Bird song dialects in homogeneous landscapes

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Overview

- Introduction
- Model 1: postdisperal learning
- Model 2: predispersal learning
- Model 3: adaptive songtypes
- Model 4: including space
- Outlook

Introduction

- song dialects are common in birds that learn song
- 45 years of research, (practically) no modelling
- ‘learning’ is all important. Why?

long term goals: understand how the main forces at play shape dialects: formation and stability

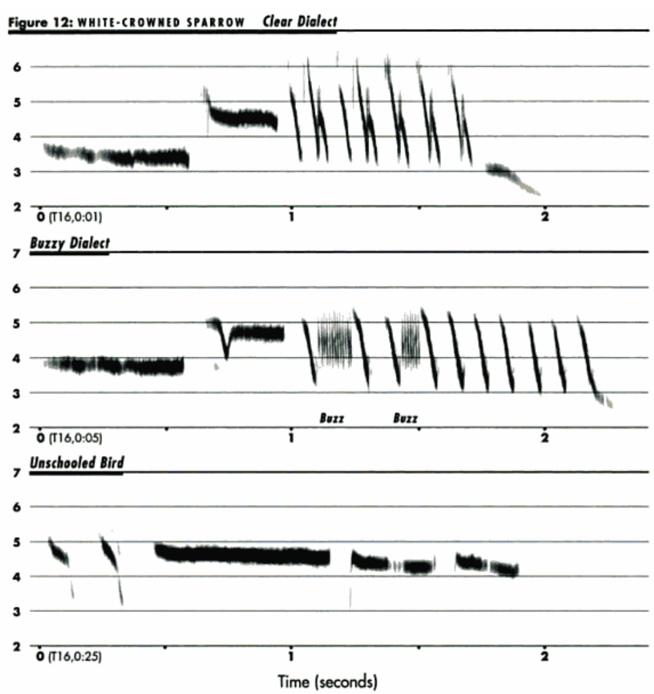
here: maintenance of dialect borders

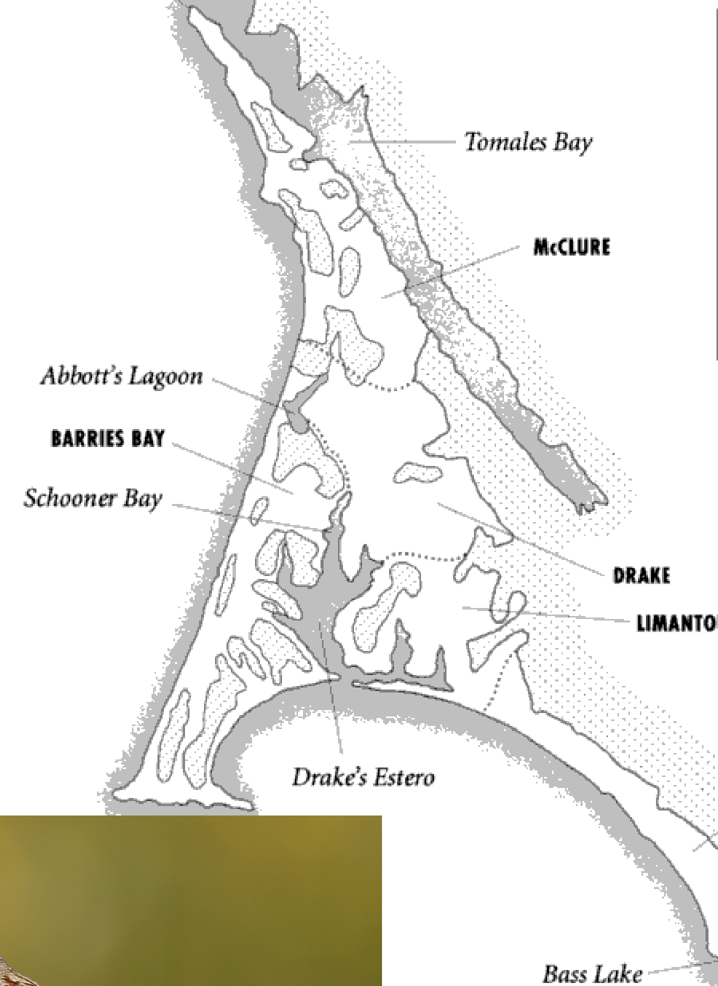
Importance of geographic variation in bird song

