

**Cultural variation and usage of coda vocalisations  
by sperm whales, *Physeter macrocephalus***

by

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for the degree of Doctor of Philosophy

at

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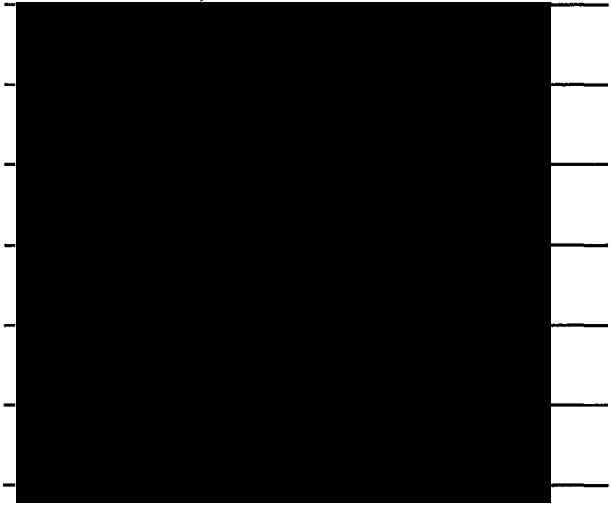
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*Andábamos sin buscarnos, pero sabiendo que andábamos para encontrarnos*

Julio Cortázar

Dedico esta tesis a la hermosa Claudia,  
quien siempre estaba a mi lado.  
Gracias por todo su apoyo y amor.  
Qué seguimos andando juntos.

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## *Abstract*

Studies of animal culture have normally not included a consideration of cetaceans. However, cultural transmission may be a significant source of variation in the behaviour of whales and dolphins, especially as regards their vocal signals. There is good evidence for cultural transmission in several cetacean species. There have been suggestions of gene-culture co-evolution in cetaceans, and culture may be implicated in some unusual behavioural and life history traits of the whales and dolphins. One such species is the sperm whale (*Physeter macrocephalus*). I studied variation in the vocal output of 'codas', short repeated patterns of clicks, recorded from sperm whale social groups.

I evaluated five methods of comparing repertoires of 'codas' and concluded that using multiple techniques concurrently allows the drawing of relatively robust conclusions about repertoire similarity. Using these methods, I showed that the coda repertoires of all 18 known social units, and 61 of 64 groups (about two social units in temporary association) that were recorded in the South Pacific and Caribbean between 1985 and 2000 can be reliably allocated into six acoustic 'clans', five in the Pacific and one in the Caribbean. Clans have ranges that span thousands of kilometres, are sympatric, contain many thousands of whales, and most likely result from cultural transmission of vocal patterns. Culture may thus be a more important determinant of sperm whale population structure than genes or geography; this has major implications for our understanding of the species' behavioural and population biology.

I used the multi-pulse structure of sperm whale clicks to estimate the size of animals producing codas in recordings of a single social unit. These data showed that more than one animal was producing codas and that several coda types were shared. Thus the codas recorded from these animals represent a shared repertoire, with coda production not limited to a single animal and coda types shared between individuals within the unit.

Playback studies are an important technique in elucidating the function of vocal signals. I attempted to test for differential response to the playback of clan and non-clan codas to sperm whale social groups off Chile, but found little evidence for such a response. However, the study had low power and was based on a fairly simplistic hypothesis.

Exploring the clan dialect system further, I found little evidence for unit-specific repertoires within clans or change over time in the repertoires of any unit. I did find good evidence for geographic variation within clans that relates well to what we know of sperm whale movement and ocean ecology. These patterns were repeated when I analysed variations within a single coda type, suggesting that clan membership also affects the structure as well as the usage of coda types.

Surveying similar phenomena in other taxa leads to the conclusion that the only non-human parallels of sperm whale vocal clans are the vocal clans of killer whales (*Orcinus orca*).

### *List of abbreviations and symbols*

$\alpha$	alpha, the probability of incorrectly rejecting a true null hypothesis
$^{\circ}\text{C}$	temperature in degrees centigrade
$\text{cms}^{-1}$	velocity in centimetres per second
dB	decibel
dB//1 $\mu$ Pa	decibels relative to one micro-Pascal of pressure (peak-to-peak measure)
dB//1 $\mu$ Pa-m	decibels relative to one micro-Pascal of pressure at a distance of one metre
d.f.	degrees of freedom
DNA	deoxyribonucleic acid
$F$	$F$ -ratio
Hz	Hertz, frequency in cycles per second
kHz	kilohertz, frequency in thousands of cycles per second
ms	millisecond
$\text{ms}^{-1}$	velocity in metres per second
m	metre
n.m.	nautical mile
$p$	probability
Q	photograph quality for identification purposes
$r$	coefficient of relatedness
$r_m$	matrix correlation, as used in Mantel test
$r_s$	Spearman correlation coefficient
$r^2$	proportion of total variance about the mean explained by a regression analysis
s	second
$t$	$t$ statistic, used to calculate probability in a $t$ -test

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*If I have seen further it is by standing on the shoulders of giants*

Isaac Newton

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I obtained most of data in this thesis by using software called Rainbow Click, provided by the International Fund for Animal Welfare's *Song of the Whale* research team; I warmly thank them and in particular Doug Gillespie who repeatedly and uncomplainingly modified the software to meet my needs.

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## CHAPTER ONE

*Introduction: An evolutionary ecological perspective on cetacean culture*

## INTRODUCTION

The starting point for this thesis are the combined evidence and suggestions of Weilgart & Whitehead (1997), Whitehead *et al.* (1998) and Whitehead (1998) that sperm whales, *Physeter macrocephalus*, have culturally transmitted group-specific dialects, and that matrilineal culture could have played a role in reducing mtDNA diversity in this species. The presence and nature of cultural processes in non-human animals is an area of some controversy (de Waal 1999; Galef 1992), not least because of the differing perspectives offered by disciplines that each bring their own cultural context to the subject. This debate, which started in Japan well before McGrew (1978) brought it to western attention (de Waal 2001; McGrew 2001), is currently expanding to incorporate a body of compelling evidence for cultural processes in cetaceans, the whales and dolphins.

Cetaceans provide an interesting contrast to the study of culture in humans and other terrestrial animals, since they inhabit a radically different environment and represent an independent evolution of social learning and cultural transmission. The evidence now available describes some interesting and rare patterns of behavioural variation in the wild, that most likely result from cultural transmission (Rendell & Whitehead 2001). There can be little doubt that cetaceans are among the most socially and cognitively complex non-humans. For example, the only non-human example of second-order social alliances (that is, alliances between alliances) comes from the bottlenose dolphin, *Tursiops* spp., (Connor *et al.* 2001; Connor *et al.* 1998). This same dolphin can use abstract representations of objects, actions and concepts to guide behaviour (Herman *et al.* 1993; Herman *et al.* 1994); it also parallels humans and great apes in being capable of mirror-self recognition (Reiss & Marino 2001). To what extent is this social and cognitive complexity reflected in the cultures of cetaceans? In this thesis, I argue that culture may have an important impact on the behaviour, genetic evolution and population structure of cetacean species, and, further, that the importance of cultural identity is not just a human attribute.

This chapter draws heavily on a previously published discussion of cetacean culture (Rendell & Whitehead 2001). While culture and cultural transmission have been briefly discussed in the context of cetaceans by a number of authors (Felleman et al. 1991; Ford 1991; Norris & Dohl 1980; Norris & Schilt 1988; Norris et al. 1994; Osborne 1986; Shane et al. 1986; Silber & Fertl 1995), there has until recently been little exchange with other disciplines. For example, anthropology is anthropocentric by definition, and so the study of non-human culture is most often seen as an attempt to understand human culture by understanding that of our evolutionary ancestors and close current relatives; hence small wonder that most attention is given to primates. However, the study of culture is wider than this, and we find ourselves at an exciting point of inter-disciplinary contact where anthropologists, psychologists and, increasingly, evolutionary ecologists like myself, are seeking to forge a common conception of what culture is and how to study it across species.

Before reviewing culture in cetaceans, I discuss the differing approaches that have been taken to the study of non-human culture, and explicitly set out the influence that my own academic cultural inheritance has upon my reading of the culture concept. I then briefly review the evidence for, and the evolution of, culture in cetaceans, and suggest that cultural processes may explain some unusual behavioural, life-history, and genetic patterns of whales and dolphins.

#### **HOW DOES ONE STUDY CULTURE IN WHALES AND DOLPHINS?**

My own cultural inheritance as a behavioural ecologist gives a certain perspective on culture, and this of course will be radically different from some others. I work quite happily from within the neo-Darwinian paradigm, see no need to dispense with it, and consider it quite capable of explaining the evolution of cultural faculties up to and including human culture. To be useful to cetologists, a concept of culture must be concerned with things that can be observed empirically, without the necessity of knowing about internal states or constructs (for example, beliefs or values). It must at least allow for non-human culture, and should not exclude things that we commonly consider

cultural in humans. The definition I consider most useful is:

*Information or behaviour – shared by a population or sub-population – which is acquired from conspecifics through some form of social learning.*

(Rendell & Whitehead 2001)

Whiten & Ham (1992) list a range of “social processes” as supporting cultural transmission, and in the definition of culture I use, the term “some form of social learning” refers to these processes. These comprise exposure, social support, matched dependent learning, stimulus enhancement, observational conditioning, imitation, and goal emulation as listed and defined in Whiten & Ham (1992).

Rendell & Whitehead (2001) were criticized for adopting such an inclusive and, to some, simplistic definition. Many suggestions have been made to narrow the definition, none of which I consider defensible (Table 1.1). This definition should not be seen as an attempt to *describe* culture, rather as setting out *minimum conditions* for what we should include in a study of culture. In humans, culture is more than this - more than just social learning, more than just group level behavioural variation; it is tied up intimately with our own sense of identity. But are we the only species with cultural identities? Here, I argue that we are not.

From an evolutionary perspective, the important questions surrounding culture in humans and non-humans concern how cultural faculties and the behavioural complexes to which they give rise (which we would call cultures by our definition) vary in extent and form within and across species, and how this may be related to evolutionary ecology. In nature, one finds what approaches a continuum between animals that appear acquire only a single behavioural pattern culturally – for example, bluehead wrasse, *Thalassoma bifasciatum*, use traditional mating sites (Warner 1988) – through animals that acquire suites of behaviours through cultural processes (including chimpanzees, *Pan troglodytes*, and killer whales, *Orcinus orca*) to humans, where culture has enabled us to radically alter our own environment. I maintain that drawing a line on this continuum and labelling

one side ‘culture’ and the other ‘not culture’ is essentially an arbitrary exercise, leading to the current variability in attributions of culture to non-humans. A broad definition allows us to concentrate on comparing cultures across species, and relating these comparisons to ecology.

Table 1.1: Failed attempts to raise the culture bar

<b>Proposed criterion</b>	<b>Why it doesn’t hold</b>
To be culture, it must be transmitted by imitation or teaching <i>only</i> (Galef 1992).	Many social learning processes can support culture (Whiten & Ham 1992); not clear that <i>all</i> human culture is transmitted this way (McGrew 1998).
Only homologues to human culture are relevant (Galef 1992).	Nonsensical to exclude analogues – un-evolutionary approach.
To be culture, it must be adaptive (Slater 2001).	Much human culture is non- or mal-adaptive (e.g. celibacy vows).
To be culture, it must be stable across generations (e.g. Freeberg 2001).	Some human culture is not at all stable.
To be culture it must “ratchet” over time (Tomasello 1994).	Not all human culture ratchets
To be culture, it must perform the same function as culture in humans (Premack & Hauser 2001; Ripoll & Vauclair 2001)	Anthropocentric, and what is the function of human culture anyway!

This concept of culture is not greatly removed from those to be found in introductory cultural anthropology textbooks - if anyone should know what culture is, it is cultural anthropologists. Consider the following definitions (gleaned from Cronk 1999):

1. “The patterned and learned ways of life *and thought* shared by a human society” (Bodley 1994).
2. “The learned set of behaviors, *beliefs, attitudes, values, or ideals* that are characteristic of a particular society or population” (Ember & Ember 1990).
3. “That complex of behavior *and beliefs* we learn from being members of *our* group”

(Moore 1992a).

4. “The socially transmitted knowledge and behavior shared by some group *of people*” (Peoples & Bailey 1997).

I have highlighted criteria that necessitate insight into the internal worlds of ones’ subjects (e.g. beliefs, thoughts, attitudes, ideals), and also specific reference to humans. When these are removed, the above definitions become:

1. “The patterned and learned ways of life ... shared by a ... society.”
2. “The learned set of behaviors ... that are characteristic of a particular society or population.”
3. “That complex of behavior ...(individuals) learn from being members of (a) group.”
4. “The socially transmitted knowledge and behavior shared by some group ...”

Note the similarity between these and Rendell & Whitehead’s (2001) definition. I submit that the gap between what I and cultural anthropologists consider to be culture is not as wide as it first seems; perhaps the major difference is the assumption of humanness understandably inherent in the latter. Accusations that of ‘lowering the bar’ for culture (see commentaries on Rendell & Whitehead 2001, Table 1.1) seem not to hold given the similarity of this definition to those found in cultural anthropology textbooks.

Armed with this concept of culture, we can now proceed out of the library into the empirical world, where the really interesting things happen. The empirical study of cultural processes in animals is generally approached in two major ways: controlled laboratory experiments on social learning mechanisms and field descriptions of behavioural variation (Lefebvre & Palameta 1988). Both make important contributions to our understanding of culture. The first approach focuses on experimental study of the cognitive processes underlying cultural transmission. The second is field-based, involving the systematic assimilation of data on the behaviour of individuals and groups often over large temporal and spatial scales. This approach has been, controversially, likened to ethnography in the social sciences (Wrangham et al. 1994). Of course, we

cannot interview cetaceans - which may be a blessing in disguise (see McGrew 1998) - and neither can we describe any values or ideals that might exist, but the essential project of identifying and mapping cultural variation in nature remains. For biologists, such research is not an end in itself, but the pre-cursor for asking evolutionary questions (McGrew 1998). Why did culture itself evolve, how do specific cultural traits themselves evolve over time, and do they affect genetic evolution (Boyd & Richerson 1985)?

These two approaches have interacted in different ways in the study of culture and cultural transmission in different taxonomic groups. Culture in humans is studied largely from an ethnographic perspective, although some experimental work has been done (Meltzoff 1996; Tomasello et al. 1993). In the study of the cultural evolution of bird-song, the two approaches have generally integrated cooperatively with laboratory and field studies complementing each other in a stimulating and progressive way (see Baker & Cunningham 1985). In non-primate terrestrial mammals, there exists an impressive body of work concerning the social transmission of feeding behaviour, based mainly on an experimental approach (Galef 1996), with little reference to variation in the wild (for a notable exception, see Terkel 1996). It is in the discussion surrounding culture in non-human primates that the most severe dichotomy between these two perspectives is apparent. A lack of laboratory evidence for imitation has led to the persistent denial of culture in chimpanzees (*Pan troglodytes*) from some (Galef 1992; Tomasello 1994), while others, drawing on field evidence of variation in behaviour such as nut-cracking which cannot be explained by ecological or genetic factors, maintain that wild chimpanzees *do* have distinctive and complex cultures (Boesch 1996; Boesch et al. 1994; McGrew 1994; Whiten et al. 1999). My own perspective coincides more with the latter, because I do not think culture can be defined in terms of particular transmission processes. However, I strongly believe that research on cultural processes is best served by an approach that integrates the sometimes-opposing process and product oriented perspectives, as well as the laboratory and field approaches, taking good data from each. It will not be served by primato-centrism to the erroneous exclusion of other taxa, nor by excluding non-humans on technicalities such as the difference between imitation and



‘individually ritualising [behaviours] with one another’ (Tomasello 2000).

## **EVIDENCE FOR CULTURE IN CETACEANS**

Detailed descriptions of the evidence for cetacean culture have been published elsewhere (Boran & Heimlich 1999; Rendell & Whitehead 2001); here I summarise that evidence and present some more recent additions to the growing body. In only four (of ~80) species of Cetacea have more than a handful of papers on behaviour been published (Mann 1999): the bottlenose dolphin, the killer whale, the sperm whale, and the humpback whale (*Megaptera novaeangliae*). The four species have diverse social systems: humpback whales generally live in loose fission-fusion societies (Clapham 1993); both sexes of killer whale generally remain within their natal matrilineal group (Baird 2000); female sperm whales live in largely matrilineal groups from which males disperse to lead quite solitary adult lives (Whitehead & Weilgart 2000); while in bottlenose dolphins, males can form stable alliances while females possess a network of more labile relationships (Connor et al. 2000). Although the four well-studied cetacean species are socially diverse, they are likely unrepresentative of all cetaceans. For instance, the pelagic dolphins, beaked whales, and river dolphins may have quite different social systems (Connor *et al.* 1998), and cultural faculties.

### **Ethnographic evidence**

Three main patterns of behavioural variation have been observed in the well-studied species, and give evidence for cultural processes in cetaceans. The best evidence for each pattern is given in Table 1.2; as well as the species mentioned above it contains evidence for the bowhead whale, *Balaena mysticetus*, the beluga, *Delphinapterus leucas*, and the Irrawaddy dolphin, *Orcaella brevirostris*. The three main patterns are:

- a) **Rapid spread** of a novel and complex form of behaviour through a segment of the population, indicating a largely horizontal - within-generation (Cavalli-Sforza & Feldman 1981) - cultural process. The best known example is the song of the humpback whale; Noad *et al.* (2000) recently described a ‘cultural revolution’ in

humpback song as populations migrating along the east coast of Australia adopted the song of their western Australian counterparts, completely replacing the old song in two years. I include the songs of bowhead whales (Clark 1990; Würsig & Clark 1993) and the spread of lobtail feeding in humpbacks (Weinrich et al. 1992) in this category, although these latter examples are more controversial.

- b) **Mother-offspring similarity** in a complex form of behaviour, indicating vertical - parent-offspring (Cavalli-Sforza & Feldman 1981) - cultural transmission. Here the best example is 'sponging' by bottlenose dolphins, where individuals carry sponges on their rostra. Thought to be a foraging specialisation (Smolker et al. 1997), it is practised by a mostly female subset of the bottlenose dolphin community of Shark Bay, Australia; currently only calves whose mothers sponged went on to become spongers themselves; Mann & Sargeant (2003) describe this and other examples of mother-offspring behavioural similarity in the Shark Bay population.
  
- c) **Group level differences** in complex behaviour between stable groups of animals that are hard to explain by genetic differences, shared environments, or the sizes or demographic structure of the groups. Such patterns could arise through vertical or oblique - learning from a non-parental model of the previous generation (Cavalli-Sforza & Feldman 1981) - transmission within strictly matrilineal groups, or through a combination of vertical, oblique and horizontal within-group transmission in a system with conformist traditions - individuals aligning their behaviour with that of other group members (Boyd & Richerson 1985) - within more labile groups. By far the best evidence comes from killer whales around Vancouver Island, where sympatric killer whale pods have distinctive dialects and foraging specialisations (Baird et al. 1992; Barrett-Lennard 2000; Barrett-Lennard et al. 1996; Deecke et al. 2000; Ford 1991; Yurk et al. 2002). There are also compelling accounts of dolphin-human cooperative fishing that has persisted for generations (Pryor et al. 1990; Simões-Lopes et al. 1998). Additionally, sperm

whale groups have distinctive dialects, discussed below.

