

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

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Chatham Islands – Geography & Ecological History

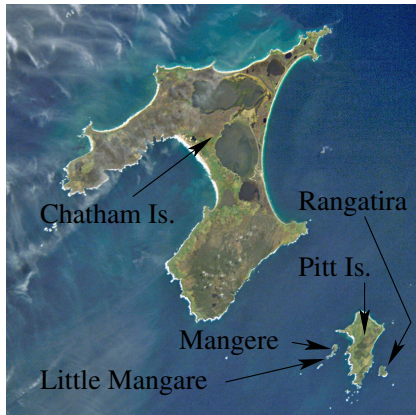
Ecological History of Black Robins

Likelihood of the Phenotypes on the Pedigree

Testing Heritability of Rim-laying

Part I

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



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- ▶ the accompanying sheep and cattle farming and the feral rabbits and pigs released by sailors resulted in over-grazing and destroyed the indigenous flora
- ▶ the introduced predators such as cats, rats and stoats destroyed the indigenous fauna (especially birds that evolved in the absence of land-based predators)

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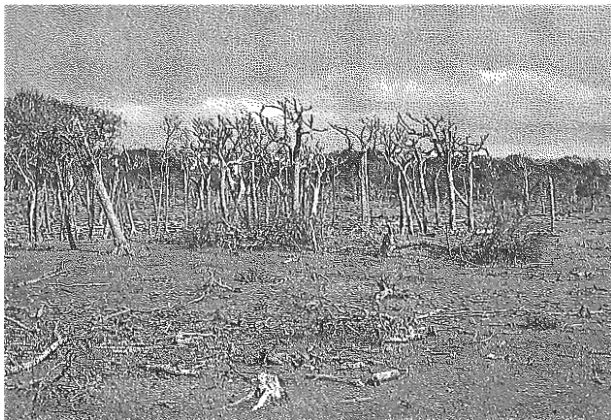
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- ▶ The more ecologically devastated Mangare island was also turned into a nature reserve with an ecological restoration effort of native flora

Pictures...



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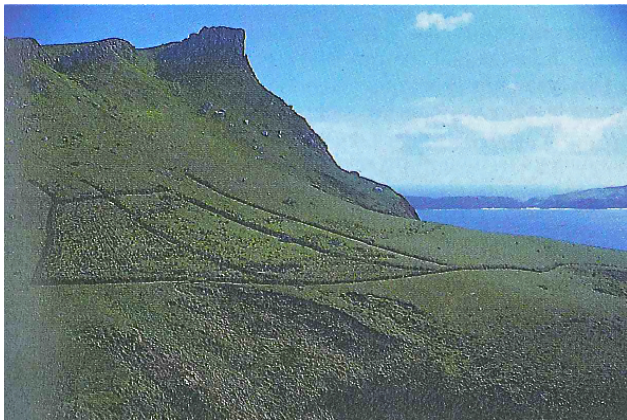
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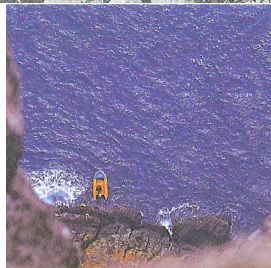
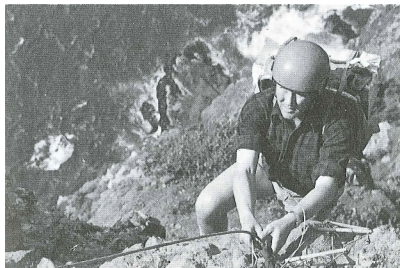
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Early Studies and Relocation in 1980s

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

- ▶ Eggs were removed after being laid to encourage egg-laying
- ▶ the removed eggs were hatched by foster species (tomtits)
- ▶ the foster-cared chicks were transferred to black robin nests for sexual imprinting
- ▶ each nest was monitored, managed and logged as unintrusively as possible in its native habitat
- ▶ Unfortunately, a maladaptive behavioural trait of “rim-laying” also increased with the population
- ▶ Managements ceased when the population reached about 100 birds