- Speciation: 4600 song birds, all learn
- Bird species often defined by song
- Song differences may allude to isolating mechanisms through assortative mating
  - female mate choice, sexual selection
  - male-male competition
  - habitat differences

Enigma 1

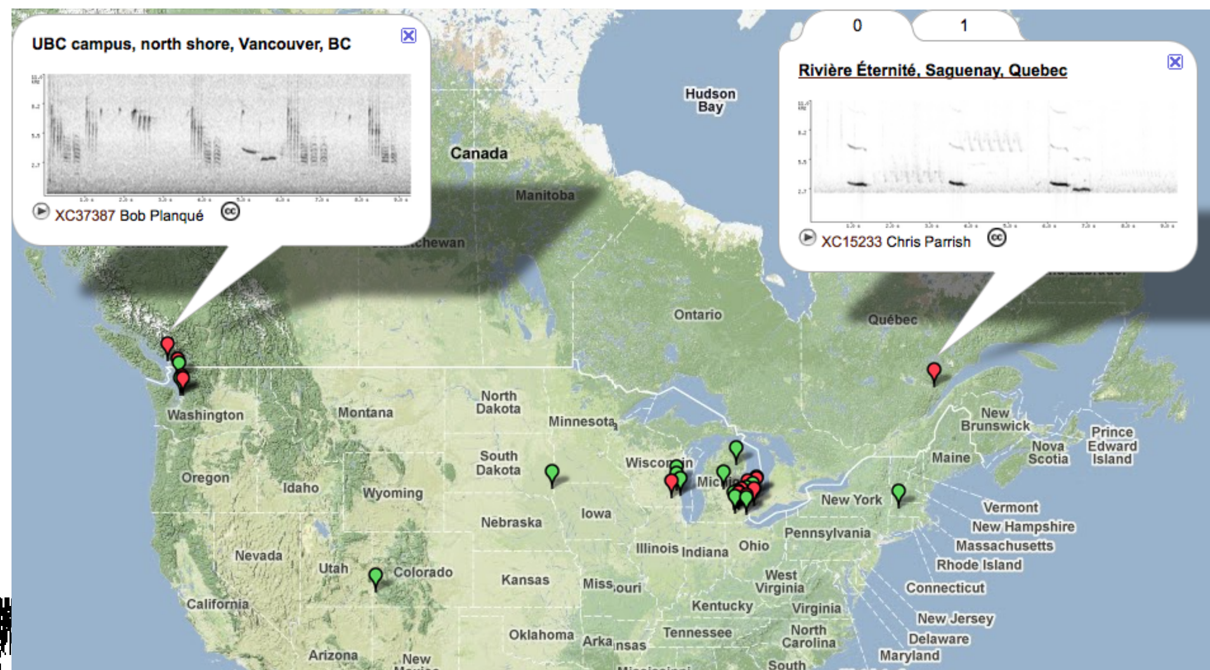
white crowned sparrow: persistent dialects over decades in seemingly homogeneous habitat





