Local adaptation in the wedge-tailed shearwater (*Puffinus pacificus*).

Thesis submitted by

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“I may not have gone where I intended to go, but I think I have ended up where I needed to be.”
Douglas Adams
(1952 - 2001)

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PAPERS ARISING FROM THIS THESIS

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Peck, D. R., Smithers, B. V., Krockenberger, A. K. & Congdon, B. C. (2004) Sea-surface temperature constrains wedge-tailed shearwater foraging success within breeding seasons *Marine Ecology Progress Series* 281, 259-266.

Peck, D. R. & Congdon, B. C. (2005) Colony-specific foraging behaviour and co-ordinated divergence of chick development in the wedge-tailed shearwater *Puffinus pacificus Marine Ecology Progress Series* 299, 289-296.

Chapter 4

Peck, D. R. & Congdon, B. C. (2006) Sex-specific chick provisioning and diving behaviour in the wedge-tailed shearwater *Journal of Avian Biology* 37, 1-7.

Chapter 5

Peck, D. R., Bancroft, W. & Congdon, B. C. (in review) Disassortative mate choice, bill morphology and sexual dimorphism in wedge-tailed shearwaters (*Puffinus pacificus*)

Chapter 6

Peck, D. R., Bancroft, W. & Congdon, B. C. (in review) Morphological and molecular variation within an ocean basin in wedge-tailed shearwaters (*Puffinus pacificus*).

SUMMARY

Models of speciation that involve adaptation to local environmental conditions rather than physical barriers have rarely been examined in vertebrate taxa. Seabirds offer a unique opportunity to test such models because they have the potential to disperse widely. This means that large-scale geographical barriers to gene flow are less likely. In addition, breeding colonies are constrained to forage locally, thus promoting the optimisation of life history and fitness-related morphological traits among colonies. Ultimately, these changes may lead to a reduction in gene flow and genetic divergence may ensue: the first step towards speciation. To explore adaptive models of speciation, the role of local foraging conditions in promoting molecular, morphological (including physiological) and behavioural divergence among breeding colonies of the wedge-tailed shearwater (*Puffinus pacificus*) was examined.

To this end levels of variation in morphology and neutral genetic markers were measured among four spatially disjunct breeding colonies located in Australian waters (Rottnest Island, Raine Island, Heron Island and Lord Howe Island). In addition, data on foraging behaviour, chick developmental patterns and sensitivity to background environmental conditions (sea surface temperature) were obtained from two of these colonies representing climatic and oceanographic extremes for this species: the sub-tropical 'reef' colony (Heron Island) and Lord Howe Island, a temperate 'oceanic' colony.

Results from the foraging behaviour and chick developmental component of this research suggests that wedge-tailed shearwaters are sensitive to fluctuations in sea surface temperature, and consistently use different foraging strategies during the chick rearing period in accordance with where they breed. Specifically, at Heron Island, birds use a 'dual-foraging' strategy involving alternative 'short' and 'long' trips. This strategy is consistent with adults self-provisioning from distant locations and chick-provisioning from near colony locations. However, at Lord Howe Island, a dual foraging strategy was not observed, suggestive of a more productive environment.

As an indirect result of divergent oceanographic regimes, chick developmental patterns between the two locations also differed; chicks at Lord Howe Island grow faster than those at Heron. However, when the differences in meal mass per night were accounted for, Heron Island chicks were consistently heavier than those at Lord Howe Island.

Overall, the foraging and chick development data suggest that; (1) chick developmental patterns and foraging behaviour are coordinated in wedge-tailed shearwaters, (2) the foraging environment experienced by wedge-tailed shearwaters at Heron Island is less productive than at Lord Howe Island and (3) chicks at Heron Island appear to 'store' mass as an adaptation to consistently poor provisioning rates (driven by poor foraging conditions experienced by adults). The chick developmental pattern is likely to be driven by an obligate rather than a facultative mechanism because it is doubtful chicks can react to changing provisioning rates over the (small) period of time that the response took place.

Within the general patterns of foraging, sex-specific differences were also evident. Females spent more time at sea resulting in a lower provisioning rate compared to males. The average maximum dive depth also differed according to sex, with males diving consistently deeper than females. The most parsimonious explanation for the differences is that competition has lead to niche partitioning at the foraging grounds, although direct evidence will be required to substantiate this hypothesis. Subtle differences in the extent of sex-specific foraging between Heron Island and Lord Howe Island could promote a barrier to gene flow via. reinforcement if inter-colony pairings result in lower provisioning to chicks. Again, further evidence will be required to test this idea.

Morphological analyses highlighted significant variation within (sex-specific) and among breeding colonies. A canonical discriminant functions analysis was conducted using four traits: wing, tarsus, culmen and tail. Discriminant function 1 (CV1) explained 57.46 % of the variation among groups and was correlated most strongly with tarsus (a measure of skeletal size) followed by tail. CV2 explained a further 38.30 % and was strongly correlated with culmen. In general, birds from Rottnest

Island are significantly larger in overall body size compared to east-coast colonies, however Raine Island birds have significantly longer culmens than elsewhere.
Within colonies males are subtly larger than females, but relative to overall size, only bill morphology was significantly larger. A novel form of mate choice (disassortative) based on bill width was also observed at both Heron and Lord Howe Islands. Patterns of morphological variation and pair formation do not fit with those expected if environmental conditions alone (i.e. plasticity) are responsible. Instead, the results suggest that morphological diversity is more likely to involve selection.

Finally, levels of gene flow were gauged and compared to morphological variation to determine if gene flow constrains morphological divergence among colonies. Three intron and three microsatellite loci were used. Gene flow estimates differed according to the type of marker. Introns suggest substantial inter-colony movement whereas microsatellites imply that gene flow is restricted. The different estimates reflect differences in the mutation rates of the two markers. Consequently, introns (evolving more slowly) likely reveal historical connections during the Pleistocene, with microsatellites representing more contemporary patterns. A lack of congruence between the amount of morphological and genetic differentiation suggests that genetic drift alone can not explain all of the observed morphological diversity in wedge-tailed shearwaters.

Taken together, the results from this study clearly suggest that oceanographic/environmental regimes have an important function in the development and maintenance of seabird diversity and can substantially influence the direction of micro-evolutionary change. This has important implications from a management perspective, as some colonies will need to be considered independently. Future work should focus on assessing the role of selection in causing the observed patterns by evaluating the relationship of behavioural, morphological and physiological (chick development) traits to fitness in alternative habitats.