Species Recovery Program in 1980s

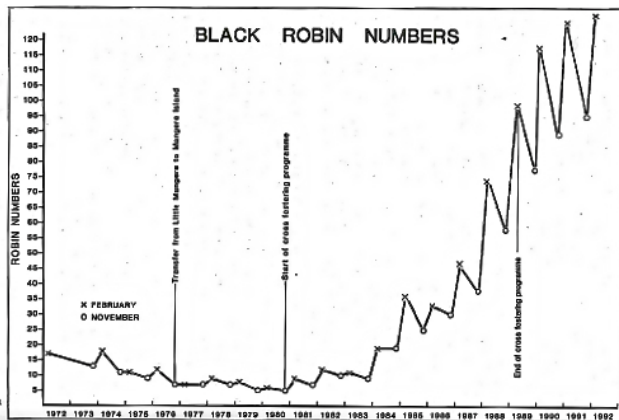


Fig. 22. Black robin numbers

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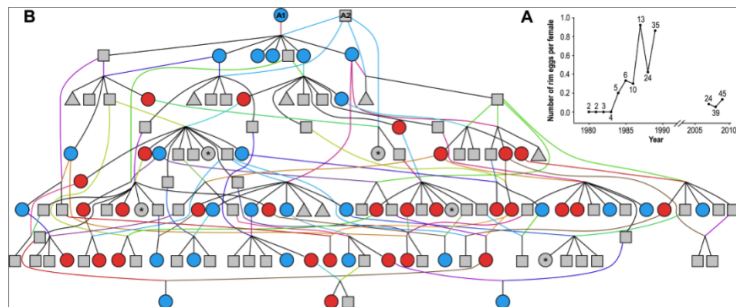
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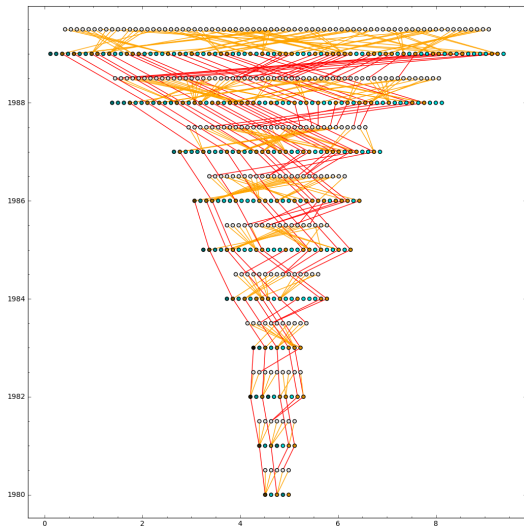
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- ▶ In the sequel, we will add temporal and spatial aspects to the classical notion of pedigree

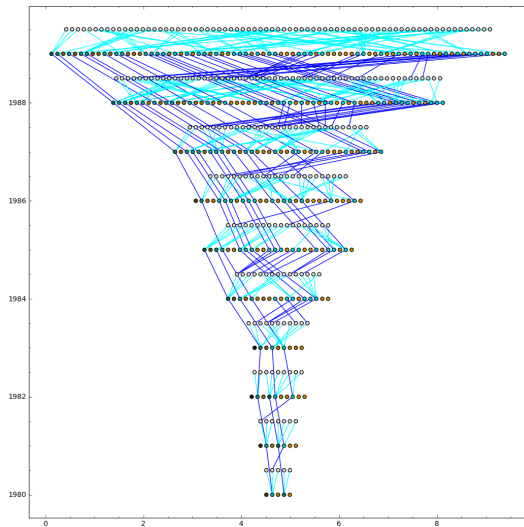
Highly Looped Black Robin Pedigree in 1980s