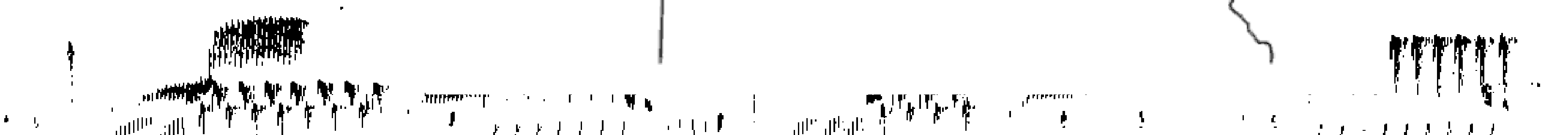
Enigma 2

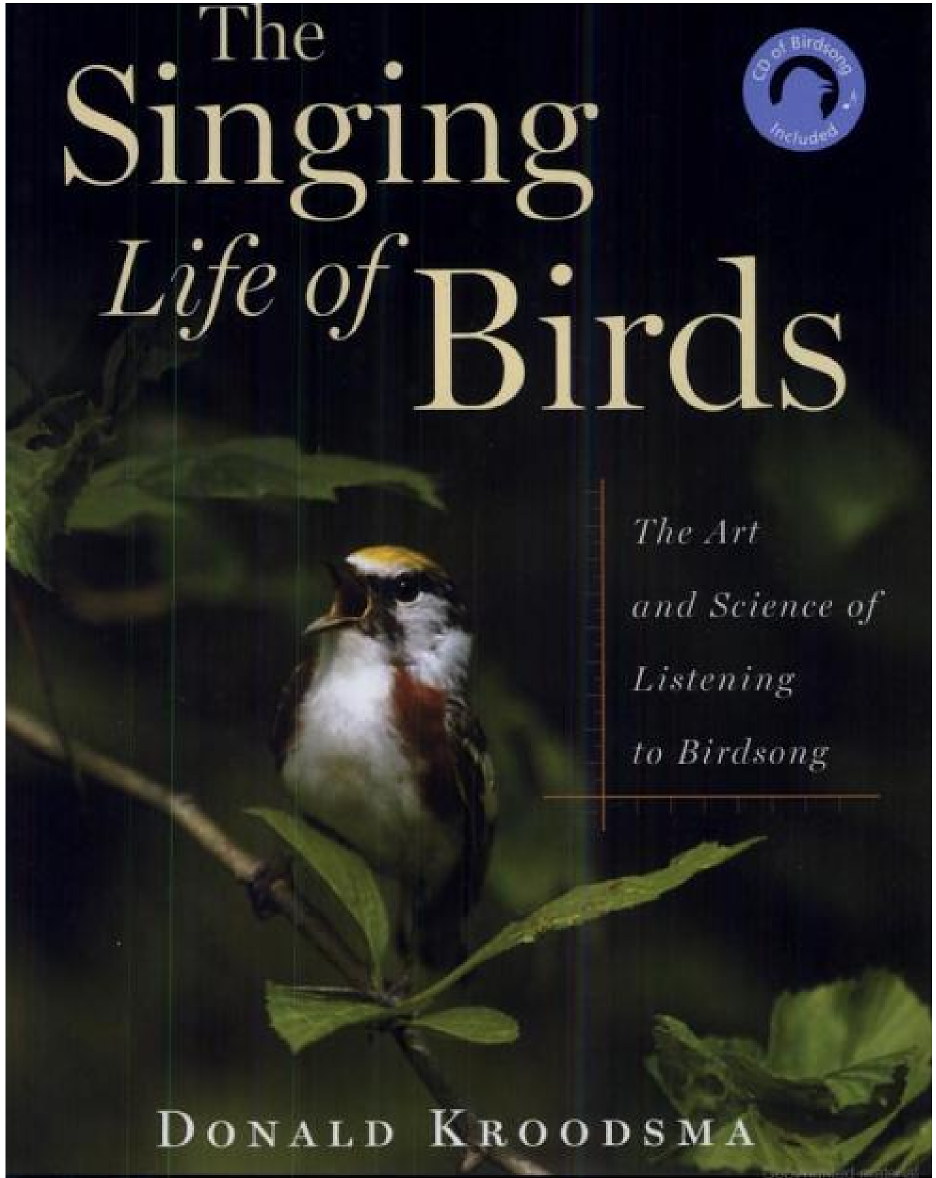
Some species have no dialects over huge ranges, although they learn (chickadee)



Enigma 3

Marsh Wrens: two huge dialect regions, meeting along a long edge




The Singing Life of Birds
CD of Birdsong Included
The Art and Science of Listening to Birdsong
Donald Kroodsma

Learning

- juveniles learn from parents
- period of early flexibility varies (~50 days)
- innate part
- can be entirely plastic, but with preference for own species’ song

Reproduction

- song is important for choosing mates
- large repertoire: old bird
- song as marker for location
- singing much: fit male

- females prefer locally sung songs
- males more successful when singing local songs

=> assortative mating based on song

Main hypotheses

- Local adaptation:
  - choose local male (based on song) as it is more likely to be adapted to local environment
- Social adaptation
  - sing songs that are alike to other local songs, or incur social penalties
- Epiphenomenon
  - byproduct of the dispersal, mating strategies and learning, nonfunctional selection

