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

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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

Allele frequency heterogeneity



Possible explanations



Mantel tests



Mantel tests



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



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

T = 0.35

- Secondary contact ~15 kya
- 2-3 yr generation time
- Degradation of cline:

Cline width (1/max slope)

 $W_{\lambda} 2$



Endler (1977)

Gene flow (mean parent-offspring geographic distance)



Time since secondary contact (generations)

Neutral introgression

Observed hybrid zone width compatible with

– contact established 15 kya (2-3 yr generation time)

– mean parent-offspring dispersal <240 m</p>

- 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 specieslevel
 - Likely to be common at the intraspecific level





Larus occidentalis x glaucescens

The "so what?"

- Failure to recognise
 hybrid zones may lead to
 spurious correlations
 regarding gene flow
 - Importance of spatial sampling





The "so what?"

3. Historical legacies may also lead to the underestimation of contemporary gene flow, rather than just the over-estimation





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Tension zone

- Microsatellite and mtDNA clines coincident
 - 27 km apart; χ²=0.034,
 d.f.=1, *P*=0.84
- Analysis suited to biallelic loci
 - "Coincident coincidence"?