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



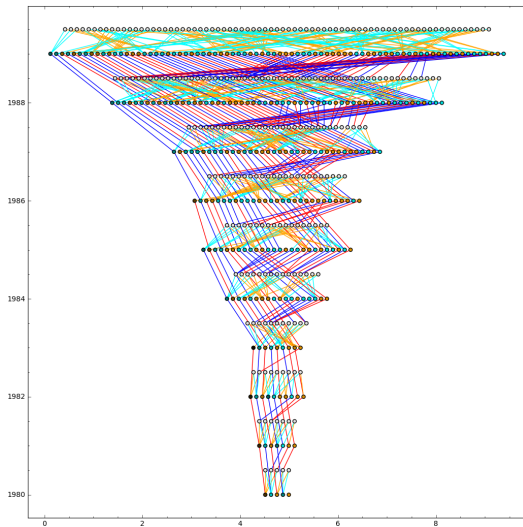
Female Population Tree during Field Conservation in 1980s



Male Population Tree during Field Conservation in 1980s

Population pedigree process of the Chatham island black robin

Ecological History of Black Robins



Population Pedigree during Field Conservation in 1980s

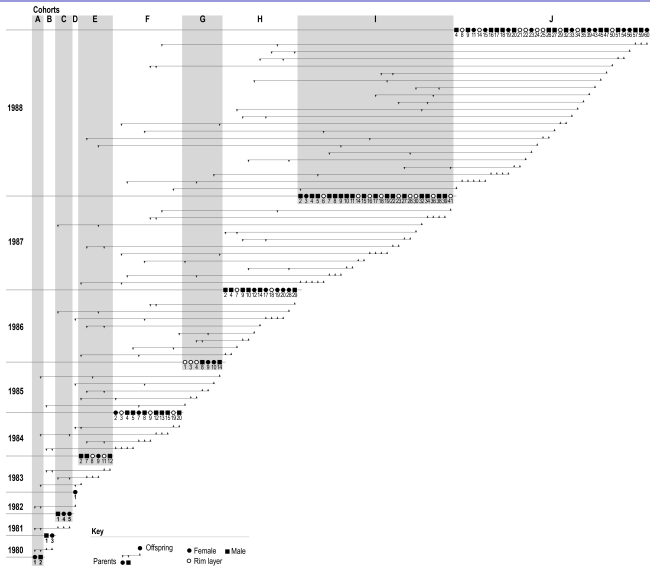
Coalescent Sub-Pedigree of the 1989 population



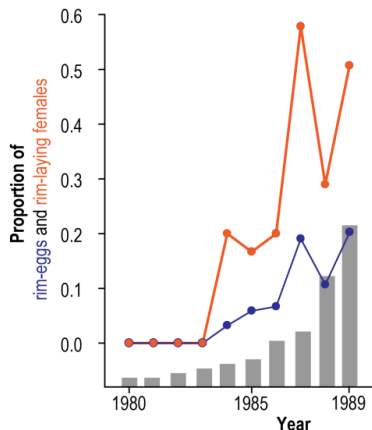
Rim-laying Behaviour during Field Conservation in 1980s

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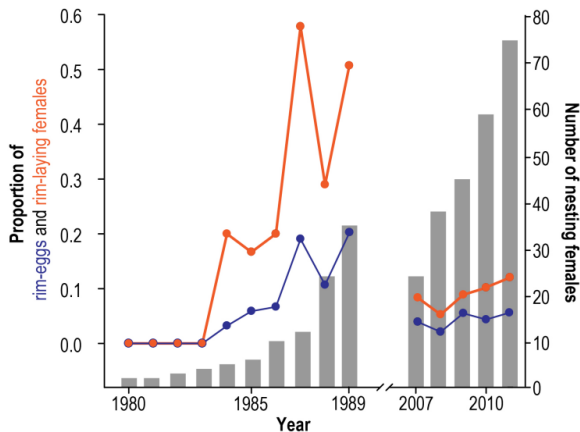


Temporal Pedigree (with rim-layers) during 1980s



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?