Main model ingredients

- dispersal
- assortative mating and selection
- learning

distinguish order: predispersal or postdispersal learning

Model 0

- birds age, disperse, learn (vary song)
- song of newborn birds is average of parents'

$$v(x,t,s,a) \qquad V = \int v(x,t,s,a)da$$

$$\frac{ds}{dt} = f(s, V(x,t,s)) \ = k\Big(\frac{\int V(\bar{s})\bar{s}d\bar{s}}{\int V(\bar{s})d\bar{s}} - s\Big)$$

$$\boxed{\begin{aligned} v_t &= -v_a + D_1(a)\Delta_x v - D_3(a)\nabla_s \cdot (f(s,V)v), \\ v(x,t,s,0) &= \frac{1}{\int_0^{\bar{a}} \int_S v(s,a)dsda} \int_S v(x,t,s-\sigma,\bar{a})v(x,t,s+\sigma,\bar{a})F(s-\sigma,s+\sigma)d\sigma \end{aligned}}$$

Model 1: postdispersal learning

- two song types
- two locations
- P_{ij} fraction of males singing songtype *i* in patch *j*
- juveniles mature in one year
- census before reproduction
- annual mortality rate μ
  - replacement with exact same number of one-year-old birds, keeping the population at carrying capacity

Model 1

- reproduction: assortative mating

$$p_{i1} = \frac{P_{i1}^2 + \sigma P_{i1} P_{i2}}{P_{i1}^2 + 2\sigma P_{i1} P_{i2} + P_{i2}^2}$$

- σ determines how often birds form mixed-song matings
- newborns learn dialect from one of their parents (at random)

Model 1

- dispersa'

$$p'_{1j} = (1-\varepsilon)p_{1j} + \varepsilon p_{2j}$$
$$p'_{2j} = (1-\varepsilon)p_{2j} + \varepsilon p_{1j}$$

- ε is the fraction of *successful* colonizers

- Learning

$$p''_{ij} = (1-\lambda)p'_{ij} + \lambda P_{ij}$$

Model 1

Put together

$$P'_{ij} = (1-\mu)P_{ij} + \mu p''_{ij}$$

In new variables

$$Q_i = P_{i1} - P_{i2},\ q_i = p_{i1} - p_{i2}$$

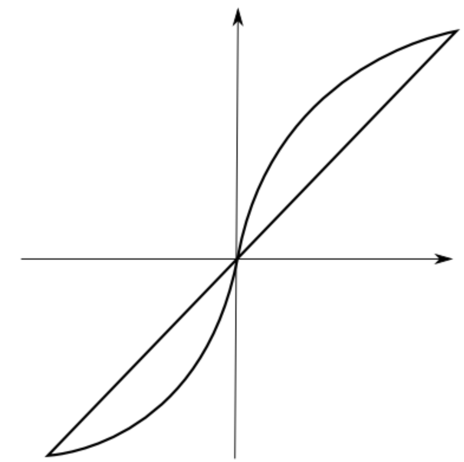
$$\boxed{Q'_i = (1-\kappa)Q_i + \kappa q'_i = (1-\kappa)Q_i + \kappa((1-\varepsilon)q_i + \varepsilon q_j)}$$

$$\kappa = \mu(1-\lambda)$$

Analysis model 1

Using that $q_i = f(Q_i)$ where

$$f(Q) = \frac{Q}{\frac{1}{2}(1+\sigma) + \frac{1}{2}(1-\sigma)Q^2}$$



we get

$$Q_i' = (1-\kappa)Q_i + \kappa((1-\varepsilon)f(Q_i) + \varepsilon f(Q_j))$$

Analysis model 1

- Three equilibria:
  - (0,0) fully mixed
  - (1,1) only dialect type 1
  - (-1,-1) only dialect type 2
- Also equilibria (*Q**,-*Q**) where
- these exist if $Q^* = (1-2\varepsilon)f(Q^*)$

