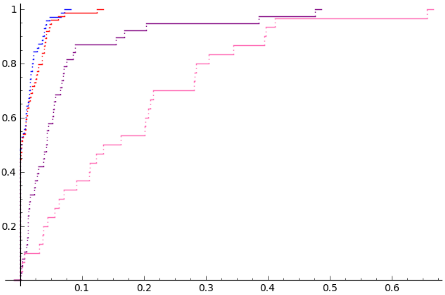
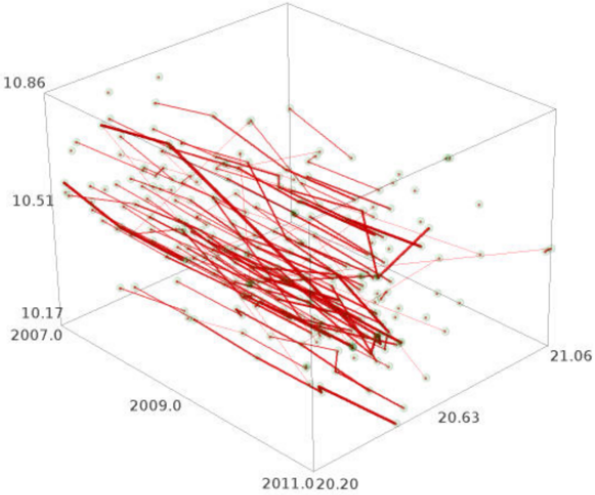


- Permutation Test to Reject H_0 : male dist = female dist (10^5 MC samples)
- Strongly reject H_0 for home to first nest (pv = 0.00025)
- Fail to reject H_0 for nest at age ≥ 1 to next nest (pv = 0.14)

male / female distance from home nest to first nest

male / female distance from nest at age $\geq$ 1 to next nest

Need Models of Spatio-temporal Population Pedigrees



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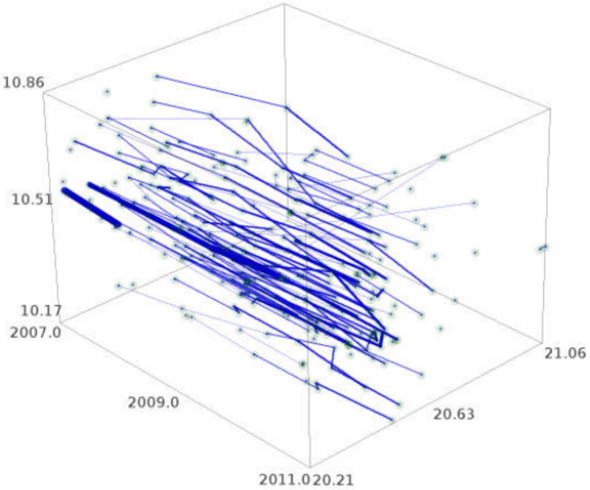

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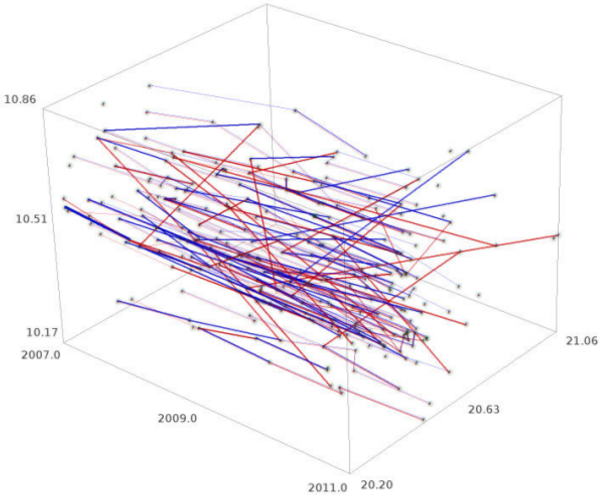
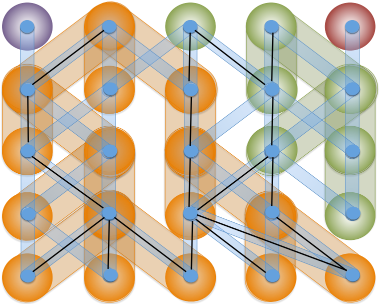


Step I: Notions of Molecular continuums within W-F Population Pedigrees

a homotopy between Kingman Coalescent Trees and Chang's Pedigree (RS, B. Thatte & A. Veber)



Zygotic, cytoplasmic, karyotic and sub-karyotic pedigrees of a Wright-Fisher population with five eukaryotic diploid individuals

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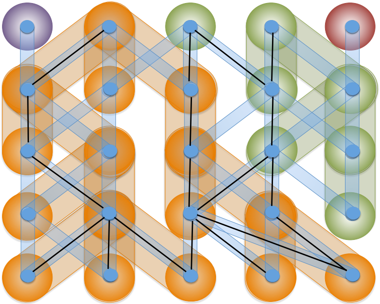

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Prob. Seminar on October 6th 2014 4:00PM in Malott Hall

Ancestries of Recombining Population Pedigrees: A Discrete Structural Perspective

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  A paradigm for "Population Structure From Behavior"

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- PLAN: continue to work on Part II @Cornell in 2014

Thank you!

Funds for Theory:

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