Rim-laying increases in 1980s

but between 2007 and 2011 (unmanaged phase) seems lower

Our Question: Is rim-laying a heritable trait?

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.

Likelihood of the Phenotypes on the Pedigree

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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

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A pedigree $\mathcal{G} := (\mathbb{V}, \mathbb{E})$ is a mathematical graph over a set of individuals (males, females, unknown-sex):

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

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

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

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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

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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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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

- ▶ 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 $\prod_{t=0}^T \hat{Z}_t$, $\hat{Z}_t = \frac{1}{N} \sum_{i=1}^N W_t^{(i)}$.

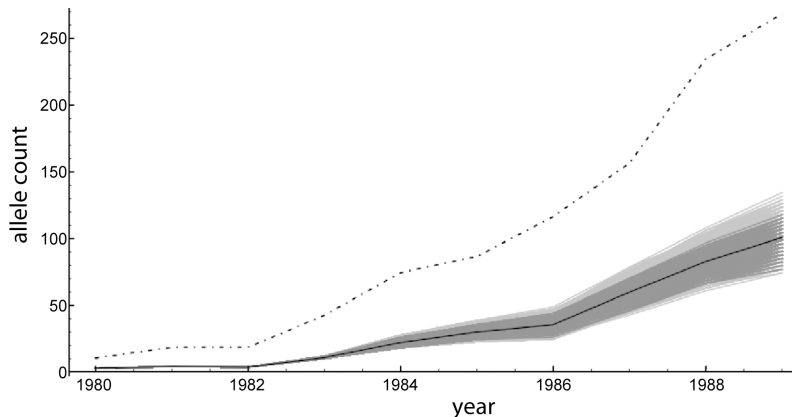
Model Selection – Results

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

- ▶ 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

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- ▶ In the case of black robins the managers seemed to have succeeded by stopping management when half the population were rim-layers
- ▶ Merton suspected rim-laying was heritable (persn. commn. to Massaro)

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Conclusions - Part I contd...

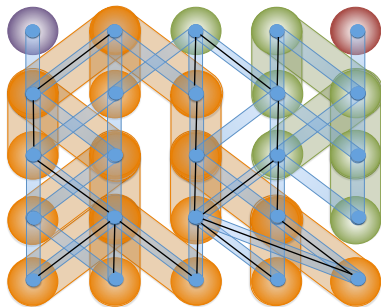
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- ▶ To appreciate the intensity of field operations and limitations of biomathematical models read: *The black robin: saving the world's most endangered bird*, David Butler and Don Merton, Oxford University Press, 1994.

Part II – Current & Future Plans

Insights from field work in November 2011

Notions of Molecular continuums within Population Pedigrees

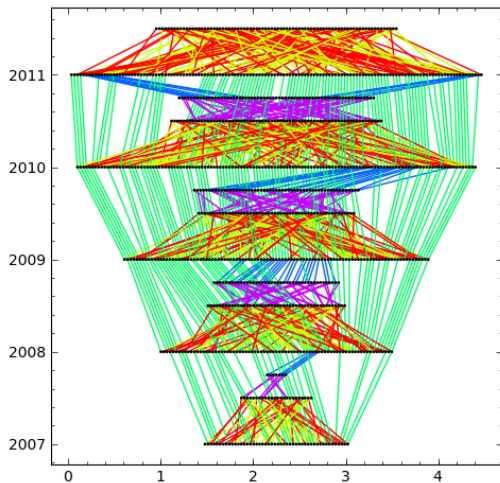
a homotopy between Kingman Coalescent Trees and Chang's Pedigree (RS & Bhalchandra Thatte)