Examples of cetacean culture, and new problems, are emerging regularly. One example concerns the two communities of bottlenose dolphin inhabiting Moreton Bay, Australia (Chilvers & Corkeron 2001). Members of one of these communities forage by following trawler nets, members of the other do not. Containing 154 and 88 members respectively, these two communities are socially isolated even though their geographic ranges overlap almost completely – only 3 of 463 sightings were of animals from both communities, and two of these were likely attempts by males of one to mate with females of the other, indicating the potential for gene-flow between the communities (Chilvers & Corkeron 2001). It is thus unlikely in the extreme that behavioural differences between these communities are anything but cultural. Unlike previous evidence for social learning in bottlenose dolphin that has highlighted individual specialisations, Chilvers & Corkeron (2001) provide evidence for *community-level* variation that more closely matches anthropological notions of culture (McGrew 2003). This example adds to the already large body of evidence for culture in bottlenose dolphins, and highlights the often sympatric nature of cetacean cultural variants, in direct contrast to the strong geographic patterning of primate and early human culture.

Further evidence for sympatric cultures has recently emerged from an ongoing study of sperm whales in the South Pacific. Sperm whales make distinctive, stereotyped patterns of 3-12 clicks termed ‘codas’, which are thought to function in communication (Watkins & Schevill 1977). Distinctive coda dialects (consisting of very different proportional use of about 30 different types of coda) are a feature of partially matrilineal, but interacting, groups of about 20 female sperm whales (Weilgart & Whitehead 1997). This phenomenon is the main topic of this thesis, and I discuss these observations in more detail later in this chapter (see also Chapter 3).

Table 1.2: Ethnographic patterns suggesting cetacean culture. For detailed argument against genetic or ecological variation coupled with individual learning as causes for these patterns, see Rendell & Whitehead (2001).

Species	Phenomenon	Causation: Ecological?	Genetic?	Comments	Reference(s)
Humpback whale	Songs	No	No	Continuously evolving in large and dispersed population	(Noad <i>et al.</i> 2000; Payne & Guinee 1983)
Bowhead whale	Lobtail feeding	Unlikely	No	Rapid spread through population	(Weinrich <i>et al.</i> 1992)
	Migration	No	Unlikely <sup>1</sup>	Calf repeats mother's migration	(Katona & Beard 1990)
	Songs	No	No	Continuously evolving; some evidence for imitation	(Clark 1990; Würsig & Clark 1993)
Beluga whale	Migration	No	Unlikely <sup>1</sup>	Calf repeats mother's migration	(O'Corry-Crowe <i>et al.</i> 1997)
Bottlenose dolphin	Sponging	Unlikely	Unlikely	A few animals in one study site, seems to be passed from mother to female offspring	(Mann & Sargeant 2003; Smolker <i>et al.</i> 1997)
Killer whale	Use of human provisioning	?	Unlikely	Recent phenomenon in one study site	(Mann & Sargeant 2003)
	Human-dolphin fishing cooperative	Unlikely	No	Complex coordinated behaviour pattern of both species has persisted for generations	(Pryor <i>et al.</i> 1990; Simões-Lopes <i>et al.</i> 1998)
	Feeding from trawlers	Unlikely	Unlikely	Two sympatric communities	(Chilvers & Corkeron 2001)
	'Kerplunking', and other foraging specializations	?	Unlikely	Probably other foraging specializations at this and other sites	(Connor 2001)
Intentional stranding	Unlikely	Unlikely	Intriguing evidence for teaching	(Guinet & Bouvier 1995; Hoelzel 1991)	

Table 1.2 (continued)

	'Resident' call dialects	No	No	Sympatric dialects are quite stable but show small coordinated changes. Recent genetic analyses show most mating is <i>between</i> pods.	(Barrett-Lennard 2000) (Deecke <i>et al.</i> 2000; Ford 1991)
Killer whale	Pod-specific foraging specializations	No	Unlikely <sup>1</sup>	Consistent specializations of both 'resident' and 'transient' pods, sometimes sympatric	(Baird <i>et al.</i> 1992; Barrett-Lennard <i>et al.</i> 1996)
	Pod-specific migration patterns	No	Unlikely <sup>1</sup>	Sympatric	(Nichol & Shackleton 1996)
	Community-specific greeting ceremonies	Unlikely	Unlikely	Not sympatric	(Osborne 1986)
Sperm whale	Group-specific coda repertoires	No	Unlikely <sup>1</sup>	Groups have distinctive coda usage dialects	(Weilgart & Whitehead 1997; Whitehead <i>et al.</i> 1998)
	Group-specific movement patterns	Unlikely	Unlikely <sup>1</sup>	Sympatric groups show evidence of characteristic movement patterns	(Whitehead 1999)
	Group-specific communal defence methods	?	Unlikely <sup>1</sup>	Indirect evidence	(Dufault & Whitehead 1998)
Irrawaddy dolphin	Human-dolphin fishing cooperative	Unlikely	Unlikely	Complex coordinated behaviour pattern of both species has persisted for many generations	(Smith <i>et al.</i> 1997)

<sup>1</sup>For these patterns to be genetically determined demands inheritance entirely or principally from the mother; this is unlikely

### **Social learning abilities**

So how do they do it? What kinds of social learning are cetaceans capable of? Some scientists (e.g. Galef 1992; Tomasello 1994) will only admit culture when it can be shown that behavioural patterns are being transmitted between animals by either imitation or teaching, and not by other types of social learning such as stimulus enhancement (in which individual learning is enhanced when one animal directs the attention of another towards a stimulus). While I do not subscribe to this particular view, I do think that understanding process (cultural transmission) is important to our understanding of the product (culture) – for example some forms of social learning may be more likely to produce cultures capable of building upon themselves, producing the “ratchet effect” (Tomasello 1994).

One species, the bottlenose dolphin, can lay fair claim to being the best known non-human imitator. Experimental work on the learning abilities of cetaceans has been largely confined to this species because it makes up the vast majority of the captive population. A number of studies have shown that bottlenose dolphins are capable of vocal and motor imitation (Bauer & Johnson 1994; Herman & Pack 2001; Kuczaj et al. 1998; Richards 1986; Richards et al. 1984), and the impressive results led Whiten (2001) to comment that dolphins can apparently ‘ape...better than apes’. To my knowledge, bottlenose dolphins are the only non-human animals for which both vocal imitation, *and* motor imitation at *both* action and program level, has so far been demonstrated (Herman 1986; Kuczaj *et al.* 1998). The absence of evidence for other species reflects a strong and unfortunate taxonomic bias towards bottlenose dolphins in this work; I, and others (e.g. Herman & Pack 2001), suspect that studies of other cetacean species will reveal more species with advanced social learning abilities.

Also in need of further study is what Rendell & Whitehead (2001) suggest are killer whales teaching their offspring how to hunt by self-stranding. Killer whales in the Crozet Islands and off Punta Norte, Argentina, swim ashore to capture pinnipeds (Guinet

1991; Guinet & Bouvier 1995; Hoelzel 1991; Lopez & Lopez 1985). Guinet & Bouvier (1995) describe young killer whales apparently learning from their mothers, and sometimes other animals, the feeding technique of intentional stranding on pinniped breeding beaches. The behaviour of adult killer whales towards juveniles during intentional stranding appears to (unusually for non-humans) fit Caro & Hauser's (1992) definition of teaching (Boran & Heimlich 1999). While some commentators think that there are not sufficient data to come to this conclusion (e.g. Day et al. 2001; Galef 2001; Maestripieri & Whitham 2001), I still think the evidence intriguing. What is not clear is what evidence *is* required for a conclusive demonstration of teaching. A consensus on this rather thorny issue is urgently needed.

In cetaceans then we find evidence for culture in many ways as compelling as that available for primates: a wealth of ethnographic examples of behavioural variation for several species, and sophisticated social learning abilities where studied. Cetacean cultures appear to possess attributes that have otherwise been restricted to humans. In particular, I am aware of no phenomena outside humans comparable to the distinctive, stable and sympatric vocal and behavioural cultures that exist at several levels of killer whale society.

### **CONTEXTS OF CETACEAN CULTURE: ECOLOGY AND EVOLUTION**

The relationship between culture and ecology is complex; many of the most interesting aspects of human culture are ecologically based. Our houses, food, clothes, religion and even music are based upon, or incorporate, the surrounding environment. Many characteristics of human populations result from the social learning of behaviour that relates to the environment. As Boesch (2001) notes, such behaviour is accepted as cultural in humans, but not in non-humans. The foraging specializations of bottlenose dolphins described above and by Connor (2001) likely result from just such interactions between ecology and social learning, but critics will point out, correctly, that individual learning in different environments has not been formally ruled out, and so deny culture. Thus we are likely missing a large part of non-human culture if we restrict to those cases

in which there are no ecological differences between populations (Boesch 2001; Day *et al.* 2001). There is no easy solution to this conundrum, although very careful study and sophisticated model-fitting techniques may allow forward movement (Day *et al.* 2001; e.g. Lefebvre 1995a; Lefebvre 1995b; Rendell & Whitehead 2001).

### **The evolution of cetacean culture**

All four of the best-studied cetacean species show strong evidence, from either the experimental or ethnographic approach, for social learning and culture. Why? They do possess those biological attributes which Roper (1986) suggests favour social learning: long lifetimes (~20-90yr), prolonged parental care and advanced cognitive abilities (Herman *et al.* 1994; Reiss & Marino 2001; Tyack 1986; Whitehead & Mann 2000). However, while there probably is a minimum cognitive capability required for social learning, the relative fitness of those individuals within a given species which are better than average at social learning likely depends ultimately on the ecological situation in which that individual must make a living; thus it is important to look to ecology when attempting to explain species differences in social learning (Lefebvre & Palameta 1988). I think that ecological factors may have a strong role to play in explaining the social learning abilities, and cultures to which they give rise, in cetaceans.

Compared with life on land, marine ecosystems are more likely to switch into alternate states over time scales of months or longer (Steele 1985). This increased low-frequency temporal variability of marine systems may significantly increase the adaptive benefits of culture to cetaceans, as the benefits of cultural transmission, relative to individual learning or genetic determination, are thought to be strongly related to environmental variability (Boyd & Richerson 1985; Boyd & Richerson 1988; Laland *et al.* 1996). The scale of spatial variation relative to animal ranging patterns may also be important; spatial autocorrelation in oceanic ecosystems weakens at ranges of about 500km (Myers *et al.* 1997), so that one way to deal with radical changes in the environment in any place is to move a few hundred kilometres, less of a challenge for aquatic mammals (e.g. Whitehead 1996b; Whitehead *et al.* 1997; Williams *et al.* 1992).



Alternatively, or additionally, the high variation of prey availability in the ocean over medium spatial (kilometres) and temporal (hours to days) scales may have driven the evolution of cetacean culture, as animals used socially-acquired information, or perhaps social conformity, to optimise their behaviour in these challenging environments (Barrett-Lennard et al. 2001). Extensive mobility, while often primarily a function of the need to reduce variation in one key environmental variable (usually food intake, availability of water, or temperature), tends to increase variance in other aspects of an animal's environment, including its social environment (Janik & Slater 1997). Tyack & Sayigh (1997) argue that the relatively greater mobility of cetaceans may be one reason why they show extensive capabilities for vocal flexibility and vocal learning, while terrestrial mammals do not. Consider group-living species; there are substantial advantages for individual cetaceans living in groups, be it through cooperative foraging (Similä & Ugarte 1993), food sharing (Hoelzel 1991) or communal defence (Arnbom et al. 1987; Pitman et al. 2001), but there is also the risk of sharing food with, or being injured in defending, individuals who are not members of the same group and hence are unlikely to reciprocate. Group signatures are one way to minimize this risk. However, as Tyack and Sayigh (1997) point out, when highly mobile animals regularly interact with conspecifics of different groups, signature systems need to be flexible and sophisticated - a demand that culturally transmitted dialects meet.

So the mobility of cetaceans may have created selection for vocal learning, perhaps providing the roots for sophisticated social learning of other types of behaviour (Moore 1992b; Moore 1996; Rendell & Whitehead 2001), while the spatial and temporal variability of the marine environment made social learning highly adaptive. In long-lived animals that form stable social groups, the opportunities for cultural transmission are greatly increased, and if most other group members were kin, such information exchange would also accrue inclusive fitness benefits - leading, perhaps, to the remarkable cultures of killer whales.

### **Evolutionary effects of culture**

Culture, once evolved, can enter a complex and dynamic co-evolutionary interaction with genetic evolution, and has done in humans and birds (Boyd & Richerson 1985; Feldman & Laland 1996; Grant & Grant 1996). There have been two suggestions that substantial gene-culture co-evolution has occurred in whales and dolphins; since both involve historical explanation neither can be empirically proven. However, this is no different from posited cases of gene-culture co-evolution in humans (Feldman & Laland 1996).

Firstly, both Baird (2000) and Boran & Heimlich (1999) propose that culturally-transmitted group-specific foraging techniques initiated the divergence of the forms of killer whale, which now show genetic and morphological differences, and may well be in the process of speciation given the apparent reproductive isolation of the two forms (Baird *et al.* 1992). This is a plausible explanation for the ongoing sympatric speciation; however, since the genetic differences between the two forms are now so evident (Hoelzel *et al.* 1998; Hoelzel *et al.* 2002), it cannot be proven that culture was responsible for the divergence.

Secondly, in the cultural hitchhiking proposed by Whitehead (1998), gene-culture co-evolution is suggested as a mechanism to produce strikingly low mtDNA diversity in matrilineal odontocetes. Since mtDNA is transmitted matrilineally between generations, alleles at neutral mtDNA loci will track the spread of ('hitchhike on') successful matrilineally-transmitted cultural traits as these traits spread in the population, the mtDNA alleles associated with that matriline will also spread, giving rise to the reduced mtDNA diversity now observed.

Culture may also have had effects on the evolution of life history. Menopause is known in killer and short-finned pilot whales (*Globicephala macrorhynchus*), and there are indications of its occurrence in other cetacean species (Marsh & Kasuya 1986; Olesiuk *et al.* 1990). Like humans, and unlike any other mammal, female killer and short-finned pilot whales often live decades after the birth of their last offspring. Within-group

cultural processes may have played a part in this phenomenon, if, for instance, the role of older females in cultural transmission is very important. Menopause could be highly adaptive if the role of older females as a source of information significantly increases the fitness of her descendants, and reproduction towards the end of her life decreases survival (Boran & Heimlich (1999), see also O'Connell *et al.* (1999) and Diamond (1997) for related discussions on human evolution).

### **THE SPERM WHALE: SOCIAL COMPLEXITY AND VOCAL DIALECTS**

Sperm whales are the largest odontocetes, found in all ocean basins. Ecologically, they are an extremely successful species; feeding mainly on mesopelagic squid (Kawakami 1980) at depths generally greater than 1,000m (Whitehead & Weilgart 2000), they are thought to be responsible for the removal of around 100 million tons of biomass annually, a similar amount to that removed by all human fisheries combined (Kanwisher & Ridgway 1983). Sperm whales are clearly both a significant element in the pelagic ecosystem, particularly given recent insight into top-down ecological effects in marine food webs (Worm & Myers 2003), and very successfully adapted to exploit the highly variable resources in that system (Whitehead 1996b). Part of that success is surely due to the sperm whale's extraordinary nose, the spermaceti organ; this mass of lipid and connective tissue is a crucial element of what is likely the most powerful biological sonar system on Earth (Madsen 2002; Møhl *et al.* 2000). The organ is up to one quarter of the length of a mature female sperm whale, representing a massive developmental and metabolic investment, and in mature males it can account for fully one-third of the body length, having most likely been further expanded in this gender by sexual selection (Cranford 1999). The foraging advantages it conveys probably explain a large part of the sperm whale's ecological success, and the lack of similar, competing, mesopelagic predators (Whitehead 2003a; Whitehead 2003b). Other factors must also contribute though, and one that may be highly important in a large, patchy and systematically varying biological environment is a social structure that allows for traditional knowledge to pass between generations along matrilineal lineages (Whitehead 1998; Whitehead 2003a; Whitehead 2003b).

### **Social structure in sperm whales**

Sperm whale social structure is complex. Females, calves and immature animals of both sexes, found in sub-tropical and tropical waters, live in relatively stable social 'units' containing on average 11-12 animals that persist for decades. However, these units typically form groups with one or more other units for periods of several days, and so at sea one generally encounters groups that are temporary associations of stable units (Christal *et al.* 1998; Whitehead *et al.* 1991; Whitehead & Weilgart 2000); I will retain these meanings of the terms 'group' and 'unit' throughout this thesis when referring to sperm whales. These social units initially appeared from genetic studies to be matrilineal (Richard *et al.* 1996). However, more recent work has shown that these units may not generally be strict matrilineal; specifically, observations of social units containing large proportions of unrelated individuals (Christal *et al.* 1998; Mesnick 2001; Mesnick *et al.* 2003), and of membership changes in social units (Christal *et al.* 1998), have produced a more complex picture, such that social units may contain long-term associations between unrelated matrilineal. In contrast to females, males disperse from their natal units at a mean estimated age of 6 years, whence they migrate slowly into higher latitudes prior to attaining sexual maturity at 18-21 years, and subsequently attain social maturity at around 27 years, at which time they are generally very large (16 m, 45 metric tons) and solitary; at this point, they return to the tropics to mate (Whitehead & Weilgart 2000). This broad pattern of female philopatry and male dispersal is reflected in a high variability and lack of geographic structure in nuclear DNA relative to mitochondrial DNA (Lyrholm *et al.* 1999). The benefits of group living for females include, but may not be limited to, communal care of young and defence against predation (Pitman *et al.* 2001; Whitehead 1996a).

Population or stock structure is likewise largely unknown, due in part to the complexity of the underlying social structure (Donovan 1991). The South Pacific population is the best studied; in it females appear to have ranges of at least 1,000 km (Dufault & Whitehead 1995; Whitehead 2001a), perhaps averaging 1,500 km (Whitehead

2003a). However, recent work has pointed to a lack of geographically based structure, promoting instead the matrilineal unit as the primary structural determinant (Whitehead *et al.* 1998). This is in contrast to the broad and often arbitrary geographical stock divisions of recent management models (Donovan 1991).

### **Vocal dialects**

The sperm whale vocal repertoire is dominated by clicks (Whitehead & Weilgart 2000). Codas are repeated stereotyped sequences of 3-40 broadband (0-16kHz) clicks generally heard during periods of socialising at or near the surface (Watkins & Schevill 1977), behaviour that contrasts sharply with the prolonged dives and wide spacing of foraging groups (Whitehead & Weilgart 1991). For this reason, codas are presumed to have a social function such as re-affirming bonds after foraging bouts (Whitehead & Weilgart 2000), although there is no direct evidence regarding the role of these vocalisations. Communication systems based primarily on rhythm are unusual in mammals; the best example is the drumming of alarm signals by kangaroo rats *Dipodomys* spp. (Randall 1997), while other possible examples include drumming by chimpanzees, *Pan troglodytes* (Boesch 1996) and the use of clicks by Hector's dolphins, *Cephalorhynchus hectori* (Dawson 1991).