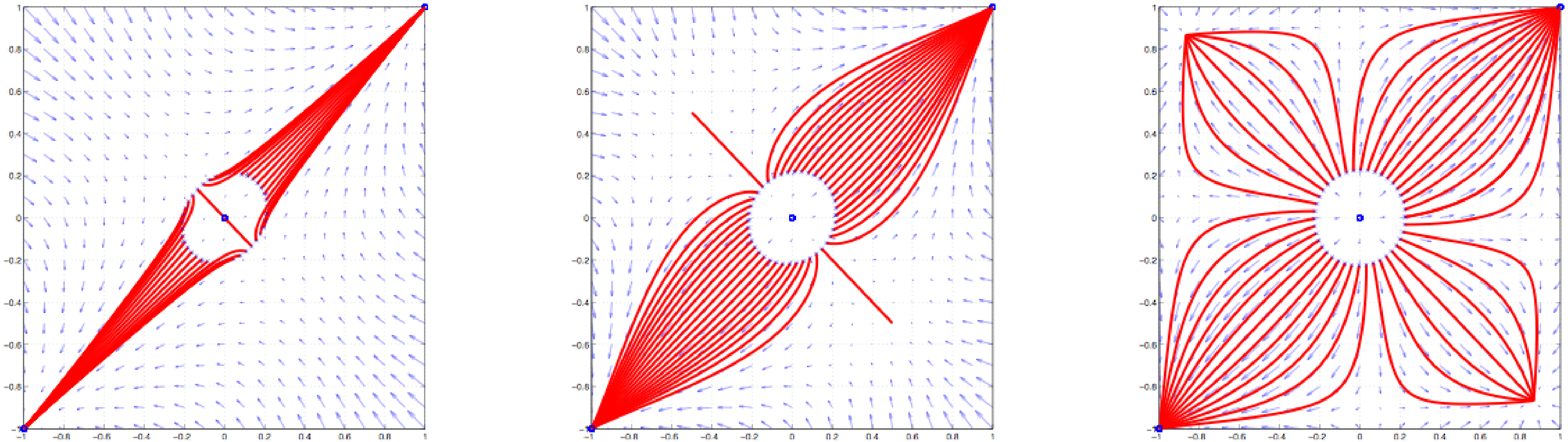
$$\boxed{\varepsilon < \varepsilon_1 = \frac{1}{4}(1-\sigma)}$$

Analysis model 1

- (-1,-1) and (1,1) are always stable
- (0,0) is always unstable
- As ε decreases past ε_1, a pair of equilibria (Q^*,-Q^*) branches off, but these are unstable
- As ε decreases further past ε_2, from each of these two a pair of eq^{a} bifurcates, conferring stability to (Q^*,-Q^*).

$$\boxed{0 < \varepsilon_2 = \frac{1}{4}(3 - \sqrt{5 + 4\sigma}) < \varepsilon_1 = \frac{1}{4}(1 - \sigma)}$$

Example dynamics model 1



Conclusions model 1

- **Assortative mating** must be sufficiently **strong**, and **dispersal** not too **weak** to allow dialects to form
- Neither learning or mortality played any role in bifurcations (but they do matter for speed)

Model 2: predispersal learning

$$\boxed{\begin{gathered} Q_i' = (1-\mu)Q_i + \lambda\mu[(1-\varepsilon)Q_i + \varepsilon Q_j)] \\ +\mu(1-\lambda)[(1-\varepsilon)q_i + \varepsilon q_j] \end{gathered}}$$

Analysis model 2

- (1,1) and (-1,-1) again stable
- anti-symmetric steady states exist if

$$\varepsilon < \varepsilon_1 = \frac{1}{4}(1-\sigma), \;\; \lambda < \lambda_1 = \frac{1-4\varepsilon-\sigma}{(1-2\varepsilon)(1-\sigma)}$$

and are stable if

$$\varepsilon < \varepsilon_2 = \frac{1}{4}(3-\sqrt{5+4\sigma}), \quad \lambda < \lambda_2 = \frac{3-4\varepsilon-\sqrt{5+4\sigma}}{(1-2\varepsilon)(3-\sqrt{5+4\sigma})}$$

Conclusion model 2

- Only real difference is in the role of song learning: it **shouldn’t be too great**
- Dispersal and assortative mating play the same role as in model 1

