

Many animals, such as birds, use multi-message mating displays that contain structurally distinct song types. A song type may be simultaneously used for mate attraction and male-male interactions since both involve the same function; conveying species identification and sender locations over long distances. These song types generally have a simple structure that consists of highly stereotyped bouts of lower frequency sounds. The lower frequency sounds propagate efficiently over long distances and the low within and between individual variations in signal structure conveys species or group identity. A different song type may be used for courtship and is therefore structurally suited for short range mate assessment and conveying male quality. Courtship songs generally have a complex structure that consists of highly variable bouts with higher frequency sounds. The higher frequency sounds have limited propagation thereby reducing the possibility of eavesdropping, and the variability in signal structure conveys information about the individual.

Male humpback whales use song as a mating display, mainly on breeding grounds and migration routes. Behavioural studies in several populations have found evidence for both inter- and intra-sexual functions in humpback whale song, which suggest that song may have a dual function in female choice and mediating male-male interactions. In fact, several researchers have put forth this dual function hypothesis for humpback whale song. Thus, the objective of this thesis was to investigate whether east Australian humpback whale song shows structural characteristics consistent with a multi-message display.

Humpback whale song has a hierarchical structure with ‘units’ sung in sequences termed ‘phrases’. Phrases are repeated a variable number of times to create a ‘theme’; therefore, themes are differentiated by their characteristic ‘phrase type’. Phrase types are analogous to the song types sung by birds. Within a theme, variation can occur due to imperfect repetition of phrases, with these inexact repeats termed ‘phrase variants’. If humpback whale song is a multi-message display, then song should contain two categories of phrase types (and therefore themes), ‘simple’ and ‘complex’.

To investigate this hypothesis, song recordings from 17 east Australian whales (8 from 2004 and 9 from 2011) were analysed for structural differences. In Chapter 2, to determine if song complexity varied between phrase types, repertoire size (defined as the number of unit types,

phrase types, and phrase variants) was used to quantify complexity. Self-organising feature maps were used to delineate unit types, and the Levenshtein distance between unit sequences was used to determine phrase types and variants. Song oscillated between periods of ‘simple’ phrase types with limited repertoires of relatively stereotypic units and phrase variants and periods of ‘complex’ phrase types with larger repertoires of variable units and phrase variants. Furthermore, the ‘simple’ phrase variants were sung by multiple males, whereas the ‘complex’ phrase variants were almost always unique to individuals.

In Chapter 3, to further characterise the structural differences between phrase types, hidden Markov models (HMM) were used to model song as a two-state stochastic process. These models partitioned phrases into two distinct states, or categories, based on eight phrase features. State 1 phrase types were primarily sung by multiple individuals, had a smaller number of units and unit types, longer average inter-unit intervals, lower, narrower range of frequencies, and either shorter or longer durations than State 2 phrase types. Furthermore, State 2 phrase types incorporated phrases that were generally unique to an individual and had a larger amount of variance in the spectral and temporal features. The results of Chapters 2 and 3 were consistent in that the HMM partitioned phrases considered ‘simple’ (based on the repertoire analysis of Chapter 2) into the same state (State 1), whereas phrases considered ‘complex’ were partitioned into the other state (State 2).

Lastly, in Chapter 4 classification tree analyses identified the modifications involved in generating phrase variants within ‘simple’ or ‘complex’ themes. These modifications were characterised by determining the numbers of substitutions, deletions, and/or insertions that occurred between phrases sung within a theme. A single type of modification (one or two substitutions, insertions, or deletions only) generated phrase variants within simple themes. In contrast, a combination of modifications (generally larger numbers of substitutions with insertions or deletions) generated phrase variants within complex themes.

In summary, contrasting types of modifications resulted in simple phrase types with a small degree of syntactic variability and complex phrase types with a larger degree of syntactic differences. The structural characteristics of simple phrase types were consistent with stereotyped, long distance mate attraction/male-male competition songs. In contrast, the complex

phrase types were structurally similar to complex, short range courtship songs. This thesis, therefore, provides robust, quantitative structural evidence that supports the hypothesis that humpback whale song is a multi-message display. Future research is needed to determine if simple and complex phrase types differ in function and propagation characteristics as hypothesised.