Codas can be classified into types according to the number and temporal pattern of the clicks they contain. For example, "2+3" is a coda containing two regularly spaced clicks followed by a longer gap before three more clicks while "5R" is a coda with five regularly spaced clicks. This classification makes intuitive sense as coda types, as defined by patterns of clicks, are more or less discrete (Moore *et al.* 1993; Weilgart & Whitehead 1993), but in no case has the significance of a classification to the animals been tested using playbacks; some studies have classified codas visually from spectrographic records (e.g. Moore *et al.* 1993), others using numerical techniques (e.g. k-means cluster analysis, Weilgart & Whitehead 1997). In a study spanning the southern Pacific Ocean, Weilgart & Whitehead (1997) gave evidence that sperm whale groups they encountered have distinctive dialects in coda usage using analyses based on inter-click intervals (ICIs), the

time intervals between clicks in a coda, standardised to total coda length. Specifically, the same groups recorded on different days produced very similar proportions of the 30 identified coda types, whereas proportional use of coda types differed between groups. A further study combining genetic and coda data from six sperm whale groups suggested a link between mtDNA and coda repertoire – groups with similar mtDNA tended to have similar coda usage dialects (Whitehead *et al.* 1998). The existence of this correlation implies that mitochondrial haplotype and coda dialect are transmitted by analogous processes through the female line and show a similar order of stability. Whitehead *et al.* (1998) suggested vertical cultural transmission – offspring learn codas from their mothers – as the best explanation for this pattern. This led us to suggest that sperm whale coda dialects were an example of cetacean culture, if culture is broadly defined (Rendell & Whitehead 2001). However, it also presents a conundrum as sperm whale groups are not themselves particularly stable; as discussed above, they usually consist of two or more stable social units that swim together for periods of days (Christal *et al.* 1998; Richard *et al.* 1996; Whitehead *et al.* 1992). These social units may themselves split or merge (Christal *et al.* 1998) and can contain unrelated matriline (Mesnick *et al.* 2003). How then can the groups possess highly stable dialects (Mesnick 2001)? This thesis is dedicated to investigating these issues in more depth.

Using methods developed and detailed in Chapter 2, I answer the above question by describing the variation in group coda repertoires in more detail in Chapter 3, showing that sperm whale units and groups in the South Pacific can be assigned to one of five vocal ‘clans’, broadly similar to clans in killer whales (see also Rendell & Whitehead 2003). Some have objected that the recording methods used to collect the data on vocal dialects cannot distinguish between group and individual behaviour (Freeberg 2001; Tyack 2001). Freeberg (2001) suggests that one cannot know from these recordings whether observed differences are really between units or between individuals that may be particularly vocal and thus consistently dominate recordings of groups, questioning the existence of unit-specific dialects in sperm whales. I provide a partial response to this concern in Chapter 4 by showing that data from one social unit are inconsistent both with

individuals dominating group vocal output and individuals making only one coda type.

Playback experiments are an important tool in understanding animal communication (Catchpole & Slater 1995; for cetaceans see Richards *et al.* 1984; Sayigh *et al.* 1998; Tyack 1983), and in Chapter 5 I report the results of playback studies on sperm whales in Chilean waters. I found no evidence of differential responses to clan vs. non-clan codas, but the study itself had low power to detect them. Finally, in Chapter 6 I look for unit-specific repertoires, evidence for temporal change and within-clan geographic variation in coda repertoires; I find little and no evidence for the two former effects respectively, but good evidence for the latter. I also look for such trends in the structure of a single coda type, again finding evidence for geographic variation but not for change over time.

The principal contribution of this thesis is the description of sperm whale vocal clans. In Chapter 7 I show that this is a form of culture for which the only known non-human analogue is the presence of vocal clans in killer whales, but sperm whale vocal clans are an order of magnitude larger both in terms of geographic scale and the numbers of animals in each clan. Clans seem to be a vital element of sperm whale societies, and their existence explains previous conundrums in the interpretation of results from studies of the vocal communication and social structure of this species, and also has major consequences for our understanding and management of sperm whale populations, as discussed in Chapter 7.

## CHAPTER TWO

### *Comparing Repertoires of Sperm Whale Codas: A Multiple Methods Approach*



## INTRODUCTION

In the study of animal vocalisations, the problem of objectively defining categories and statistically comparing repertoires between individuals or sets of animals is perennial (see for example Janik 1999b; Nowicki & Nelson 1990; Terhune et al. 1993). Here I describe and compare a number of methods developed to study the repertoires of ‘coda’ vocalisations in sperm whale social groups.

Only a handful of studies have been made of these vocalisations to date (Moore *et al.* 1993; Watkins & Schevill 1977; Weilgart & Whitehead 1993; Weilgart & Whitehead 1997; Whitehead *et al.* 1998), and none evaluated the analytical methods they used. Initially codas were assigned to classes by simple observation and judgement (e.g. Moore *et al.* 1993; Watkins & Schevill 1977); the underlying assumption that the classes were real and meaningful to the animals themselves was suggested by the extreme stereotypy of the coda patterns. More recently, Weilgart & Whitehead (1997) used *k*-means cluster analysis. Both these methods come with pitfalls. The human ‘eyeball’ method contains two assumptions: that what seems different to us is actually different to the animals, and that what seems different to one person will also seem different to another observer. The former is rarely tested in animal bioacoustics and certainly has not been for sperm whales, while the latter is testable (Janik 1999b) and must be met if the essential scientific criterion of repeatability is to be fulfilled. The *k*-means cluster analysis used by Weilgart & Whitehead (1997), for all its numerical objectivity comes with the problem of determining *k* – the number of clusters into which the data are to be grouped. Weilgart & Whitehead (1997) used a fixed number of clusters (5 for 3-click codas and 10 for >3 click codas) and then lumped all clusters with less than 50 codas into a catch-all ‘variable’ category. They then compared numbers of codas in each class between different social groups. While objective, this methodology obviously discards potentially interesting information in the form of rarer coda classes.

Both classification-based methods, while making data easier to understand given our aptitude for categorisation (Tomasello 1999 pp.17-18), carry the underlying

assumption that real ‘types’ are present. However, this is not necessarily the case for other species. In cetaceans for example, Murray *et al.* (1998) showed that the calls of false killer whales (*Pseudorca crassidens*) form a graded sequence with no clear divisions. Similarly, long-finned pilot whale (*Globicephala melas*) whistles appear to form a graded continuum between several basic types (Taruski 1979). We can use empirical cues to justify a decision to classify – for example if calls are stereotyped with few or no intermediate forms. However, if methods of comparing sets of vocalisations that do not rely on classification are available then one can employ both classification and non-classification approaches in tandem for a rigorous investigation; conclusions supported by analyses using both approaches are concomitantly stronger. Here I explore methods of classifying codas and of comparing repertoires using classification as well as non-categorical methods.

## **METHODS**

### **Data collection**

In this study I used a subset of codas recorded from field studies around the Galápagos Islands. For general field methodology see Whitehead & Weilgart (2000). Codas were recorded using one of two sets of equipment. The first was an Offshore Acoustics hydrophone (frequency response,  $\pm 3\text{dB}$ : 6Hz-10kHz) connected to a Sony TC-D5M cassette recorder, used for the 1999 recordings of social unit “T”; the second consisted of a Benthos AQ17 hydrophone (1-10kHz), connected via either Barcus-Berry ‘Standard’ or Ithaca 453 pre-amplifiers to either a Uher 4000, Sony TC770 or Nagra IV-SJ recorder, used for the 1985 and 1987 recordings of social units “A” and “B”. Recordings were digitised at 44.1kHz onto a standard desktop PC, and I analysed codas using a software package called Rainbow Click (Gillespie 1997; Leaper *et al.* 2000) specifically developed for the study of sperm whale sounds (e.g. Jaquet *et al.* 2001). The software detects clicks using a two level trigger with user-variable parameters, and then stores the detected clicks in a data file. The timing of clicks within codas can then be extracted once codas have been defined and marked individually by the user. Only codas that could be unambiguously heard (at the various playback speeds supported by the software) were

marked, so some codas that were recorded were not analysed due to a variety of factors leading to a generally poor recording quality (these included water noise, engine noise and overlapping by other clicks and codas). The resultant data for each coda were the absolute inter-click intervals, defined as the time between the onsets of consecutive clicks, so for example a four click coda that we analysed was stored as : 0.180, 0.178, 0.182 (units are seconds). These data were then standardised to coda length by dividing each interval by the total length of the coda (defined as the time between the onsets of the first and last clicks) – this was done because previous work has shown coda rhythm to be better preserved than tempo (Moore *et al.* 1993) and so most work on codas discards tempo information (e.g. Weilgart & Whitehead 1997). It is therefore an assumption of this chapter, and the methods I describe, that it is the rhythm of clicks within a coda and not the tempo that is biologically important and thus of interest. For the present analysis I used a sample of 1548 codas (Table 2.1) that were assigned to social units based on the presence of photographically identified individual whales (Christal *et al.* 1998).

Table 2.1: Data used in this chapter. Social unit codes correspond to those in Christal *et al.* (1998) and Christal & Whitehead (2001)

Social Unit Code	Number of recordings	Dates recorded (first – last)	Number of codas
A	25	24 <sup>th</sup> February 1985 – 9 <sup>th</sup> March 1987	572
B	9	23 <sup>rd</sup> January 1987 – 22 <sup>nd</sup> March 1987	97
T	22	10 <sup>th</sup> March 1999 – 10 <sup>th</sup> April 1999	879
		Total:	1548

### Observer classification

Janik (1999b; 2000) has shown that human classification, with all its pitfalls of arbitrariness, is still the best way to classify bottlenose dolphin (*Tursiops* sp.) signature whistle contours. I therefore emulated his methods by using three people (myself and two volunteers) to independently classify codas. Each observer was presented with a computer display of the coda to be classified (on a standardised scale so that tempo information was discarded for this method as well) and assigned codas to types as they

saw fit based on their perception of the types present in the dataset. There was no limit on the number of types, and at any point observers could view the mean of all codas already assigned to a given type as well as a display of the current coda alongside all the other codas with the same number of clicks in the analysis set. For this method I used only the 879 codas from social unit T, in order to keep the task manageable. Once all three independent classifications were complete, the results were scanned for common classifications and if two or more observers agreed on a type for a given coda then it was assigned to that type, while if there was no agreement then the coda was dropped from further analysis. If significant proportions of codas are rejected on this basis then it becomes clear that this methodology is not as applicable to sperm whale codas as to bottlenose dolphin whistles. Such levels of rejection may also suggest that perhaps coda types are not as discrete as once thought.

### **K-means clustering**

Using automatic classification algorithms avoids the problems of subjectivity inherent when humans classify codas. Weilgart & Whitehead (1997) used  $k$ -means clustering, where data are divided into  $k$  clusters so as to minimise the pooled within-cluster sum of squares. Such analysis has to treat codas with differing numbers of clicks separately – i.e. four-click codas will be clustered in a separate analysis from five-click codas. This is because four- and five-click codas represent multivariate datasets with different numbers of dimensions, in this case three and four dimensions, since an  $n$  click coda can be represented by  $n-1$  standardised click intervals. While codas can theoretically be represented by  $n-2$  standardised intervals (since all intervals must sum to one) this biases distance measures to emphasise differences that occur in the first  $n-2$  intervals over differences in the last interval, so we included all  $n-1$  intervals in our analyses. However, the problem of deciding  $k$  non-arbitrarily remains. Weilgart & Whitehead (1997), as noted above, adopted a technique that involved discarding some potentially important information. Schreer *et al.* (1998) attempted to use a ‘stopping rule’ based on Calinski & Harabasz’s (1974) Variance Ratio Criterion (VRC); although they found it unsatisfactory for their data, I too tried this stopping rule based on the VRC:

$$VRC = \frac{BGSS}{k-1} / \frac{WGSS}{n-k} \quad (1)$$

where  $BGSS$  and  $WGSS$  are the between and within group sum of squares respectively,  $k$  is the number of clusters and  $n$  is the number of observations. I ran an iterative  $k$ -means clustering algorithm on each coda size (4 click, 5 click etc) for  $2 \leq k \leq 10$ . In this and all the  $k$ -means analyses that I ran, initial cluster centroids were selected at random from the input data. Since the iterative  $k$ -means algorithm does not necessarily always converge on the optimal solution, each clustering was run 10 times and the solution with the lowest  $WGSS$  selected and retained. I then calculated the VRC for each solution. Calinski & Harabasz (1974) suggest that the optimal clustering solution is at the first local maximum of the VRC as  $k$  increases. However, as I shall show later, I encountered the same problem as Schreer *et al.* (1998): the VRC did not give clear, unambiguous results for the test data. In Milligan & Cooper's (1985) comparison of stopping rules, the VRC rule performed best at detecting the number of clusters in sample datasets. However, their sample data were very strongly clustered, and these authors openly attempted to let every stopping rule 'adopt the most favourable conditions' to optimise its performance while cautioning that their 'findings are likely to be somewhat data dependent'. Hence, I also tried the rule that performed next best after the VRC: Duda & Hart's (1973 pp.239-243) ratio criterion. This criterion tests the null hypothesis that the partitioning of a given dataset into two clusters is spurious at the  $p$ -percent level, and rejects that null hypothesis if

$$\frac{WGSS_{(2)}}{TSS} < 1 - \frac{2}{\pi m} - \alpha \sqrt{\frac{2(1-8/\pi^2 m)}{nm}} \quad (2)$$

where  $TSS$  is the summed squared deviation from the mean for the unclustered data,  $WGSS_{(2)}$  is the pooled within-cluster sum of squares for the same data in two clusters ( $J_e(1)$  and  $J_e(2)$  respectively in Duda & Hart's (1973) notation),  $m$  is the number of

dimensions in the data,  $n$  is the number of observations and  $\alpha$  is a standard normal score given by

$$p = 100 \int_{\alpha}^{\infty} \frac{1}{\sqrt{2\pi}} e^{-1/2u^2} \delta u \quad (3)$$

This measure compares the reduction in the squared error, as given by the ratio  $WGSS_{(2)}/TSS$ , against the distribution of reductions expected from dividing a multivariate normal population through the mean. Note that this method only makes decisions about dividing a given set into two clusters, giving one major heuristic advantage over the VRC method in that it provides a basis for deciding whether any clustering at all is justified i.e. the first split of the original data into two clusters. I used this criterion in a divisive procedure, in contrast to the VRC method, which seeks globally optimal solutions for the entire dataset. Data were repeatedly split using iterative  $k$ -means with  $k = 2$  (repeated 10 times, selecting the lowest  $WGSS$  solution, as above). Each split was then accepted or rejected with  $p = 95\%$ , and the resultant clusters again split and tested. Division continued until no cluster could be split according to the  $WGSS_{(2)}/TSS$  criterion.

Once I had arrived at two classifications based on human and divisive  $k$ -means methods (the latter were performed on the expanded dataset of 1548 codas), I compared the human classification (of codas on which at least two observers had agreed) with the  $k$ -means classification of those same codas using Cramer's  $V$  (Wilkinson et al. 1996); while this metric does not provide for any kind of significance testing, it does give a relative measure of how well two classifications coincide. I also calculated Cramer's  $V$  for each individual human against each other, against the 'consensus' human classification and against the  $k$ -means classification.

### **Classification-free approach**

One obvious way to compare codas without resorting to classification is by using

distances between codas in multivariate space. I tested two different ways of measuring distances between vectors representing points in multivariate space: Euclidean distance and the infinity-norm. The Euclidean distance ( $dE_{ij}$ ) between codas  $i$  and  $j$  is defined as

$$dE_{ij} = \sqrt{\sum_{k=1}^c (x_{ik} - x_{jk})^2} \quad (4)$$

where  $c$  is the number of standardised click intervals representing codas  $i$  and  $j$  (i.e. the number of clicks minus one),  $x_{ik}$  is the  $k^{\text{th}}$  interval of coda  $i$  and  $x_{jk}$  is the  $k^{\text{th}}$  interval of coda  $j$ . The infinity-norm distance ( $dI_{ij}$ ) is defined as the maximum absolute difference between the vectors  $x_i$  and  $x_j$  (sometimes written as  $\|x_i - x_j\|_{\infty}$ ). Both these metrics are direct measures of how dissimilar codas  $i$  and  $j$  are (i.e. low values mean that codas  $i$  and  $j$  are nearly identical in pattern). However, both can in theory lead to results that appear counter to my stated aim of comparing coda rhythms. In the case of Euclidean distance, consider a regular five-click coda (5R); perturbing all the clicks by some small amount ( $x$ ) results in a slightly irregular coda that still has a generally regular rhythm, while perturbing a single click by a large amount ( $y$ ) gives a distinctly different rhythm (such as 4+1). However, the codas resulting from these perturbations could have very similar Euclidean distances from the original if  $x \approx y/\sqrt{(n-1)}$ , where  $n$  is the number of clicks (in this case five), despite having quite different rhythms. In the case of the infinity-norm distance, consider again a 5R coda, again perturbing one of the clicks by some amount ( $y$ ) to produce, for example, a 4+1 rhythm. Then consider perturbing two of the original five regular clicks by a smaller amount ( $x$ ) to produce, for example, a 3+1+1 rhythm. If  $y > x$  then the 3+1+1 coda will have a smaller distance from the original 5R than the 4+1, even though a 3+1+1 rhythm is arguably less similar to 5R than is a 4+1 rhythm. Thus neither metric always directly quantifies rhythmic differences in a consistent way. Whether these situations are occurring enough to significantly impact results depends on the actual codas, and one way to test whether these theoretical problems have a significant impact on results is to use both on the same data – if the two techniques produce similar patterns of results, then it is unlikely that the theoretical conditions outlined above are occurring

much in practice.

The above metrics reflect the differences between pairs of codas, but I am interested in comparing sets, or repertoires, of codas. One measure of how dissimilar any one repertoire of codas is to another is the mean distance defined as the average of pairwise distances between the two repertoires. That is: for each coda in repertoire A calculate the distance to all other codas in repertoire B, and take the mean of all the (size of repertoire A x size of repertoire B) resultant values, or more formally,

$$S_{AB} = \frac{\sum_{i=1}^{n_A} \sum_{j=1}^{n_B} d_{ij}}{n_A \cdot n_B} \quad (5)$$

where  $n_A$  and  $n_B$  are the number of codas in repertoire A and B respectively and  $d_{ij}$  can be either the Euclidean or infinity-norm distance. However, this cannot be used directly because repertoires contain codas of differing sizes, that is, codas with *different* numbers of clicks – it is thus impossible to measure a direct multivariate distance between them. One could overcome this by simply taking the mean of all the distances between codas of the same size, but this would not take into the account the differences in numbers of codas of different sizes between the repertoires. Using distances, comparisons between codas with different sizes could be set to an arbitrarily high number, but then average distances would depend more on the arbitrary value of this number than any other factor. Alternatively, one can use similarity scores that are inversely proportional to distance; for example,  $b/(b + d_{ij})$  is a measure of similarity, where the value of  $b$  relative to the spread of data gives the approximate resolution at which the measure operates. If comparisons are expressed as similarities rather than distances, then comparisons between codas of different sizes can be simply set to zero. I took this approach, rendering every comparison between codas of different sizes zero, and then took the mean of all comparisons (not only those between codas of the same size). Equation (5) thus becomes



$$S_{AB} = \frac{\sum_{i=1}^{n_A} \sum_{\substack{j=1 \\ l_j=l_i}}^{n_B} \frac{b}{b + d_{ij}}}{n_A \cdot n_B} \quad (6)$$

where  $l_i$  is the number of clicks in coda  $i$  of repertoire A and  $l_j$  is the number of clicks in coda  $j$  of repertoire B.