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

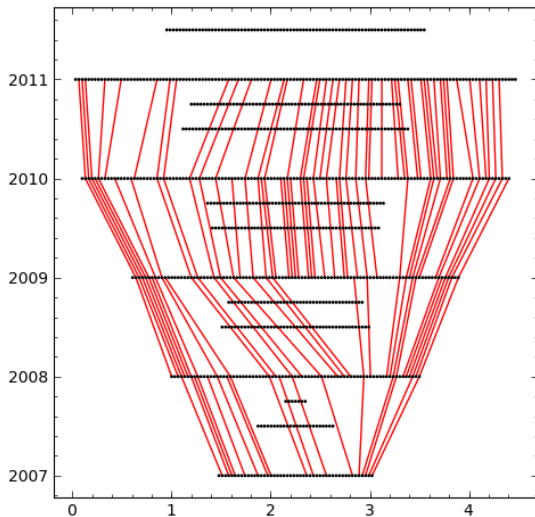
39 Connected Components (sub-pedigrees) in Pedigree Survey 2007-2011

All 39 Connected Components (sub-pedigrees) in Pedigree Survey 2007-2011



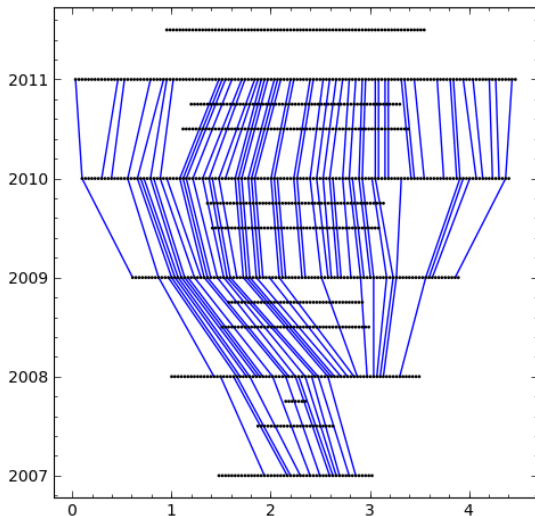
111 Maternal Life-Line Components in Pedigree Survey 2007-2011