Model 3: adaptive song types

Mortality depends on song type:

$$P'_{ij} = (1 - \mu_{ij})P_{ij} + (\mu_{ij}P_{ij} + \mu_{ik}P_{ik})p''_{ij}$$

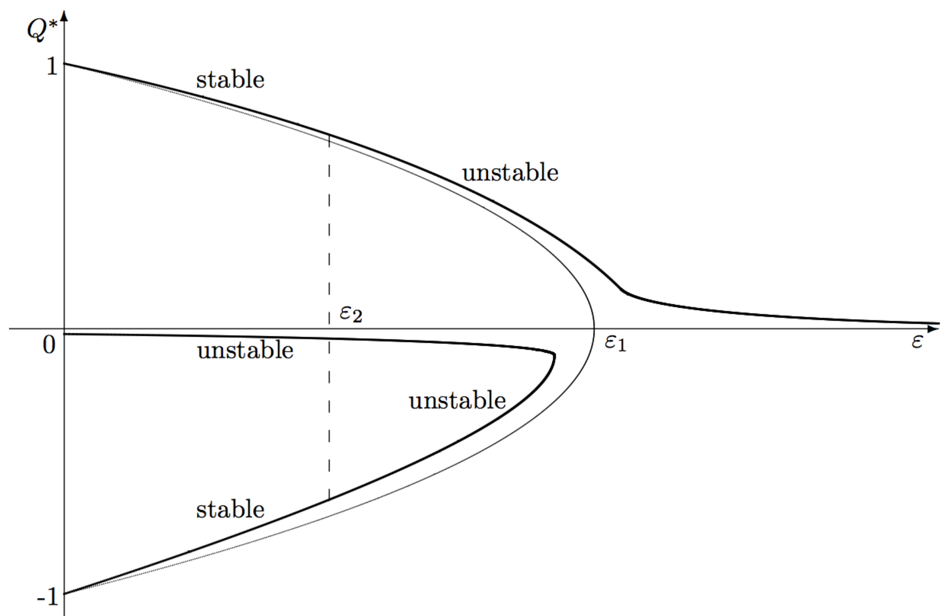
$$\mu_{11} = \mu_{22} = \mu(1 - \delta),\ \mu_{12} = \mu_{21} = \mu(1 + \delta)$$

$$Q'_1 = Q_1 + \mu(\delta - Q_1) + \mu(1 - \delta Q_1)\left\{\lambda Q_1 + (1-\lambda)(1-\varepsilon)f(Q_1) + (1-\lambda)\varepsilon f(Q_2)\right\}$$

$$Q'_2 = Q_2 - \mu(\delta + Q_2) + \mu(1 + \delta Q_2)\left\{\lambda Q_2 + (1-\lambda)(1-\varepsilon)f(Q_2) + (1-\lambda)\varepsilon f(Q_1)\right\}$$

Analysis model 3

- (1,1) and (-1,-1) are still steady states, but (0,0) is not
- For $\delta > 0$ anti-symmetric steady states