Using this approach, a repertoire can also be compared with itself; if A=B then equation (6) gives  $S_{AA}$ , the self-similarity. This is important because, unlike most similarity measures, the results of comparing a repertoire with itself using equation (6) are not readily predictable. Equation (6) does not produce one when repertoires are compared with themselves, instead it gives an approximate indication of the ‘spread’ or diversity of a given repertoire – relatively compact repertoires will have relatively high self-similarities. For this work however, the clear implication is that values of  $S_{AB}$  for between-repertoire comparisons should be interpreted alongside the values of  $S_{AA}$  and  $S_{BB}$  calculated when those repertoires are compared to themselves, unless large numbers of comparisons are being made in which case it would be more tractable to enter the similarity measures into a hierarchical cluster analysis.

I calculated comparisons between repertoires of codas recorded from different social units so as to compare the results from this technique with results from correlating classified codas as described in the previous section. I used equation (6) with both distance metrics, and  $b = 0.001, 0.01, 0.1$  and  $1$ , to look at how the different metrics and different values of  $b$  change the similarity results. I also compared repertoires using the results of the classification methods by calculating Spearman rank correlation coefficients on counts of how many codas of each type were heard in each repertoire (as in Weilgart & Whitehead 1997). When comparing repertoires between social units using both similarity and classification methods, I estimated the robustness of each measure by calculating bootstrap standard errors from 100 random samples with replacement (Sokal & Rohlf 1995). All the numerical procedures described here were implemented in MATLAB

(v12.0), with the exception of Cramer's  $V$  which was calculated in SYSTAT (v10), on a standard PC.

## RESULTS

### Observer and $k$ -means classification

After classification by three people, 861 of 879 codas (98.0%) from social unit T met the consensus criteria of agreement by at least two observers, and were classified into 49 types. 85% of the codas recorded had 6 or less clicks, and while the 8 most common types account for 82.1% of the repertoire (the single most common type accounting for 19.9%, approximately 1/5 of all the codas heard), there were many rare types – 36 of the 49 types individually made up less than 1% of the codas recorded.

As mentioned above, the VRC stopping rule did not give unambiguous results (Figure 2.1); VRC values for various  $k$  did not show unambiguous local maxima as described in Calinski & Harabasz (1974). The divisive procedure, which runs unsupervised and does not require any input apart from the initial acceptance threshold ( $p$ ) for the Duda & Hart criterion, produced 32 clusters from the entire 1548 coda dataset. Here the most common type accounted for 11% of codas recorded, the 8 most common types for 45%, and 21 types individually made up less than 1% of the codas recorded. Generally, the divisive method produced clusters that match reasonably with observable clumping of the data (Figure 2.2).

Cramer's  $V$  statistics for each combination of classifications are given in Table 2.2. It is noteworthy that all three human observers individually produced results more similar to the  $k$ -means procedure than to any of the other observers. To illustrate how this relates to the actual data, Figure 2.3 compares the classification of codas with four clicks by the  $k$ -means and observer consensus methods. Note both the clear structuring of the data in the plot, and also how the '4R' type in the observer classification considerably overlaps the '3+1' cluster, while the  $k$ -means results produce (not surprisingly) relatively well-separated clusters.

Figure 2.1: Variance Ratio Criterion values from  $k$ -means solutions for  $2 \leq k \leq 10$ , calculated using codas with 3-6 clicks. Note the lack of clear local maxima.

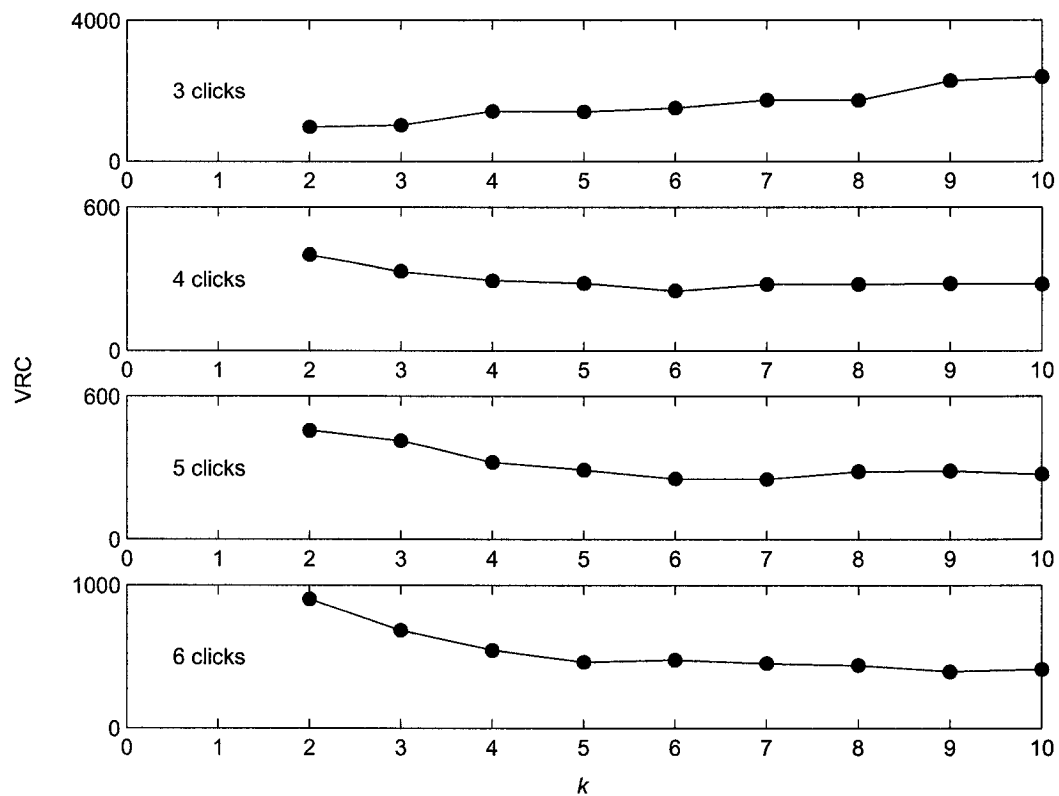


Table 2.2: Cramer's  $V$ , for each combination of classifications. Observer A, B and C are individual classifications, Human-All is the consensus and  $k$ -means the results of the divisive  $k$ -means procedure. Higher values represent a relatively higher correspondence between classifications.

	$k$ -means	Human - All	Human - A	Human - B
$k$ -means				
Human - All	0.95			
Human - A	0.95	0.95		
Human - B	0.93	0.96	0.91	
Human - C	0.96	0.91	0.88	0.87

Figure 2.2: Results of divisive  $k$ -means clustering using the Duda & Hart criterion. For 3 click codas, the plot shows frequency distribution of the first standardised click interval (SCI), with different clusters having different shaded bars. For 4 click codas, first SCI is plotted against the second SCI. All the other plots show the first two principal components derived from SCIs, along with the percent variance accounted for by those first two principal components. Different clusters are represented by different symbols.

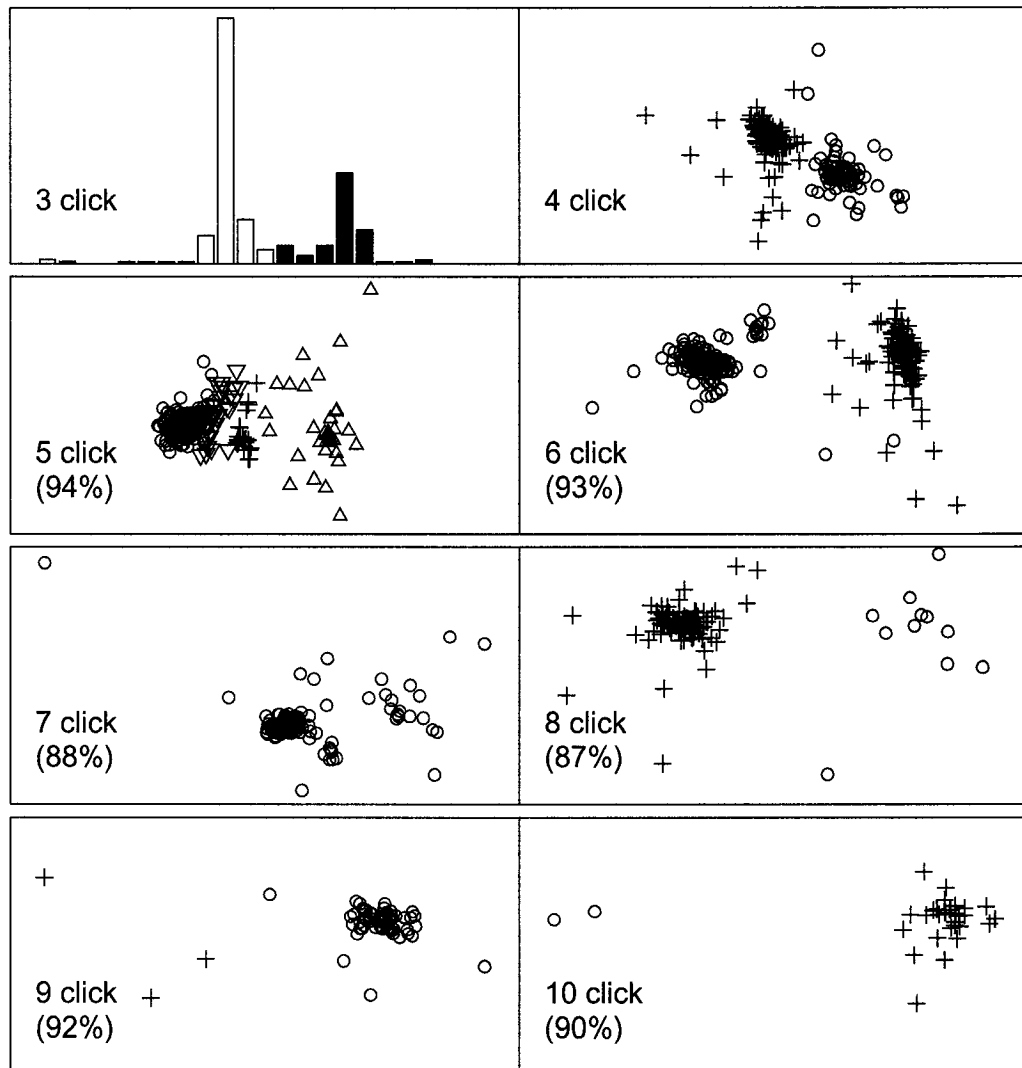
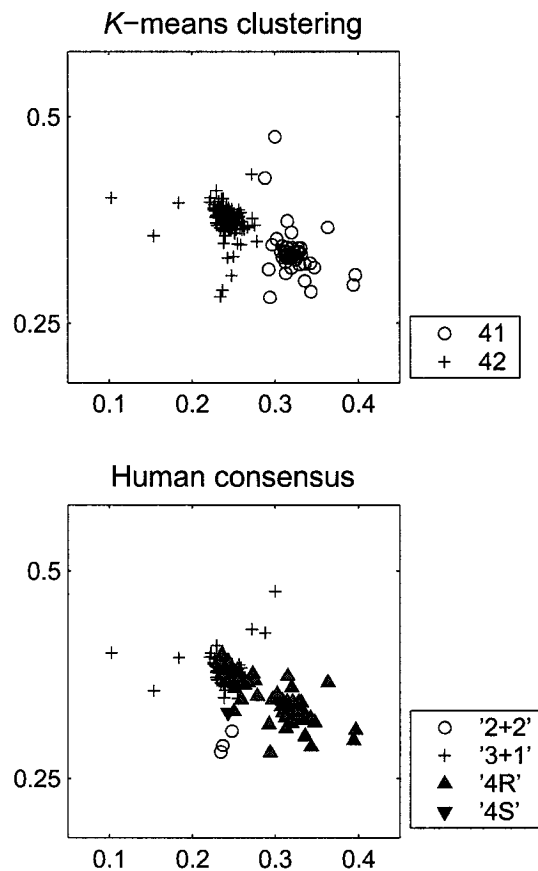


Figure 2.3: First SCI plotted against the second SCI for all four click codas from social unit T, plotted by cluster membership as determined by divisive  $k$ -means or human consensus classification.



### Multivariate similarity

Figure 2.4, (a) and (b) show the results of employing the similarity measures to compare repertoires between social units, using Euclidean and infinity-norm distances respectively, and for a range of  $b$ . The results are plotted along with the self-similarity scores for each repertoire. I would consider any result where the comparison value lay in the bootstrap standard error range of the two self-similarity values to indicate that the two repertoires were statistically indistinguishable (at the resolution set by the value of  $b$ ). The pattern of results is identical for both distance metrics and for all values of  $b$  – the repertoires of social units A and B are more similar to each other than either are to unit T,

although when using Euclidean distance with higher values of  $b$  the repertoires of A and B are indistinguishable. This pattern agrees well with comparisons using correlations between repertoires of codas classified using the divisive  $k$ -means method, where the correlation between A and B are higher than either with T (Figure 2.5). To show how these results reflect the true nature of the underlying data, Figure 2.6, (a) and (b) show plots of three to ten-click codas for social units A and B, and A and T respectively. It is clear from these plots that the repertoires of A and B overlap each other considerably. In contrast, while there is some overlap between A and T, there are also clear areas of non-overlap, particularly with four, five, and six click codas.

Figure 2.4: Repertoire similarities calculated between social units for various values of  $b$ . Each dotted line joins the comparison similarity to self-similarity values for both social units in the comparison – for example the leftmost line in each plot joins the self-similarity of unit A, the comparison similarity between A and B and the self-similarity of B. Error bars are standard errors from 100 bootstrap samples.

(a) Similarities calculated using the Euclidean distance.

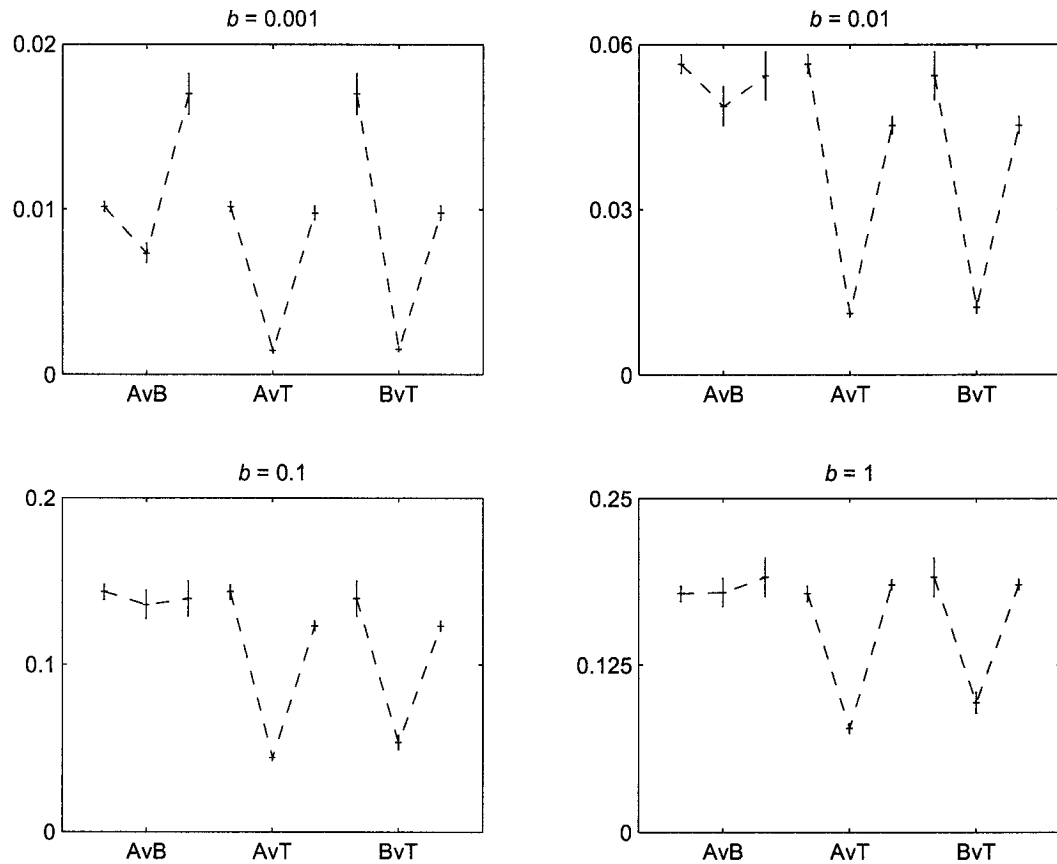


Figure 2.4: (b) Similarities calculated using the infinity-norm distance.