Life-Lines of all 107 Mothers in Pedigree Survey 2007-2011

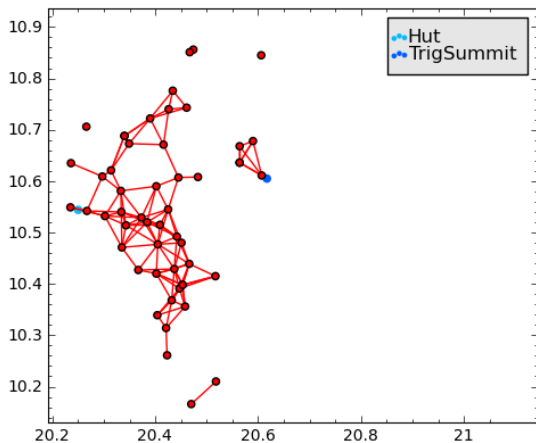


117 Paternal Life-Line Components in Pedigree Survey 2007-2011

Life-Lines of all 113 Fathers in Pedigree Survey 2007-2011

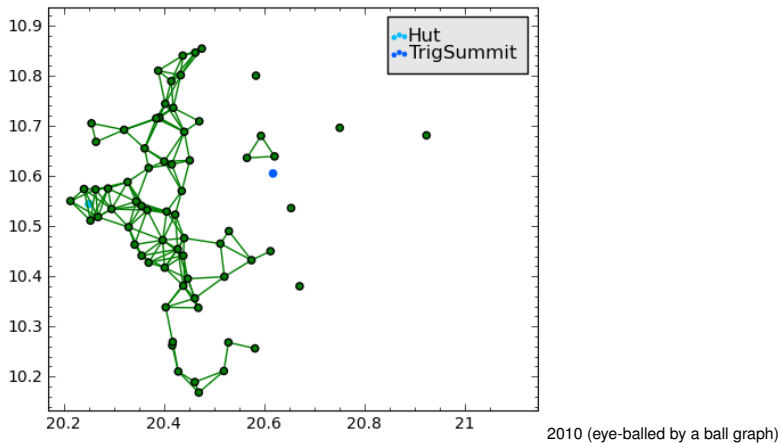


Male Territory Graphs by year

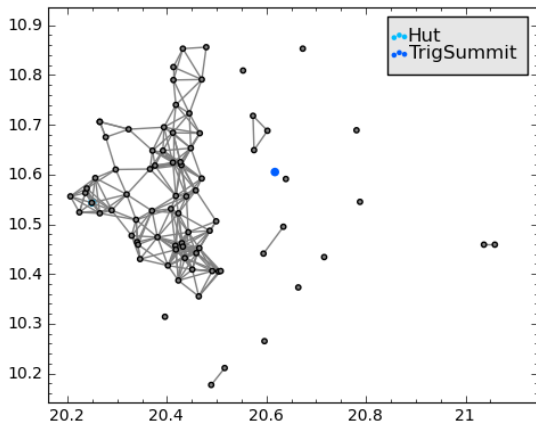


2009 (eye-balled by a ball graph)

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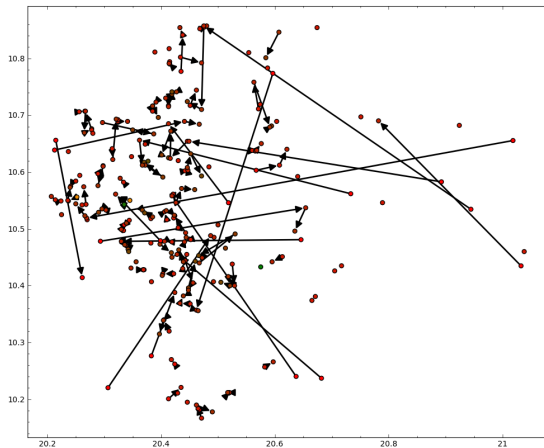


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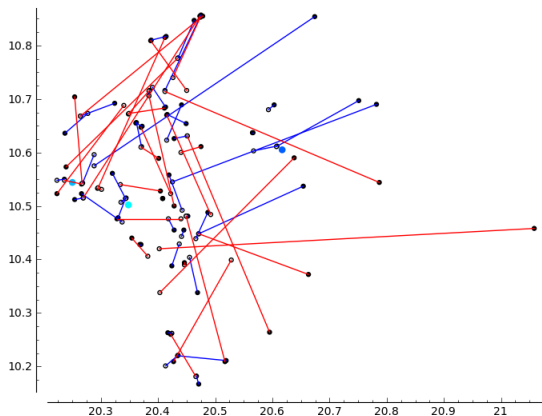
2011 (eye-balled by a ball graph)

Male Territorial Dynamics – yearly nest site relocation



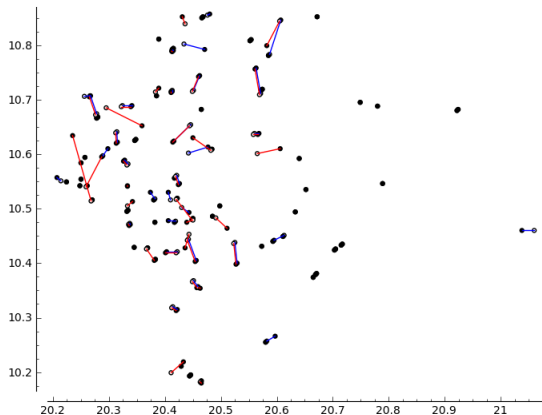
Male / Female yearly nest to nest distance