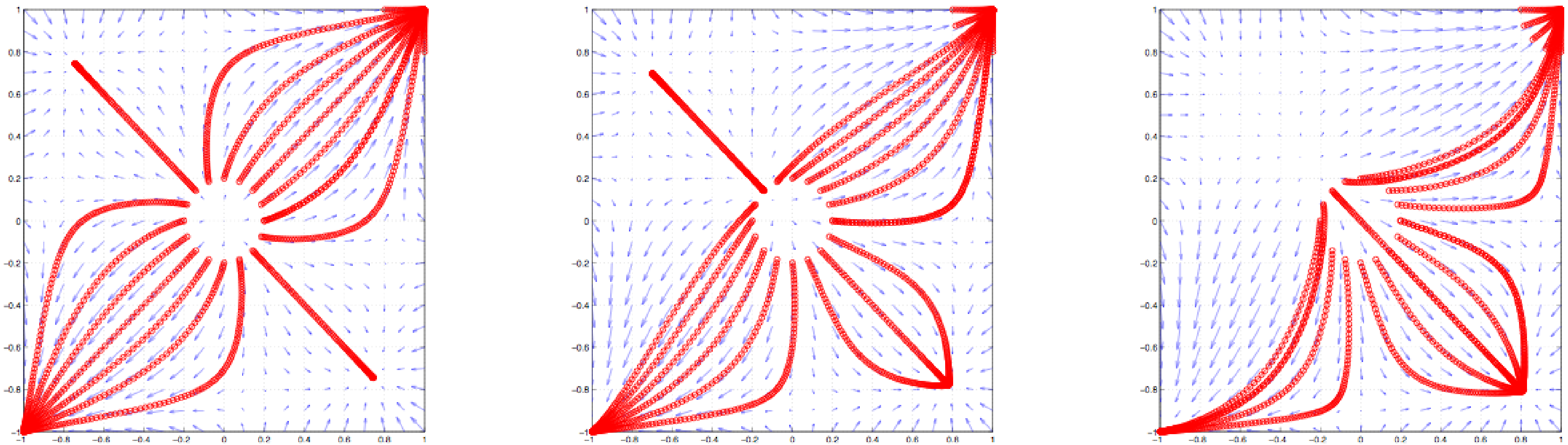


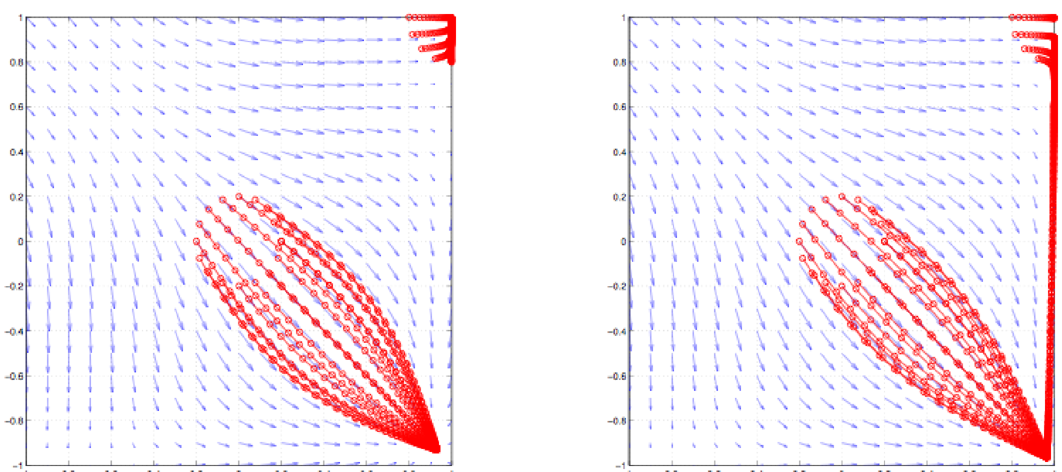
Analysis model 3

- For $\delta > \delta_1$, (1,1) becomes unstable. Presumably solutions converge to the anti-symmetric steady state in the fourth quadrant

$$\delta_1^2 = (1-\lambda)^2 \frac{(1-\sigma)(1-(1-2\varepsilon)\sigma)}{(1+\lambda)+(1-\lambda)\sigma)((1+\lambda)+(1-2\varepsilon)(1-\lambda)\sigma)} < 1$$

- The other anti-symmetric steady state seems to cease to exist for sufficiently large δ





Model 4: taking space into account

- *N*-patch postdispersal model, space periodic:

$$Q_i' = (1-\kappa)Q_i + \kappa((1-2\varepsilon)q_i + \varepsilon(q_{i-1} + q_{i+1})$$

- Set $v_i = f(Q_i)$ so that $Q = f^{-1}(v) =: h(v)$

$$h(v) = \frac{1}{(1-\sigma)v}\left(1 - \sqrt{1-(1-\sigma^2)v^2}\right)$$

Analysis model 4

- Linearisation around *v=0*

$$\frac{dv_i}{dt} = \kappa\Big(\frac{1-\sigma}{1+\sigma}v_i + \frac{2\varepsilon}{1+\sigma}(v_{i+1} + v_{i-1} - 2v_i)\Big)$$