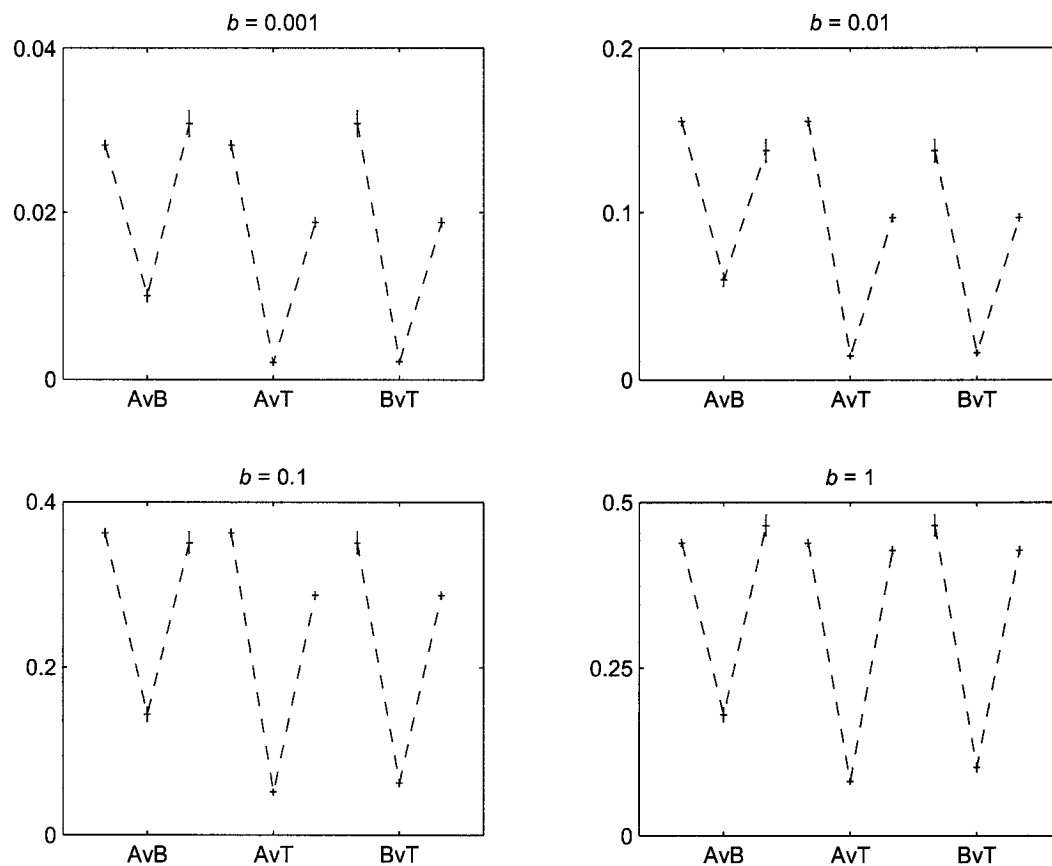
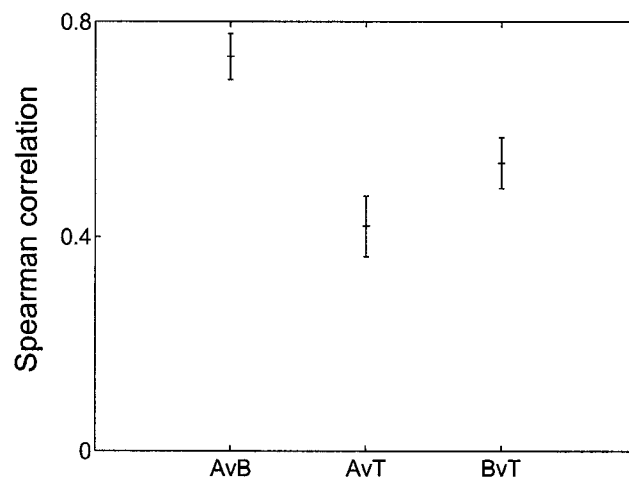
Figure 2.5: Spearman correlation coefficients for comparisons between repertoires of codas classified by divisive  $k$ -means, calculated as in Weilgart & Whitehead (1997). Error bars show standard errors from 100 bootstrap samples.



Figure 2.6: Plots comparing coda repertoires between social units. For 3 click codas, the plot shows frequency distribution of the first standardised click interval (SCI). For 4 click codas, first SCI is plotted against the second SCI. All the other plots show the first two principal components derived from SCIs, along with the percent variance accounted for by those first two principal components.

(a) Unit A (+, shaded bars) and unit B (o, clear bars).

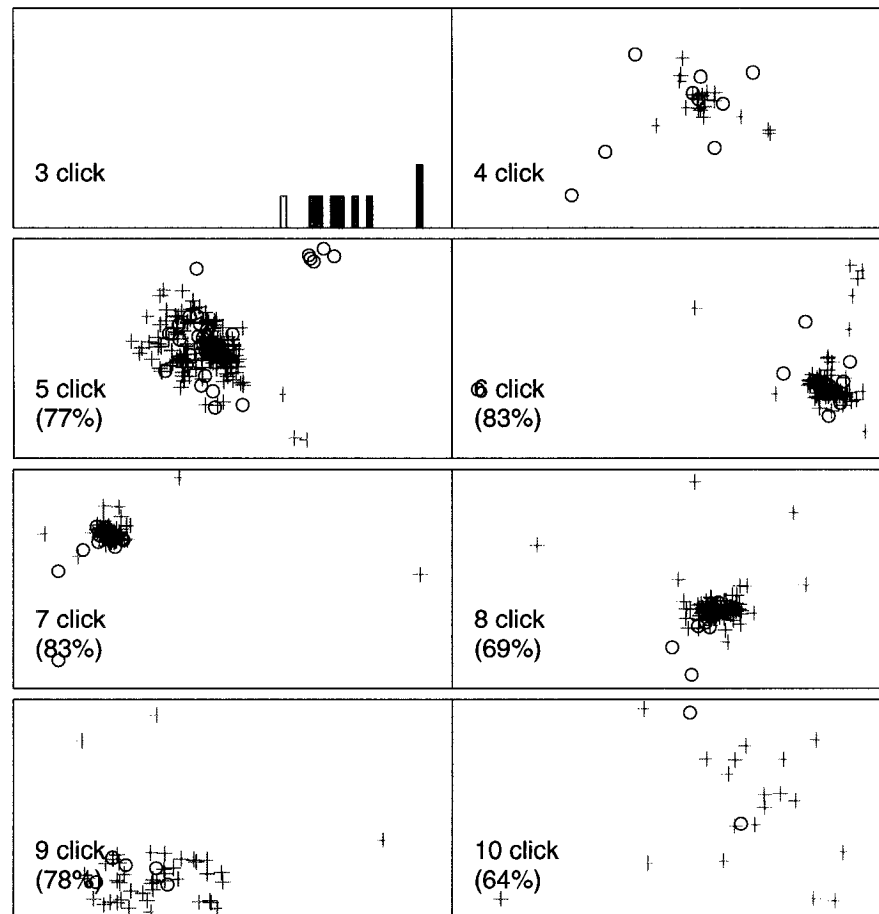
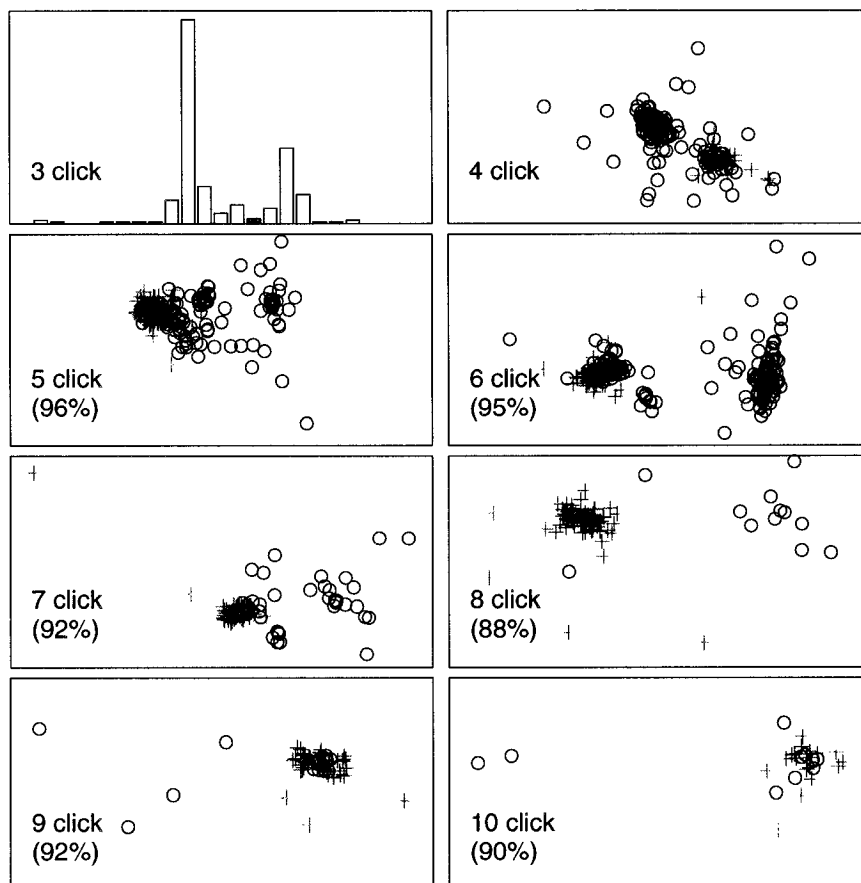


Figure 2.6: (b) Unit A (+, shaded bars) and unit T (o, clear bars).



## DISCUSSION

Of the methods that I implemented or attempted to implement – observer classification, VRC  $k$ -means, divisive  $k$ -means using the Duda & Hart criterion, and multivariate similarity – only the last three are likely to be useful in future studies of sperm whale codas. While observer classification has been shown to work rather well for other cetacean vocal studies (Janik 1999b; Janik 2000), it is apparently not so useful for studying sperm whale codas, for several reasons. Firstly and most importantly, humans did not pick out the naturally occurring groupings in the data as well as divisive  $k$ -means method – for example, the human defined classes stretch across the two main clusters evident in the four-click codas (Figure 2.3). Secondly, the Cramer's  $V$  results for the classifications show that the human classifications were inconsistent with respect to each other, suggesting that the repeatability of these measures would not be especially robust. If the acceptance criteria were raised to require agreement from all three observers, only 34% of the codas would be accepted, which casts further doubt on the robustness of the technique. One can only speculate as to why this might be so, but one possible reason might be the large amounts of data used here – I asked volunteers to classify 879 codas, while Janik (1999b) used only 104 bottlenose dolphin (*Tursiops* sp.) signature whistles in his study. Remembering one's previous classifications is likely much easier for smaller datasets, particularly since Janik (1999b) also printed hard copies of each whistle spectrogram for the comparison exercise, something which was unfeasible for the 879 codas used here and more so for the larger datasets for which I plan to use these methods. Finally, the observer classification method also involved the rejection of an albeit small number of codas; it is hard to justify throwing away information in this way given the difficulty and expense of making these recordings in the first place, nor given the possibility of introducing bias if classifiers are more likely to disagree over certain forms of coda than others. Hence I do not see observer classification as a useful method in this particular case.

I do think that some form of classification is justified, given the structure present

in the data (Figures 2.2, 2.3 and 2.6) – there do seem to be some very tightly defined coda ‘types’. Both the  $k$ -means methods potentially provide a robust method for classifying codas that will produce repeatable results. However, the VRC stopping rule did not seem to work well here; while it performs excellently with well-defined clusters (Milligan & Cooper 1985), I found that the rule produced ambiguous results for the test data. In contrast, the divisive  $k$ -means method assigned data to clusters that matched the structuring of the dataset quite well (Figure 2.2). In addition, comparisons between the three social units based on this classification produced results that make sense with respect to the underlying data (Figure 2.6). While this latter technique is clearly better in this case, I would add the caveat that it might not always be better. As Milligan and Cooper (1985) point out, the performance of any such criterion is very likely to be data dependent, and while it appears that for the present data the VRC rule is not the most appropriate, this may not always be so. For example, a dataset with several clear clusters may not produce a significant difference in Duda & Hart’s ratio criterion on the first split into just two groups and thus the split may be rejected even though clustering is obviously present to a human observer. I therefore suggest that the results of both techniques be checked against the raw data to ensure that logical clusters are being retrieved. The ultimate choice of technique will be data dependent, and somewhat arbitrary based on an observer’s judgement of how well the clustering solution fits the data. One disadvantage with these clustering methods is that care must be taken with the *ad-hoc* addition of new data. One could classify new data using Mahalanobis or Euclidean distances to assign new codas to the cluster with the nearest centroid, but only for small amounts of new data. Visual inspection (e.g. as in Figure 2.2) would be necessary to ensure that new, very different, codas were not being ‘forced’ into existing categories, and the entire procedure should be run again if large amounts of new data are added. While there are many other clustering algorithms available, as well as more recent developments in artificial neural networks (see e.g. Deecke *et al.* 2000) it is for other interested researchers to investigate their viability in this application; the simplicity and wide recognition of  $k$ -means, along with the reasonable results given here, make it suitable for the present purposes. In the only such study of which I am aware on

biological data, Schreer *et al.* (1998) concluded that *k*-means was the best classification technique for dive profile data in an analysis that included performance comparisons with artificial neural networks, although obviously there are major differences between dive profile and coda data.

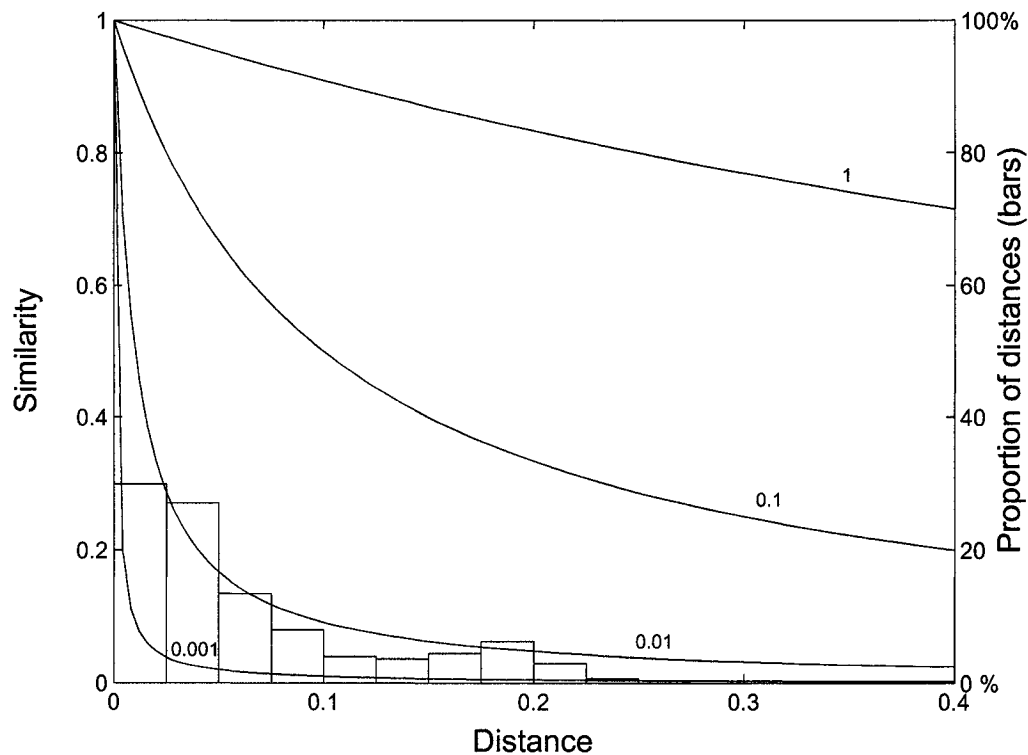
It is encouraging that the multivariate similarity measures show the same pattern as the classification methods – this agreement gives a greater confidence that the results are robust, particularly since the pattern of results is repeated across all values of *b*. It is also encouraging that the similarity results comparing social unit repertoires reflect rather well the degrees of overlap evident in Figure 2.6. The two distance metrics tested produced very similar patterns of results, with the main difference being that the infinity-norm distance was perhaps the better discriminator across all values of *b*, and so may give a more precise measure of repertoire similarity. I also argue that the similar patterns of results suggest that the theoretical limitations of both distance metrics are not substantially affecting results. While the possibility that unforeseen combinations of codas may produce results dissonant with our stated aim of comparing coda rhythms still exists, I have shown that the methods produce results consistent with a different analysis method, *k*-means clustering (Figures 2.4 & 2.5), and with observable patterns in the raw data (Figure 2.6); the aggregative nature of the measure likely leads to specific anomalies being subsumed in broader scale patterns. One drawback of this method is that it is computationally demanding, especially for high numbers of bootstrap resamples: I performed the analyses again with 1,000 bootstrap resamples (as opposed to the original 100), which took a desktop computer approximately three days to complete. The bootstrap standard errors for 1,000 resamples were nearly identical to those for 100 samples, but sometimes smaller.

The slightly different results produced by various values of *b* are interesting; with similarity defined as in Equation (6), the value of *b* is an approximate measure of the *resolution* at which comparisons are being made, in terms of normalized inter-click interval. Considering Figure 2.3, and noting that the two obvious clusters present are

about 0.1 standardised-click-interval-units apart suggests that calculating similarities with  $b = 0.1$  will likely give us information on whether the two social units make codas in similar or different clusters. Decreasing  $b$  to 0.01 or even 0.001 gives a very fine scale comparison of exactly how well the codas in each repertoire coincide within clusters, since each cluster in Figure 2.3 is approximately 0.05 data units across. Plotting the functional form of the similarity transformation against an actual distribution of coda distances shows how the transformation emphasis shifts to smaller distances as  $b$  decreases (Figure 2.7). It therefore doesn't make sense to recommend a fixed value for  $b$  as different values can provide information at different scales of analysis. Actual coda lengths (defined as the time between the onsets of the first and last clicks) in the present data ranged from 0.189s to 9.510s, with a mean of 1.228s, so  $b = 0.001$  corresponds on average to a resolution of 1.2ms (range 0.2-9ms), which roughly equals the maximum resolution of our analysis system. Whether sperm whales can detect rhythmic differences of this scale remains a moot question.

During this work I also developed and tested another approach to measuring similarities between codas of different sizes. This approach arose from the observation that certain coda 'classes' identified by Weilgart & Whitehead (1997) seem to span various coda sizes – for example the '+1' codas (click-click-click-pause-click would be a 3+1 coda) are heard with differing numbers of clicks (i.e. 3+1, 4+1, 5+1). To reflect such classes in the similarity measure I 'cross-correlated' codas of different sizes using a technique best explained by example. Consider two codas, A and B; A contains four clicks, and B contains six. Without disturbing the order or neighbour-relationships of clicks in B, one can extract 3 different four-click codas from it –  $B_1$  with clicks one to four,  $B_2$  with clicks two to five and  $B_3$  with clicks three to six – each of which can be standardised by dividing each click interval by the sum of the absolute click intervals of each given subset ( $B_1, B_2, B_3$ ). One can then 'cross-correlate' the two codas by calculating the Euclidean distance between A and ( $B_1, B_2, B_3$ ) and taking the minimum distance (hence maximum similarity).

Figure 2.7: Plot of the functional form of the similarity transformation at various  $b$  (labelled lines; distance on the x axis and resultant similarity on the y axis) overlaid with a histogram of distances between the five click codas on our dataset calculated using the infinity-norm (data are proportion of total).



This similarity was then ‘discounted’ by an amount related to the difference in number of clicks between codas (otherwise, for example, a 3R and a 15R coda could have equal similarity to a 3R and another 3R, which few would consider useful), and so instead of having similarities between codas of different size rendered zero as in Equation 6, a discounted distance would be entered into the averaging. Thus a 3+1 coda would be scored more similar to a 4+1 coda than to a 5R coda. However, reviewers of a manuscript based on this chapter pointed out that this method is biased toward uniform rhythm patterns, and does not always give results consistent with the aim of comparing rhythm. For example, consider a 4+1 and a 5R coda compared to a 4R coda – the 4+1 and 5R

coda could produce identical similarities to the 4R by using only the first four clicks of each, despite having quite different rhythms. This theoretical inconsistency together with a more than three-fold increase in computation time to produce results that had the same pattern as Figure 2.4 led to deciding that this was unlikely to be a useful method in the future.

In conclusion, I have developed and/or tested potentially useful ways to compare collections, or repertoires, of codas. The methods can be used in a variety of ways such as comparing social unit repertoires as here, or to compare the coda output of the same group recorded at different times, or in different ecological or behavioural situations. In addition, the methods can be employed at levels both below and above that of the group – from individual repertoires (if codas can be reliably assigned to individual whales) through to comparisons between oceans. In future studies it would be advisable to use both categorical and non-categorical techniques in tandem in order to minimise concerns that results are simply due to spurious categorisations or weaknesses in the distance metrics. I hope that these techniques will be helpful in future studies of sperm whale codas and other studies that face similar problems in comparing vocal repertoires represented by multivariate datasets.