sex-specific distance between home nest and first nest

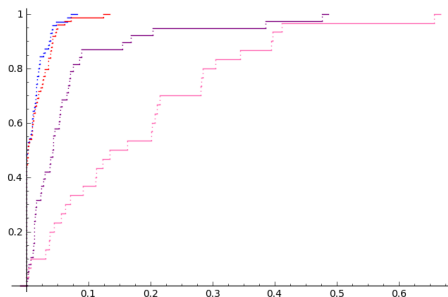


Male / Female yearly nest to nest distance

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



Male / Female yearly nest to nest distance

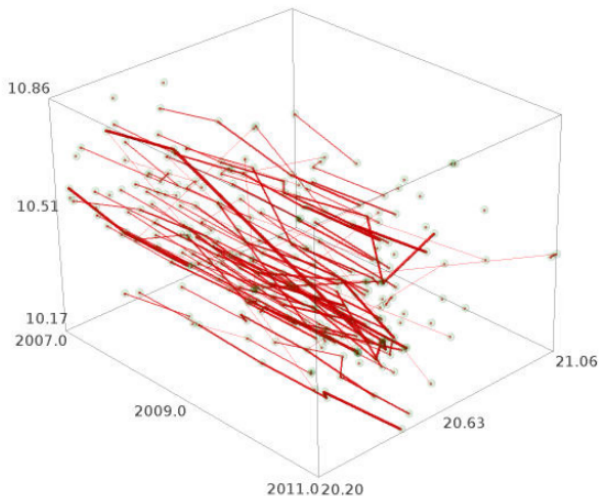


- ▶ Permutation Test to Reject H_0 : male dist = female dist (10^5 MC samples)
- ▶ Strongly reject H_0 for home to first nest ($p_v = 0.00025$)
- ▶ Fail to reject H_0 for nest at age ≥ 1 to next nest ($p_v = 0.14$)

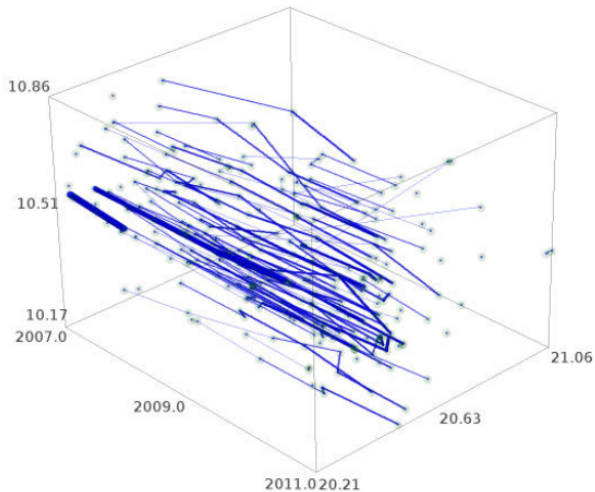
male / female distance from home nest to first nest

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

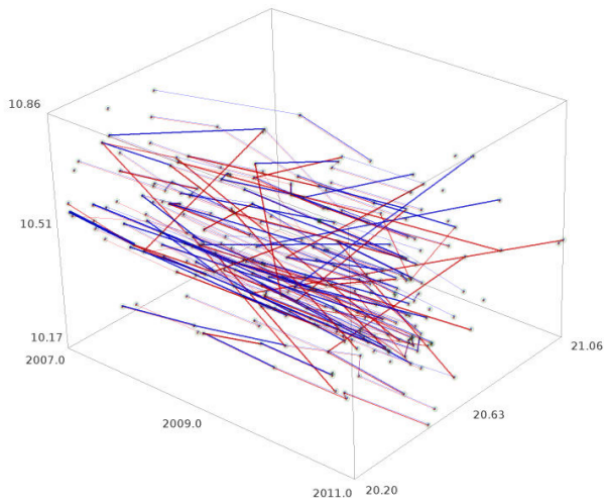
Need Models of Spatio-temporal Population Pedigrees



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Conclusions - Part II

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- ▶ PLAN: continue to work on Part 2 during my visit to Andrew Clark's Lab, Genetics@Cornell in 2014

Thank you!

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- ▶ School of Maths & Stats (solar panels for remote computing in 2011; Sabbatical grant 2014),
- ▶ Brian Mason Foundation,
- ▶ Vieol Environment - French Natural History Museum - Ecole Polytechnique.