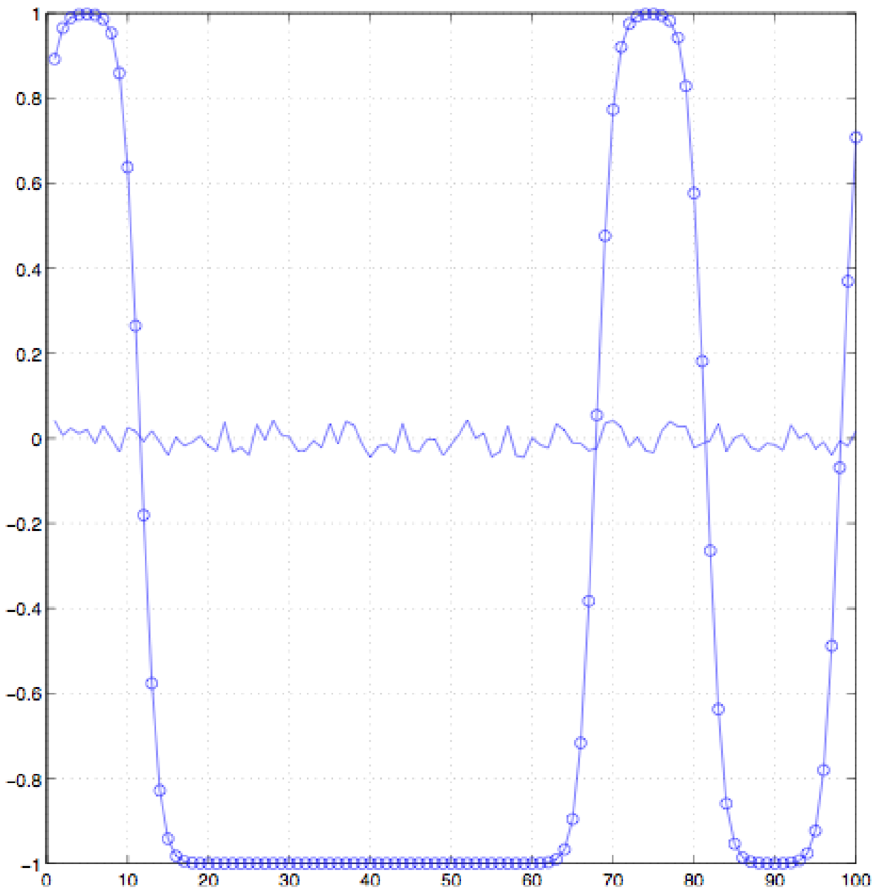
- In Fourier variables, $w_i = \frac{1}{N}\sum_{j=1}^{N}\exp\Big(-\frac{2\pi ij}{N}\Big)v_j, i = 0, \ldots, N-1$

$$\frac{dw_i}{dt} = \kappa\Big(\frac{1-\sigma}{1+\sigma} - \frac{8\varepsilon}{1+\sigma}\sin^2\frac{\pi i}{N}\Big)w_i$$

Analysis model 4

- Origin unstable if $\varepsilon < \frac{1}{8}(1-\sigma)$
- Anti-symmetric steady state (Q*,-Q*) now alternating (Q*,-Q*,Q*,-Q*,..) (if N is even)
- Existence and stability of this steady state is same as for *N*=2 model

Analysis model 4



metastable steady states

Analysis model 4

- In continuum limit of large *N*

$$Q_t = \tilde{\kappa}(f(Q) - Q + D(f(Q))_{xx}$$

- in *v* variable $h'(v)v_t = \kappa(v - h(v) + Dv_{xx})$

- *v=1* and *v=-1* are the only stable uniform equilibria, but solutions close to heteroclinics between *1* and *-1* can be metastable

Analysis model 4

- Short term pattern formation controlled by

$$\alpha := \frac{1}{D}\frac{1-\sigma}{1+\sigma} = \frac{N^2(1-\sigma)}{\varepsilon(1+\sigma)}$$

- If $\alpha \gg 1$: patterns expected
- If $\alpha \ll 1$: patterns not expected

Conclusions model 4

- Formation of local dialects promoted by
  - more patches
  - less dispersal
  - stronger assortative mating

Overall conclusions

- Mortality has little influence on dialects
- Learning (as modelled here) has either no influence, or a negative one (?)
- A combination of **little dispersal** and **strong assortative mating** promotes dialects
- Linking song type to mortality rates allows for **invasion of novel song types**

Outlook and open questions

- Longevity/stability of song dialect regions?
- Necessary ingredients for novel song types to establish themselves?
- Song learning as a ***positive*** force in dialect formation? Introduce e.g.
  - copying errors, novelties
  - selective attrition

Thanks to

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NDNS+

examples

habitat

Cinereous Tinamou, David Edwards

Sky Lark, Patrik Aberg

sexual selection

Tui, Patrik Aberg

Capuchinbird, Nick Athanas

speciation

Chiffchaff, BP

Willow Warbler, BP

source: xeno-canto.org