## CHAPTER THREE

### *Vocal clans in sperm whales*

## INTRODUCTION

There is an ongoing debate about the existence and nature of culture - defined as group-level information or behaviour transmitted by social learning (Rendell & Whitehead 2001) - in non-humans (Boesch & Tomasello 1998; Galef 1992; McGrew 1998; Whiten *et al.* 1999). This debate has recently widened to include cases of cultural variation in the behaviour of cetaceans (Noad *et al.* 2000; Rendell & Whitehead 2001; Chapter 1; Whitehead 1998), a group noted for its social (e.g. Connor *et al.* 2001) and cognitive (e.g. Reiss & Marino 2001) complexity. There may be examples of gene-culture co-evolution in cetaceans unique outside humans. For example, in killer whales, some have suggested that the cultural transmission of differing foraging techniques initiated the split between the so-called 'resident', fish-eating, and 'transient', mammal-eating forms that may be in the process of speciation (Baird 2000; Baird *et al.* 1992; Boran & Heimlich 1999). More broadly, cultural and genetic processes may have interacted to greatly reduce mitochondrial DNA diversity in matrilineal odontocetes, through neutral mitochondrial alleles hitch-hiking on successful cultural traits (Whitehead 1998).

One such species is the sperm whale (*Physeter macrocephalus*), a key player in meso-pelagic ecosystems that can be found in the deep waters of every ocean (Whitehead & Weilgart 2000). Sperm whale groups vary in their usage of different coda types (Weilgart & Whitehead 1997), and among six groups this variation correlated with mitochondrial DNA variation (Whitehead *et al.* 1998) – groups with similar coda output having similar mtDNA haplotypes. Whitehead *et al.* (1998) suggested that analogous inheritance processes through the female line produced this pattern, namely calves both inherit their mtDNA and learn their coda dialect from their mothers. The cultural transmission of coda dialect would have to be highly stable to produce this correlation (Whitehead *et al.* 1998). Rendell & Whitehead (2001) thus suggested that sperm whales showed culture in the form of sympatric variation in vocal dialects. However this interpretation has been challenged (Tyack 2001) because the groups that showed vocal dialects are often only temporary aggregations of two or more social units, begging the

question of how temporary social entities can maintain stable cultural characteristics (Mesnick 2001; Tyack 2001).

Here I answer this question by using codas recorded over 15 years of research on sperm whales in the South Pacific and Caribbean to investigate variation in coda usage among groups. I find strong evidence for a higher level of social structure based on variation in vocal output, somewhat similar to the acoustic clans of killer whales. Sperm whale populations may thus be structured more along cultural lines than on a geographic basis, which has major implications for understanding the behavioural and population biology of this species.

## **METHODS**

### **Coda recording**

Recordings were made using one of several sets of equipment; either an Offshore Acoustics hydrophone (frequency response 6Hz-10kHz,  $\pm 3$ dB) connected directly to a Sony TC-D5M cassette recorder, or either a Benthos AQ17 or modified AQ21B hydrophone (frequency response 1-10kHz,  $\pm 3$ dB) connected via either Barcus-Berry 'Standard' or Ithaca 453 pre-amplifiers to either a Uher 4000, Sony TC770 or Nagra IV-SJ reel-to-reel tape recorder. I extracted inter-click time intervals (the time between the onset of one click and the onset of the next) of codas in one of two ways: either from a DSP Sona-Graph, Model 5500 (coda data contributed by L. Weilgart, as published in Weilgart & Whitehead 1997), or by digitising the recordings at 44.1kHz onto a desktop PC and extracting inter-click intervals using software custom written for analysing sperm whale sounds (Gillespie 1997; Leaper *et al.* 2000). The resultant click intervals were then standardised to coda length, thus discarding tempo information but retaining rhythm (see Moore *et al.* 1993, for justification).

### **Assigning codas to units or groups**

I selected codas recorded from sperm whale social units whose members were photographically identified around the Galápagos Islands during the period 1985-1999;

units were defined by repeated associations (in time and space) between individuals over months and years (for details see Christal *et al.* 1998). I assigned codas in a given recording to a known social unit if at least one member of that unit had been photographically identified within two hours of the recording start time. Only photographs with a quality rating, Q, of three or more out of five were included (Arnbom 1987; Christal *et al.* 1998). If members of more than one known unit were identified in that same period, then the codas were assigned to a joint unit (e.g. A&B). Note that, with the exception of unit T, there were also always non-unit members identified in these periods. I included only units from which at least 25 codas had been recorded. 3,943 codas were included in the analysis.

I then widened my analysis to include recordings made across the South Pacific, and some made in the Caribbean, using codas assigned to groups based on photo-identification records so that I was not restricted to known social units nor to just the Galápagos Islands. All codas recorded on a given day were assumed to have come from the same group. Codas recorded on two different days were considered to be from the same group if  $m_{ab} > 0.25 * \min\{n_a, n_b\}$  where  $m_{ab}$  is the number of individuals photographed on both days,  $n_a$  the number photographed on the first day and  $n_b$  the number photographed on the second day (as in Weilgart & Whitehead 1997). Again, I included only groups from which at least 25 codas had been recorded. 13,941 codas from 64 groups were included in this analysis, incorporating those from the unit analysis.

### Repertoire comparisons

I used MATLAB (v12.0) for all numerical analyses. I used an averaged multivariate similarity method to compare sets of codas, based on the infinity-norm distance between two coda vectors (Chapter 2):

$$S_{AB} = \frac{\sum_{i=1}^{n_A} \sum_{\substack{j=1 \\ l_j=l_i}}^{n_B} 0.001}{n_A \cdot n_B + \sum_{i=1}^{n_A} \sum_{\substack{j=1 \\ l_j=l_i}}^{n_B} 0.001}$$

where  $S_{AB}$  denotes the similarity between coda sets A and B,  $l_i$  is the number of clicks in coda  $i$  of set A,  $l_j$  is the number of clicks in coda  $j$  of set B and  $d_{ij}$  the maximum absolute distance (or infinity-norm) between the vectors containing the standardised inter-click-intervals of the codas  $x_i$  and  $x_j$  ( $\|x_i - x_j\|_\infty$ ). The similarity between two codas containing different numbers of clicks was 0. I chose the basal similarity, 0.001, as being approximately the maximum resolution of the most accurate analysis system given a median coda length of 0.93s and a maximum time resolution of 0.001s. This figure is also approximately 10% of the distance across most of the obvious clusters in the coda data (these clusters generally representing coda types) such that analysis at this resolution examines not only the use of different types, but variation within a given type (see Chapter 2). For both the unit and group analyses I calculated similarities between sets of codas assigned to each unit or group and entered these similarities into an average linkage cluster analysis (see e.g. Manly 1994). I tested the robustness of the resultant clustering using 100 bootstrap resamples (codas resampled with replacement within sets) of the original data; for a given branch I counted the number of bootstrap resamples in which that branch was reproduced perfectly, that is, contained exactly the same groups as the original clustering.

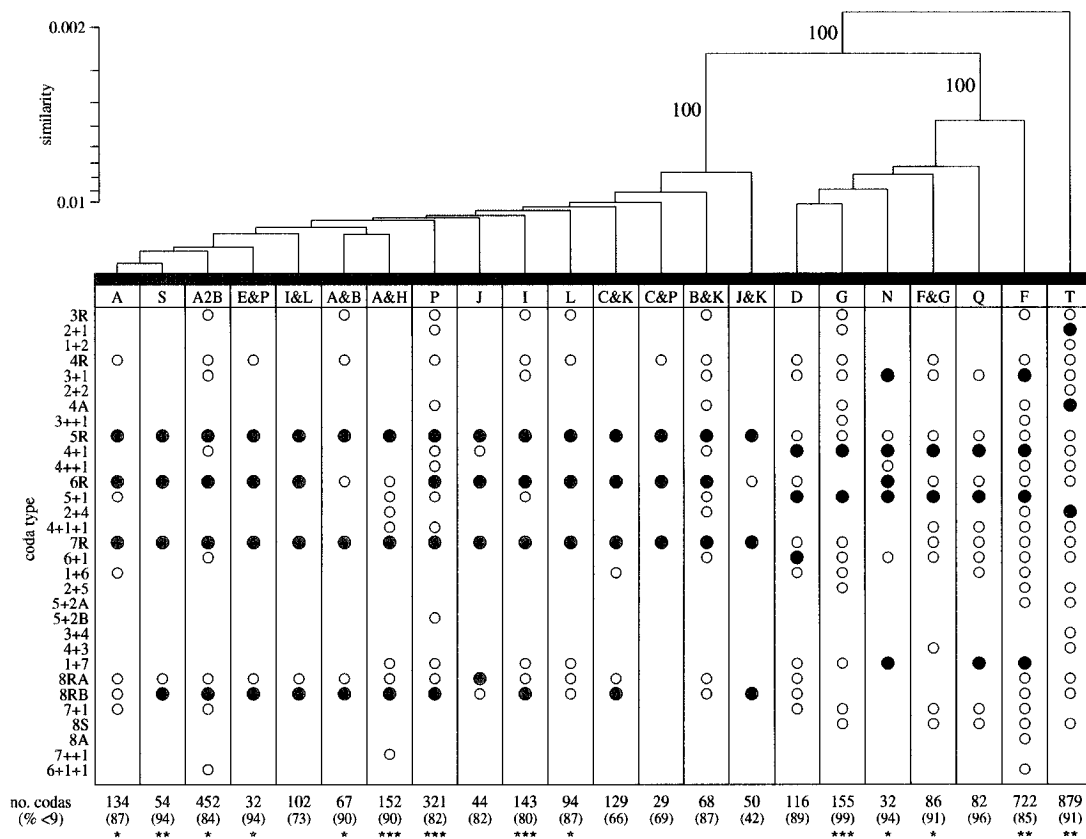
In order to illustrate observed differences I also classified codas containing the same number of clicks using  $k$ -means clustering and the Variance Ratio Criterion (VRC) (Milligan & Cooper 1985) to select an appropriate  $k$  (Chapter 2). Each coda type was then given a descriptive name based on the pattern of clicks in that type; for example '5R' denotes a coda with five regularly spaced clicks, while '4+1' signifies four regular spaced clicks followed by a longer gap before the fifth click (Weilgart & Whitehead 1997). The VRC produced unambiguous estimates of  $k$  for all but the five-click codas, where the splitting of one very large cluster - the 5R codas - led to misleading VRC values at  $k > 4$ . The splitting of large clusters is a known weakness of  $k$ -means analysis (Duda & Hart 1973), and in this case the 5R cluster contained 84% (4111 of 4879) of all the five click codas, such that splitting it necessarily produced a large reduction in the

sum of squared errors on which the VRC is based. Hence in this case I randomly sampled 10 five-click codas from each recording day and ran the VRC analysis on this subsample; in 20/20 repeats of this procedure the VRC unambiguously indicated  $k=3$ , so I classified the entire five-click dataset into three clusters. This classification did not split the 5R cluster.

## RESULTS

The coda repertoires of all social units clustered into one of three acoustic groupings based on coda usage patterns (Figure 3.1). I term these groupings ‘clans’. One clan made predominantly regular spaced codas (5R, 6R, 7R), the second made predominantly codas with an extended last interval (4+1, 5+1, 6+1) and the third, represented here by just one unit, made predominantly short codas (containing three or four clicks). I termed these clans ‘Regular’, ‘+1’ and ‘Short’ respectively. This division is apparent whether analysis is based on discrete classification or continuous measures, and, like all the patterns I describe here based on the infinity-norm distance, was reproduced when the analysis was repeated using Euclidean distance as a measure of dissimilarity between the inter-click-interval vectors of codas containing the same number of clicks instead of the infinity-norm. The clustering was reproduced in all 100 bootstrap resamples, giving confidence that the division is not data-dependent. The results are consistent across units – in cases where units were recorded grouped with one or more other identified units (e.g. A, A&B; F, F&G), they always clustered in the same clan. Clan coda usage is stable over time – some units were recorded over periods of years yet still retained a clear clan signal; the longest such period was for unit G, which was recorded in 1987 and 1993 with the same pattern of coda usage; data on the coda repertoires of this and the three other units recorded over different years are given in Appendix 1.

Figure 3.1: Coda repertoires of sperm whale groups containing known social units recorded around the Galápagos Archipelago compared using multivariate similarity (top) and *k*-means classification methods (bottom). Unit codes are retained from previous studies (Christal *et al.* 1998; Whitehead 2001b); more than one code is given when members of more than one unit were identified within 2 hours of recording. Numbers next to dendrogram branches are the number of bootstrap resamples in which that branch was recreated (/100). Circles in the classification table indicate coda types present in a unit's recorded repertoire, while filled markers indicate types that made up 10% or more of a unit's repertoire. The raw data underlying the classification table can be found in Appendix 1. Numbers below each column are the number of codas recorded from each unit and in brackets the percentage of that number with less than nine clicks and hence shown in the table (note that all codas are included in the hierarchical cluster analysis). Units flagged with \* were recorded on more than one day, with \*\* had 30 or more days between first and last recording, and with \*\*\* had >1 year between first and last recording. Colours represent clan assignments; green = 'Regular', blue = '+1' and red = 'Short'.



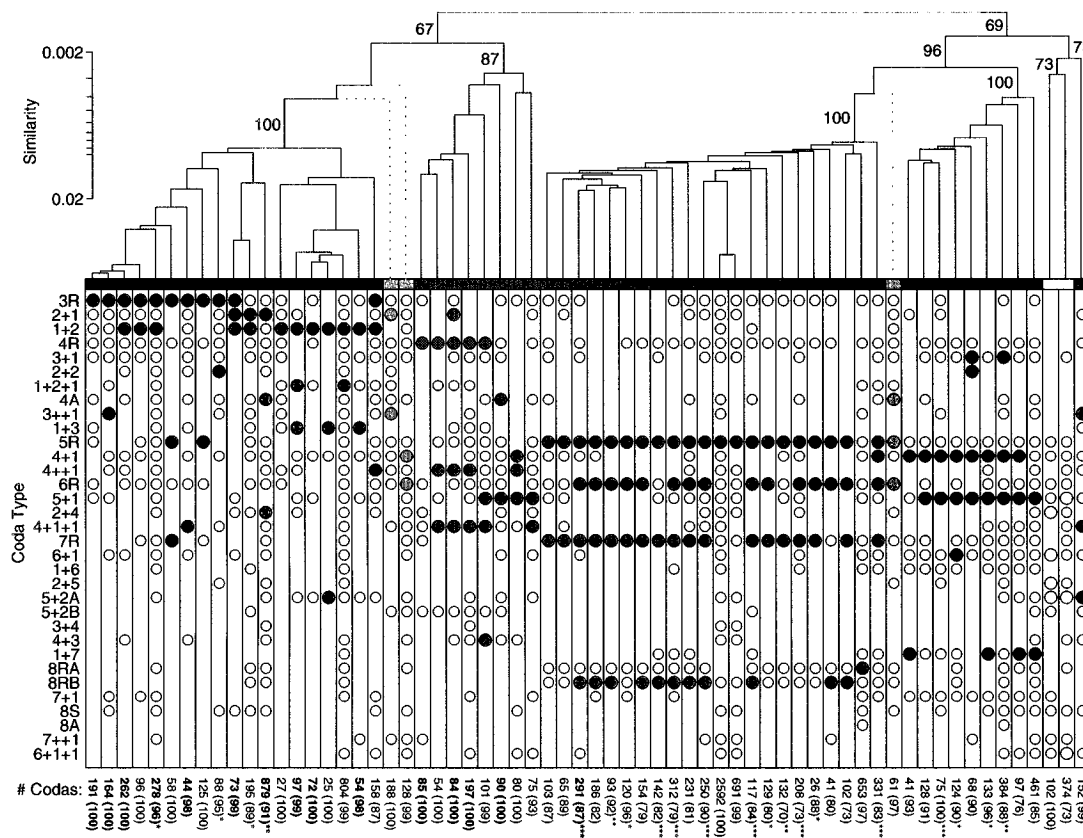
Units generally associated with other units of the same clan. Of 27 encounters in which members of different units were identified within two hours of each other, only

one involved units of different clans (23 were between 'Regular' clan units, and two were between '+1' clan units). This was on 27 April 1993 when two members of unit G ('+1 clan') were identified between 06:32-06:35, eight members of unit L ('Regular' clan) between 06:48-07:46, and 12 members of unit G between 08:10-12:50, including the two first sighted. A recording made at 11:26, assigned to unit G using my method, gave a clear '+1' signal; given that this unit had been assigned to the '+1' clan by independent recordings on other dates, the consistency of results here provides some *post-hoc* justification of the 2 hour criterion for assigning codas to groups or units. Unit L was assigned to the 'Regular' clan based on recordings from other dates. Members of other units were identified throughout this time, but for at least one hour on this day members of units from different clans were within a few kilometres of one another.

The clan structure is reproduced in a similar analysis of groups across the South Pacific and Caribbean (Figure 3.2). Although data on unit membership is generally not available for these groups, I assume that the general pattern found in the Galápagos, where groups consist of temporary associations of long-term social units, applies across the Pacific. I also assume that clan signatures recorded from these groups are, as in the Galápagos data, an accurate reflection of the clan membership of the underlying units. All the Galápagos clans are present, with more groups representing them (particularly the 'Short' clan). However there is also evidence of two more clans in the Pacific, bringing the total to five, and a distinct clan recorded only in the Caribbean (Figures 3.2 & 3.3). The most common of these I termed '4+' because the dominant coda types were based on a root of four regular clicks (e.g. 4R, 4++1, 4+1+1). The fifth Pacific clan ('++1/+1+1') is represented by a single group. I termed the Caribbean clan '+2' because of the 5+2A and 6+1+1 types commonly used. These terms are meant for descriptive purposes only and do not necessarily represent the most important differences between clans. Three of the 64 groups had ambiguous clan membership – in bootstrap samples they were often assigned to different clans. Hence I excluded these groups from the bootstrap analyses reported here, which give high support (at least 73%) to the clusters found at the clan level.

