Presence of a cryptic hybrid zone explains spatial variability in population genetic structuring of a colonial nesting seabird

Chris Burridge¹
Amanda Peucker²
Rebecca Overeem²,³
Craig Styan⁴
Peter Dann³

¹University of Tasmania
²Deakin University
³Phillip Island Nature Park
⁴University College London, Adelaide
Eudyptula minor

- Little penguin (Korora)
- World’s smallest penguin (~1 kg, 300 mm tall)
- Breeding colonies around New Zealand and Southern Australia
- First breeding at 2-3 yr
- Clutch: 2 eggs
- Longevity ~7 yr
Gene flow – Phillip Island

- Intensively studied for >40 years
- No fewer than 62,000 individuals banded
  - 23,686 fledglings

Sidhu et al. (2007). Mark-recapture-recovery modeling and age-related survival in Little Penguins (*Eudyptula minor*). *Auk* 124: 815-827
Where do banded birds go?

• 23,686 fledglings banded
  – 2979 subsequently observed (12.5%)
    • 1347 dead (45% of observations)
    • ~1600 returned alive to Phillip Island

• Observed adult philopatry also not particularly high (<50%)

• Occasional observations at non-natal colonies, but breeding rarely confirmed
  – But, low search effort at other colonies
Movements by living individuals
Question

What are the rates of movement between colonies?
Employ genetic methods to quantify recruitment dynamics

• Compare allele frequencies at putatively neutral markers among colonies
  – Dispersal (gene flow) will homogenise allele frequencies among colonies
Methods

• 17 colonies of up to 50 individuals each
  – some pooling of colonies... “Spencer Gulf”
• 12 microsatellite loci, mitochondrial DNA
• Data analysis
  – Exact tests of allele frequency homogeneity
  – Isolation-by-distance (Mantel) test
  – Non-spatial Bayesian clustering
Possible explanations

- Breeding phenology (✗)
- Oceanographic features (✗)
Mantel tests

Z=228.7760, r=0.4299, P=0.029


Comparison east of “zone”
Mantel tests

![Graph showing genetic distance (Fst) vs. geographic distance (km) for different categories: Inside "zone", Inside/outside "zone", West, and All. The graph indicates a significant correlation between genetic and geographic distance.](image)
How to explain?

• Gene flow related to distance, but different relationships in different regions
  – Different foraging distances in different regions
  – Nesting habitat specialisation and spatial heterogeneity in habitat
  – *Some magic factor that influences the relationship between gene flow and geographic distance*
A different perspective

- Non-spatial Bayesian clustering of individuals
  - "STRUCTURE" analysis
A genetic cline!
Possible origins

Origins of genetic clines

- Selection along an environmental gradient [ECOTONE]
- Isolation and secondary contact [HYBRID ZONE]
  - Selection against hybrids [TENSION ZONE]
  - Neutral introgression (incomplete)
Environmental gradients?
Isolation and secondary contact

• Northern range shift suspected for many temperate Australian marine taxa during Pleistocene glaciation

De Deckker et al. (2012) Nature Geoscience 5, 266–269

• Chance bifurcation of Australian range; loss of geographically intermediate colonies
Isolation and secondary contact

- Hybrids are inferior ("tension zone")
- Neutral introgression [prior to equilibrium]
Isolation and secondary contact

Test via...

1) Tension zone
   • coincidence of cline centres among loci
   • signatures in genetic variation

2) Neutral introgression
   • likely persistence of cline given duration of secondary contact
Tension zone

- No supporting signatures of genetic variation
Neutral introgression

- Assume isolation during glacial stages
- Secondary contact ~15 kya
- 2-3 yr generation time
- Degradation of cline:

\[ T = 0.35 \left( \frac{w}{l} \right)^2 \]

\( T \) is the time since secondary contact (generations).
\( w \) is the cline width (1/max slope)
\( l \) is the geographic distance.

Endler (1977)
Neutral introgression

• Observed hybrid zone width compatible with
  – contact established 15 kya (2-3 yr generation time)
  – mean parent-offspring dispersal < 240 m

• Plausible under a situation of leptokurtic dispersal—high natal philopatry and occasional dispersal to adjacent colonies
  – can accommodate higher dispersal if contact more recent (1 km if contact 1 kya) or generation time longer
Lack of phylogeographic structuring
Summary: *E. minor*

- Regional differences in genetic structuring may only reflect a historical legacy of isolation and secondary contact
  - Contemporary gene flow (per unit distance) could be the same across the study range
- Genetic difference increases with geographic distance
  - Predominance of self/local recruitment
The “so what?”

1. Hybrid zones increasingly reported at the species-level
   - Likely to be common at the intraspecific level

\[ \text{Larus occidentalis} \times \text{glaucescens} \]
2. Failure to recognise hybrid zones may lead to spurious correlations regarding gene flow
   - Importance of spatial sampling
3. Historical legacies may also lead to the under-estimation of contemporary gene flow, rather than just the over-estimation.
Acknowledgements

- Holsworth Wildlife Research Endowment
- Fieldwork volunteers
Tension zone

• Microsatellite and mtDNA clines coincident
  – 27 km apart; $\chi^2=0.034$, d.f.=1, $P=0.84$

• Analysis suited to bi-allelic loci
  – “Coincident coincidence”?