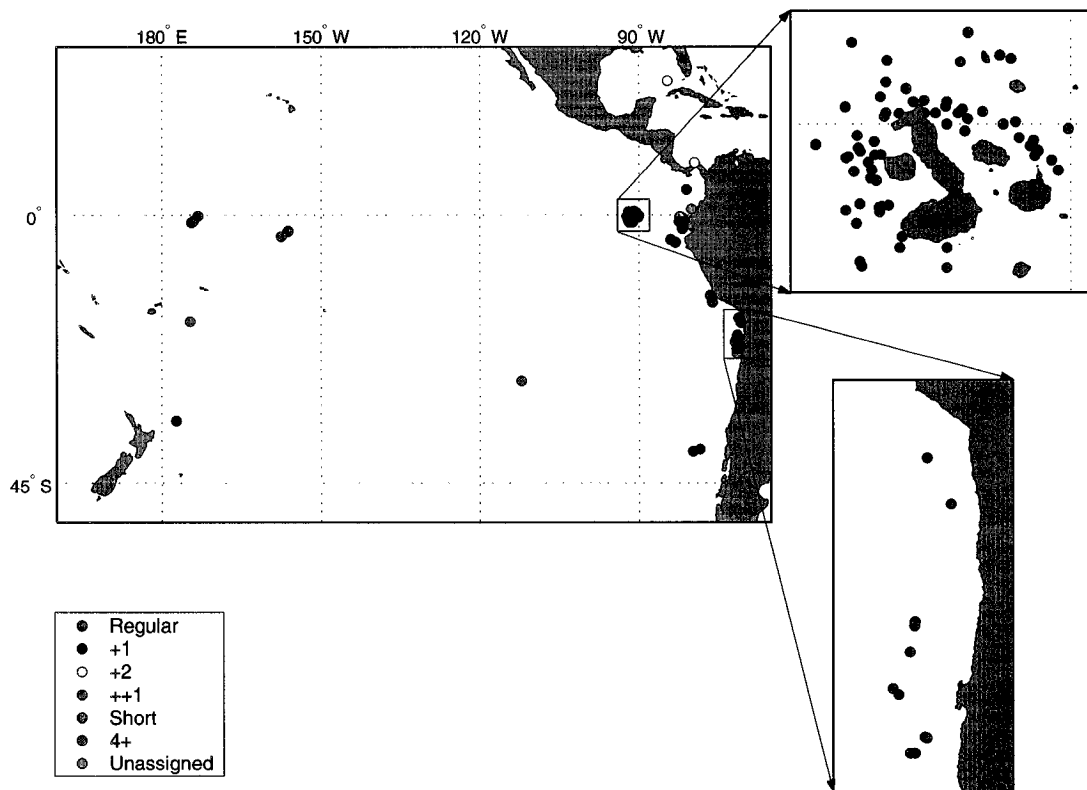


Figure 3.2: Coda repertoires of photographically identified sperm whale groups compared using multivariate similarity (top) and  $k$ -means classification methods (bottom). Grey markers and dashed lines in the dendrogram denote groups that were shown to cluster ambiguously by low bootstrap support; these groups were not assigned to a clan and were not included in the bootstrap analysis. All other notations, markers and colours are as Fig. 1, with the addition of three extra clans; yellow = '+2' (the Caribbean clan), cyan = '++1/+1+1' (recorded off Tonga only) and magenta = '4+'. The raw data underlying the classification table can be found in Appendix 1. Group data printed in bold indicates mtDNA data were available from that group (Table 3.1).



Clans are sympatric across huge geographic ranges (Figure 3). While there are differences in these ranges, no Pacific clan is restricted to a single area except for the '++1/+1+1' clan that was recorded just once near Tonga (where sampling effort was least). For example, the 'Regular' and '+1' clans are restricted to the eastern Pacific, and the '+1' clan to the tropics (although it may extend further north than the recording effort reported here), while the '4+' and 'Short' clans both span the entire South Pacific.

Figure 3.3: Map of clan distribution. Each point on the map indicates the nearest fix to the first recording time for each day a group was recorded.



## DISCUSSION

The analyses reveal a picture of sympatric vocal variation that has major implications for our understanding of sperm whale society. Results are consistent with previous studies that found large between group variations in coda usage overlaying a weaker geographic variation (Weilgart & Whitehead 1997), but add a very strong and significant factor - the vocal clan. I suggest that variation in vocal behaviour between clans is cultural, based on social learning rather than genetic variation or ecological differences plus individual learning (Boesch 1996) for the following reasons. Firstly, variation cannot be due to ecology plus individual learning, since clans are sympatric. Secondly, available genetic data points to male dispersal and female philopatry (Lyrholm *et al.* 1999) and is inconsistent with within-group mating, making genetic inheritance unlikely, although the important question is whether there is gene flow between clans. Several mitochondrial

haplotypes are shared between clans, showing that the clans are not matrilineally monophyletic (Table 3.1; mtDNA data from previous studies Whitehead *et al.* 1998). There was no greater probability for individuals in the same clan, but different groups, to have the same haplotype (19%) as for individuals in different clans (17%). Thus, albeit with a small sample (15 groups from 3 clans), I do not reject the null hypothesis that clans are undifferentiated in mtDNA. Further evidence of gene flow between clans is given by social unit dynamics; between 1985 and 1987 one individual from unit C belonging to the ‘Regular’ clan transferred to unit D belonging to the ‘+1’ clan (Christal *et al.* 1998).

Table 3.1: Mitochondrial haplotypes present in clans for which data are available.  $N_i$  and  $N_g$  are respectively the number of individuals and the number of groups sampled from each clan.  $H$  is the number of haplotypes present. Data are number of samples with a given haplotype.

CLAN	$N_i$	$N_g$	Haplotype code										H	
			#1	#2	#3	#5	#6	#7	#8	#11	#12	#13		
4+	15	4	1		7	5	1	1						5
Regular	19	1	18									1		2
Short	67	10	18	23	17		2	1	1	1	1	3		9

In answer to previous criticisms that question how labile day-to-day aggregations of sperm whales could maintain stable cultural characteristics (Mesnick 2001; Tyack 2001), I therefore suggest that cultural variation, in the form of coda usage dialects, is maintained primarily at the level of the clan rather than the level of group or unit. Units forming groups predominantly with units of their own clan explain previous findings of dialects at the group level. Clans may thus represent a higher-level social structure essentially unobservable over the short time periods for which it is possible to follow sperm whales in the field. The closest parallel to this, and from which I took the term ‘clan’, are the acoustic clans of killer whales, based on discrete pulsed calls (Ford 1991), with the important difference that killer whale clans do not share call types in the way that sperm whale clans do. Killer whale clans are also more geographically restricted, spanning about 1,000km (Ford *et al.* 2000) rather than 10,000km for the sperm whales

(Figure 3.3), and contain fewer members, about 100 (Ford *et al.* 2000) rather than of the order of 10,000 as suggested by the number of clans in the South Pacific and global sperm whale densities (Whitehead 2002). The striking conclusion is that there are only five clans present in this extensive South Pacific sample, although the relatively low effort in the western Pacific means there may well be other undiscovered clans in that region. I am aware of no similar phenomena on this oceanic scale, where stable cultural groupings persist despite being largely sympatric.

The function of codas is unknown, and the function, if any, of coda dialects is thus a matter of speculation. However, it is known that members of sperm whale groups will take considerable risks to help group-mates under predatory attack (Pitman *et al.* 2001), and also provide allomaternal care of calves within groups (Whitehead 1996a). I suggest that coda dialect performs a signature function in this context, allowing units to identify other units of the same clan within a highly mobile sperm whale society (c.f. Tyack & Sayigh 1997) and perhaps mediating seemingly altruistic exchanges such as communal defence and allomaternal care. It is important to know if clan signatures form boundaries to these exchanges; if they do, then sperm whale clans would be among the largest cooperative groups known outside humans. The erection of social boundaries through vocal variation is also considered important in human evolution and social behaviour (Nettle 1999), and may be paralleled here in sperm whales. Thus I suggest that clan signatures may give sperm whales a cultural identity that is of great importance to their individual survival and reproduction. Playback experiments are an obvious way to assess how clan signatures may affect social interactions in sperm whales.

The next research priority is to establish how clan structure relates to genetic population structure. Genetic and other studies have found little evidence for population structure in sperm whales at scales below ocean basins (Dufault *et al.* 1999; Lyrholm *et al.* 1999). Sperm whale populations may be most clearly structured culturally, in which case coda recordings may be an easy way to map population structure worldwide. This is particularly important at a time when sperm whale populations are threatened by the

resumption of commercial whaling as well as, potentially, by other anthropogenic effects such as climate change. It is therefore of obvious interest to know whether other, non-vocal, behavioural traits map onto clan structure, particularly aspects of behaviour with direct fitness consequences, as, in this case, anthropogenic effects may affect clans in different ways. Finally, if there were variation in ecologically important behaviour as well as gene differences among clans, this would potentially allow culture to drive genetic evolution at the level of the clan.

## CHAPTER FOUR

*Insights into coda usage from acoustic size measurement.*

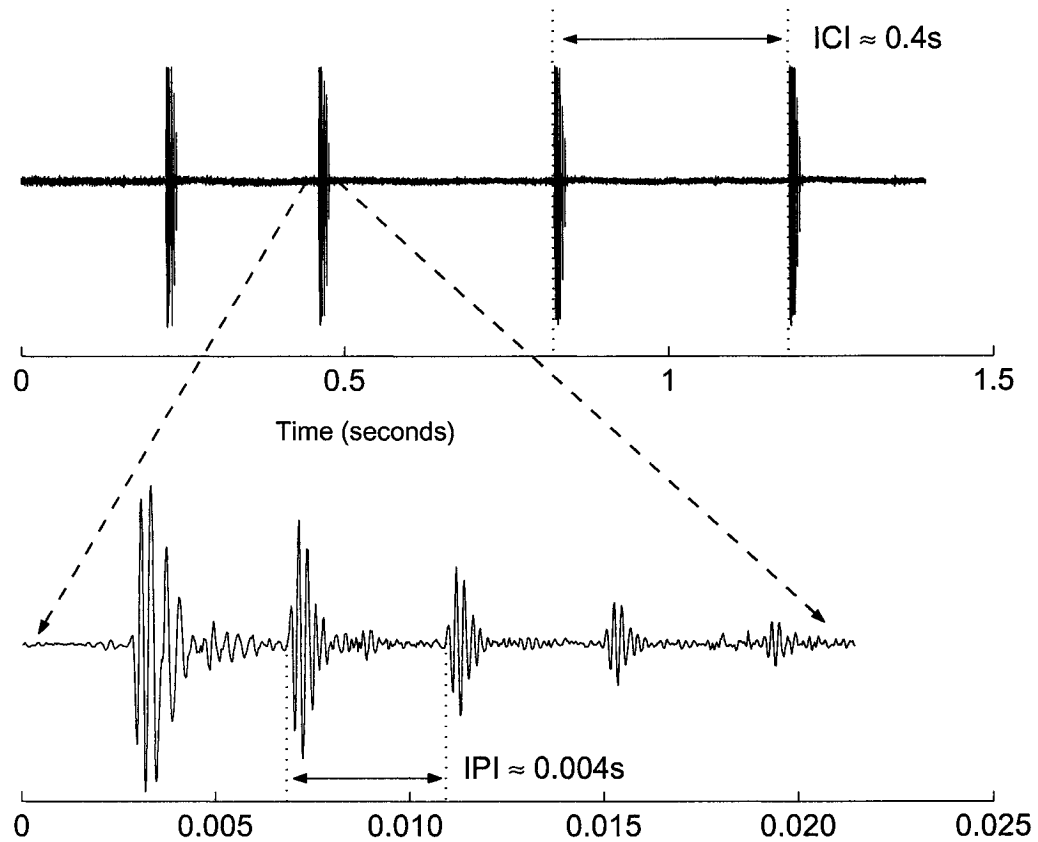
## INTRODUCTION

Evidence for group-specific coda usage dialects in sperm whales has led to the suggestion that these patterns are the result of cultural transmission (Rendell & Whitehead 2001, Chapter 3; Weilgart & Whitehead 1997; Whitehead *et al.* 1998). However, some have challenged the assertion of group-specific vocal patterns because recording techniques that sample at the level of the group and not the individual (Freeberg 2001; Tyack 2001). Given that the recordings of sperm whales used in this and previous studies on Pacific sperm whales were made from a single hydrophone recording an entire group output, without the ability to assign codas to individuals, the possibility exists that what is labelled as ‘group’ output is in fact the vocal output of, for example, a single dominant individual – hence reported ‘group’ differences would actually be differences between individuals, and we (specifically Rendell & Whitehead 2001, Chapter 3; Weilgart & Whitehead 1997; Whitehead *et al.* 1998) would have made an error in interpreting this data. Likewise, if each animal in a group made a single, ‘signature’ coda type (as initially thought by Watkins *et al.* 1985; Watkins & Schevill 1977), then ‘group’ differences could also result as the combined differences between the individual signatures of the vocalising group members, and not truly a group attribute at all.

Here I attempt to address these concerns using a fortuitous acoustic feature of sperm whale clicks – the inter-pulse interval (IPI). Sperm whale clicks have a multi-pulsed structure (Figure 4.1), thought to arise from reverberations of the initial click along the length of the spermaceti organ within the whale’s head (Møhl 2001; Norris & Harvey 1972). In agreement with this theory, it has been shown that the IPI is directly related to body length (Gordon 1991). I apply a method developed by Goold (1996), that automatically measures IPIs, to multiple recordings of codas from a single sperm whale social unit. Thus I estimate the length of the animal that produced any given coda and so examine the diversity of coda production by animals of various sizes within a single social unit. In this way I can investigate whether coda repertoires really are shared attributes or the persistent output of one or two individuals, and also determine whether

coda types are shared within social units.

Figure 4.1: Illustration of inter-click intervals (ICI) of a sperm whale coda and inter-pulse interval (IPI) in a single click. The coda illustrated is a 2+2 type recorded from the focal social unit of this study.



## METHODS

### Unit T

Unit T is a social unit of nine female and immature sperm whales that was followed during four encounters for a total of 17 days (10-20 March, 28-31 March, 6 April and 9-12 April, 1999) around the Galápagos Islands. Animals were tracked visually during the day and followed acoustically at night using a directional hydrophone (see Whitehead & Gordon 1986). Taking identification photographs of the tails whenever possible (analysed



as per Arnborn (1987) by giving each picture a quality, Q, rating from 1 to 5 based on size of the tail in the frame, how focussed the image is, and other factors) revealed the presence of nine animals in the group. All nine animals were repeatedly identified in a total of 379 identifications with  $Q \geq 3$ ; (see Whitehead 2001b). Photo-identification records from previous work around the islands revealed that all nine had been identified together one year previously, hence I considered them a long-term social unit (Christal *et al.* 1998). During the follows the only other sperm whales seen were mature males on 2 separate days; hence in contrast to the normal pattern of a group consisting of more than one social unit, here I am confident that a single social unit was followed. Sloughed skin samples yielded genetic material from five of the nine unit T members (see Whitehead *et al.* 1990). Genetic results indicate that the five unit members sampled are largely unrelated, with  $r$ -values of -0.23-0.17 from nine micro-satellite loci, and two mtDNA haplotypes present (Mesnick 2001; Whitehead 2003a).

### **Coda analysis**

During the encounters with unit T I made 21 recordings, but none on the days males were seen. Thus I am sure that only the nine members of unit T were present during recording, giving a unique opportunity for insight into the diversity of a single unit's repertoire and to examine the question of coda sharing using inter-pulse intervals. To make the recordings, I used an Offshore Acoustics hydrophone (frequency response,  $\pm 3$ dB : 6Hz-10kHz) connected to a Sony TC-D5M cassette recorder (frequency response 30Hz-17kHz). I subsequently digitised these recordings at 44.1kHz onto a standard desktop PC and analysed them using a dedicated software package called Rainbow Click (see Gillespie 1997; Jaquet *et al.* 2001; Leaper *et al.* 2000). The program detects sperm whale clicks (with user supervision) and stores them in a separate data file; the user can then mark clicks as belonging to a coda. Once the user has marked codas the software outputs the timing of clicks within the codas in seconds (so for example a regular 4-click coda could be represented as 0.180, 0.178, 0.182). I only analysed codas that could be clearly identified aurally; the recordings yielded 879 codas of sufficient quality for further analysis (Table 4.1). These data were then standardised by coda length and classified into

types using  $k$ -means cluster analysis in a divisive clustering algorithm using Duda & Hart's (1973 pp239-243) ratio criterion as a stopping rule to determine the number of clusters, or coda types (see Chapter 2). Here I set the critical level at 95%, and clustered the codas as follows: For codas with a given number of clicks (e.g. four click codas) I clustered the data using iterative  $k$ -means with  $k = 2$  (repeated 10 times, selecting the solution with the lowest within-group sum of squares); each split was then accepted or rejected according to the Duda & Hart criterion, and the resultant clusters again split and tested, with division continuing until all possible splits were rejected (see Chapter 2).

Table 4.1: Recordings of unit T

<b>Date</b>	<b>Start Time</b>	<b>Duration (mm:ss)</b>	<b>Latitude</b>	<b>Longitude</b>	<b>#Codas Recorded</b>	<b>#Codas IQR&lt;0.02ms</b>
10/03/99	10:19	01:50	0.19°S	90.36°W	26	0
10/03/99	10:52	02:34	0.19°S	90.36°W	35	1
10/03/99	11:18	00:59	0.19°S	90.36°W	8	0
13/03/99	12:55	02:49	0.14°S	90.33°W	79	8
14/03/99	10:18	01:51	0.32°S	90.17°W	22	0
14/03/99	10:40	04:21	0.32°S	90.17°W	75	4
14/03/99	15:08	01:29	0.27°S	90.26°W	10	2
15/03/99	09:20	09:38	0.23°S	90.29°W	194	17
16/03/99	11:05	02:23	0.27°S	90.27°W	29	3
16/03/99	13:10	01:54	0.28°S	90.32°W	13	0
18/03/99	11:45	05:58	0.09°S	90.45°W	76	14
18/03/99	12:51	01:16	0.12°S	90.46°W	16	5
18/03/99	12:59	02:19	0.12°S	90.46°W	33	8
19/03/99	11:41	04:56	0.06°S	90.94°W	69	5
19/03/99	13:07	01:29	0.05°S	90.96°W	24	2
20/03/99	11:16	05:06	0.07°S	90.93°W	60	15
20/03/99	12:57	01:37	0.06°S	90.94°W	8	1
28/03/99	15:37	01:58	0.41°S	90.11°W	30	1
06/04/99	15:05	02:41	0.17°S	90.34°W	36	7
06/04/99	16:30	01:40	0.17°S	90.34°W	21	1
10/04/99	12:40	01:48	0.24°S	90.29°W	15	0
<b>Total :</b>	<b>60:36</b>			<b>Total :</b>	<b>879</b>	<b>94</b>

**IPI analysis**

Repeated broadband pulses cause ‘ripples’ in the log magnitude spectrum of a signal, with a frequency equal to the time between pulses; since the multiple pulses of a sperm whale click are broadband signals, they cause ripples in the spectrum of a click with a frequency equal to the inter-pulse interval (IPI) of the click (Goold 1996). This frequency can be measured automatically by extracting peaks from the spectrum of the spectrum (termed the cepstrum) of a click (Goold 1996). The software package Rainbow Click also outputs the digitised sound data for each click in each coda, and we used these data for the IPI analysis. I wrote MATLAB (v12.0, with Signal Processing Toolbox) routines to automatically analyse large numbers of clicks by extracting the maximum value from the cepstrum, following precisely Goold’s (1996) method.

I then calculated the median and inter-quartile range for IPI measurements from all the clicks in each coda, and selected from this set those codas with IPI inter-quartile ranges of less than 0.02ms, the minimum time resolution at a 44.1kHz sampling rate (typical IPI estimates ranged from 3.7 to 4.5ms). This last step can be justified under the assumption that the ‘true’ IPI is identical for every click in a given coda, and thus large inter-quartile ranges are indicative of measurement error (e.g. due to overlapping clicks, wave-noise or poor recording conditions) rather than a genuine variation in IPI. IPIs from a given individual are expected to vary with pressure (i.e. depth) and temperature, since these factors affect the speed of sound through spermaceti oil and hence within the spermaceti organ (Goold et al. 1996). However, 99% of the codas analysed were less than three seconds in length; the potential for these factors to change significantly during the emission of a coda is thus rather limited, given that all the codas were recorded from whales at the surface. Hence my assumption of identical true IPIs.

## RESULTS

The  $k$ -means cluster analysis grouped the codas into 32 types. A ‘discovery curve’ of the number of types heard plotted against the number of codas recorded reaches an asymptote after approximately 400 codas (Figure 4.2). The seven most common types account for over 75% of the codas heard, with the two most common types accounting for 40% (Figure 4.3). However, there are many rare types; 19 of the 35 clusters each make up less than 1% of the codas recorded (Figure 4.3).

Figure 4.2: Discovery curve of coda types heard plotted against codas recorded from unit T. Solid vertical lines separate recording days, dotted vertical lines separate recordings.

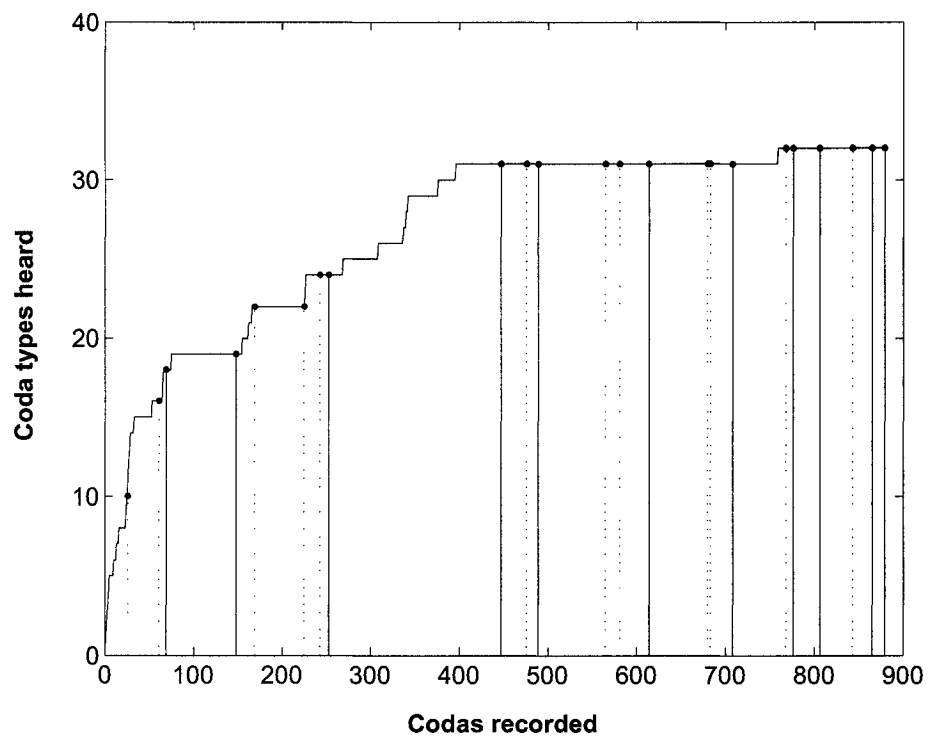
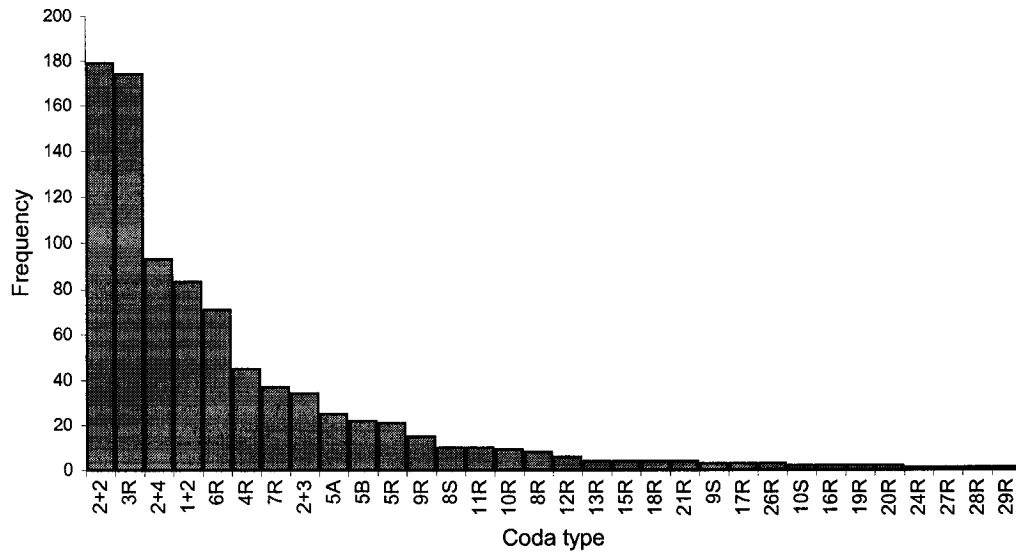


Figure 4.3: Frequency distribution of coda types heard from unit T.



Of the 879 codas recorded from unit T, 94 (~11%) had IPI measurements with inter-quartile ranges of less than 0.02ms, and these had median IPIs between 3.7ms and 4.2ms (see also Table 4.1). Using Gordon's (1991) equation to calculate estimated body length from IPI, my results indicate that we recorded animals between 10.20m and 10.92m in length. No photographic measurements were made at sea (e.g. Dawson et al. 1995; Gordon 1990) for confirmation. However, this size range is that expected for female and immature sperm whales (Rice 1989) and concurs with actual measurements of other whales in the same area (Waters & Whitehead 1990). There were clear modes in the distribution of median IPIs, showing that a number of different sized animals were vocalising (Figure 4.4, (a) and (b)).

Figure 4.4: IPI measurements from the 94 codas recorded from unit T having inter-quartile ranges of IPI estimates  $< 0.02\text{ms}$ .

(a) Histogram of median IPI for each coda; the seven peaks in the distribution are marked.

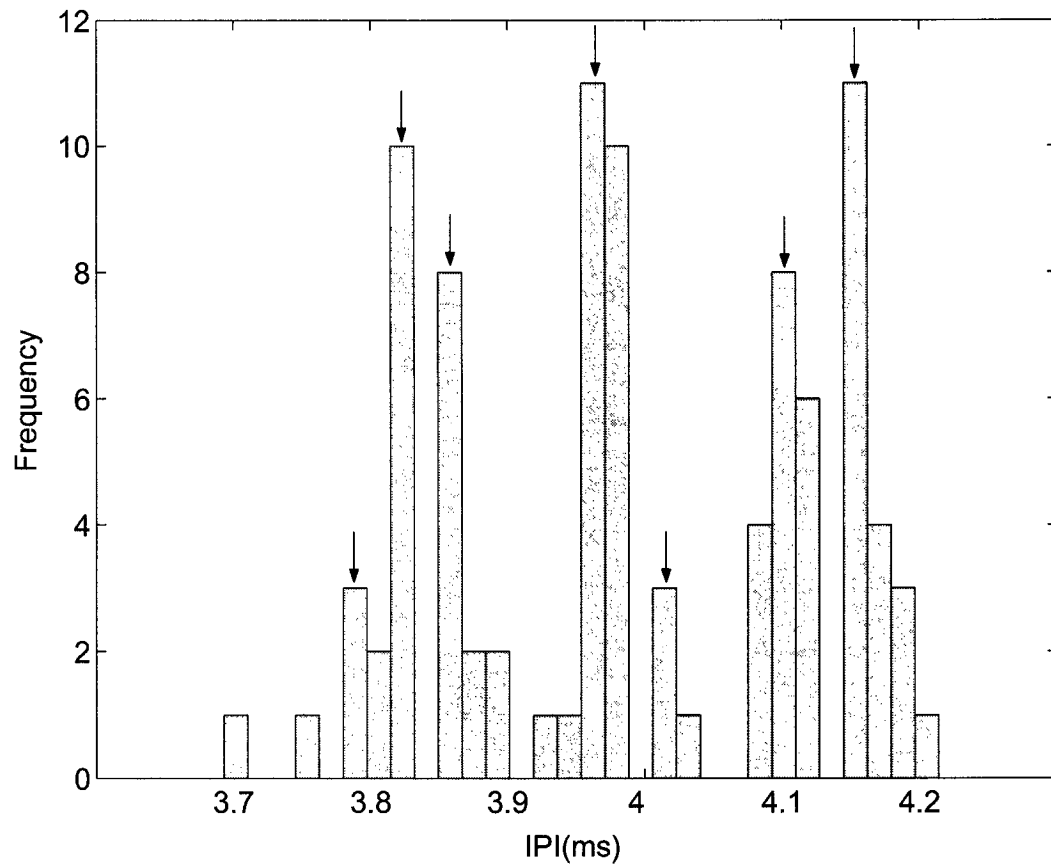
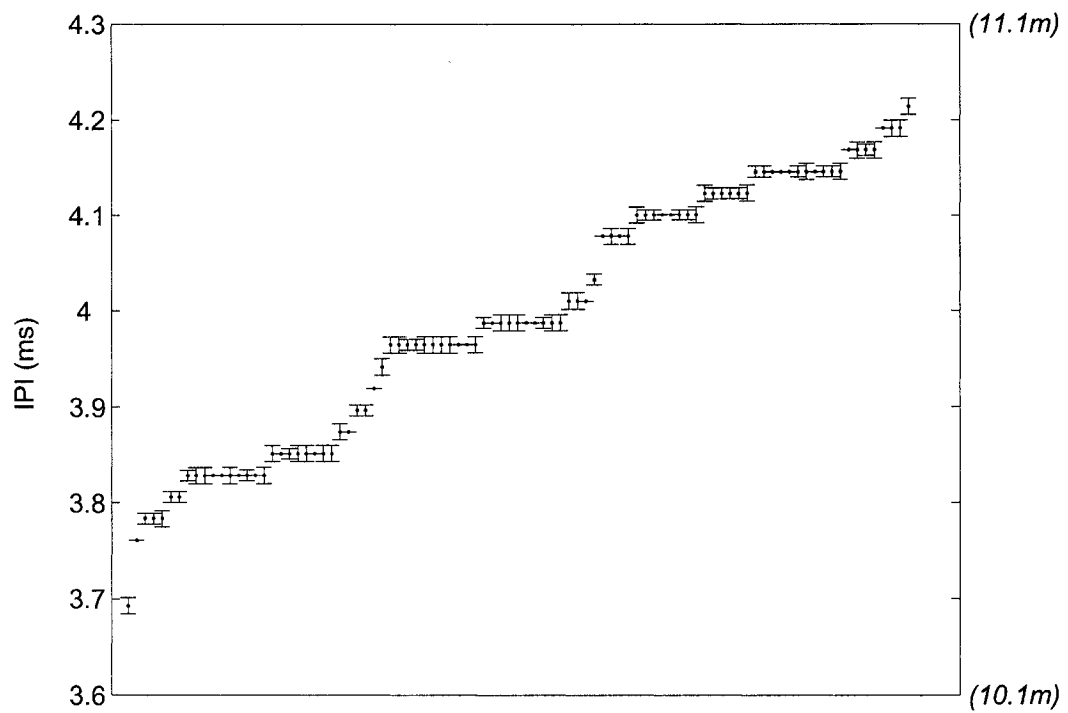


Figure 4.4: (b) IPI measurements ordered by increasing IPI. Points are median and inter-quartile range for each coda. Note clear modes in the distribution, where several codas with identical median IPIs occur. Figures on right show equivalent animal size using Gordon's (1991) equation.



For a number of types, in particular 3R, 1+2 and 2+2, there are again clear clusters in the data, showing that these coda types were made by a number of animals of differing size (Figure 4.5). A similar picture emerges if one does not classify the codas, but instead measures their proximity in multivariate space. I selected the 46 3-click codas from unit T with IPI measurements having an inter-quartile range less than 0.02ms. For each pair of codas in this set, I plotted the absolute difference in median IPI against the Euclidean distance between the two codas calculated from the standardised inter-click intervals of the codas (Figure 4.6). A number of different sized animals were recorded, since most of the pairs of codas have median IPIs that are more than 0.02ms different, and on several occasions different animals (indicated by a large difference in median IPI) made similar codas, as evidenced by points occurring in the top-left sector of the plot.

Figure 4.5: IPI measurements from unit T plotted by coda type. Each column contains one coda type. Points are median and inter-quartile range, and are jittered horizontally to illustrate codas having identical median IPIs.

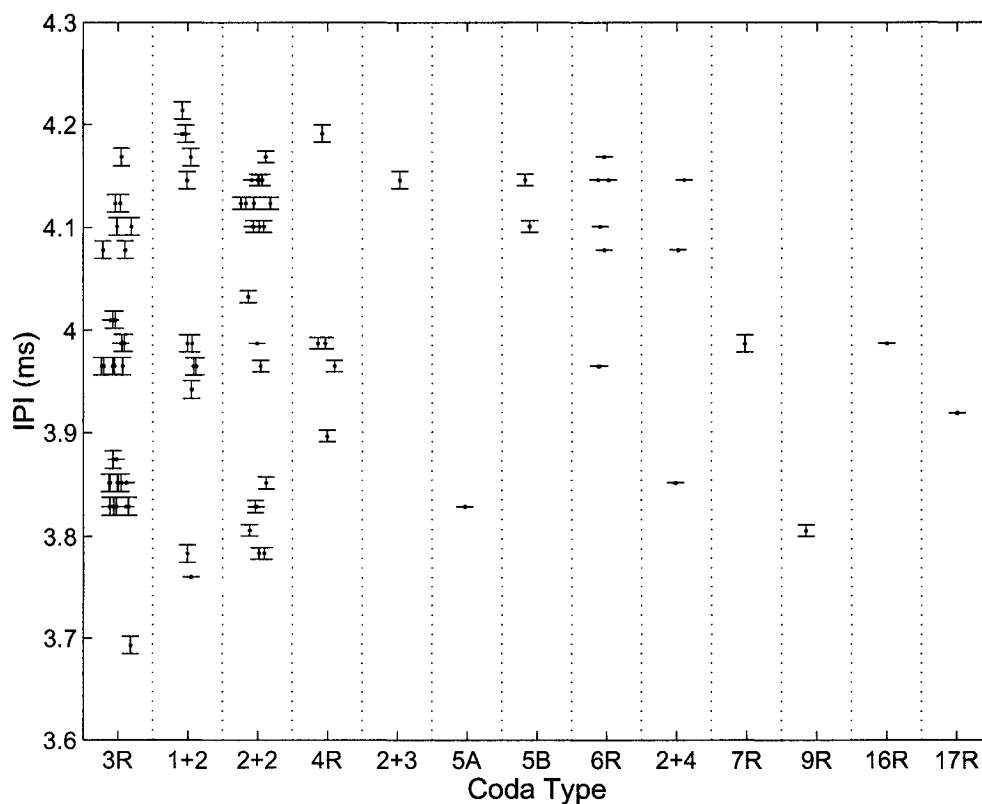
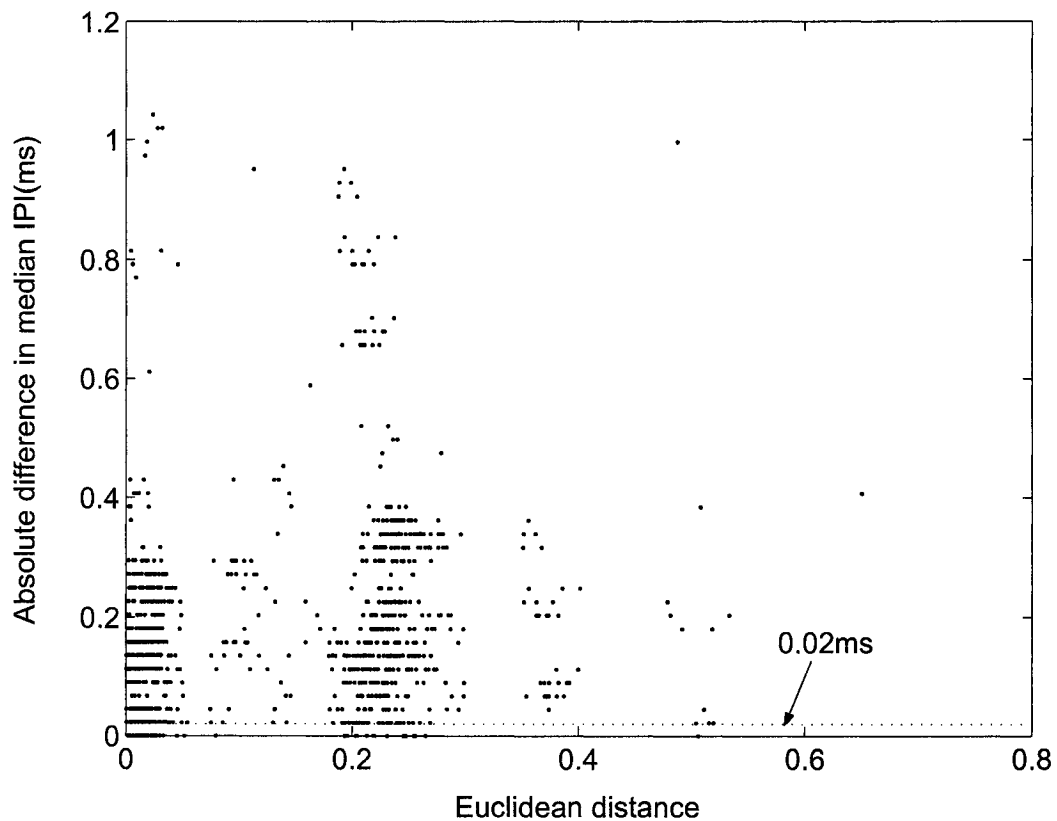




Figure 4.6: Absolute difference in median IPI plotted (high values indicate vocalizing animals of increasingly divergent size) pair-wise against Euclidean distance (high values indicate increasingly different coda rhythms) for 3 click codas from unit T. Horizontal dashed line represents a difference of 0.02ms in median IPIs – points above this line represent pairs of codas likely made by different animals.



## DISCUSSION

In this chapter I investigated whether coda types are shared across individuals, and whether coda repertoires recorded from sperm whale social units are genuinely unit repertoires, in that they are an attribute of the unit as a whole rather than of one or two vocal individuals. The data presented here show that, for unit T at least, the answer to both these questions is yes. The results of the IPI measurement are inconsistent with a scenario of vocalisations recorded from unit T being produced by a single individual. Instead, they are consistent with several animals vocalising, given the modes present in

the data. Similarly, a given coda type can be produced by more than one animal – sperm whales in unit T share at least some of their coda types. This conclusion is robust to varying coda classification as it holds true when no classifications are made; very similar codas were recorded with IPI estimates that clearly indicate they were made by different animals. Also, different codas were recorded with IPI estimates close enough (i.e. medians less than 0.02ms different) to be from the same individual (Figures 4.5 and 4.6). While this suggests that individual sperm whales have repertoires containing several coda types, I cannot eliminate the possibility that the different codas could have been made by different, but very similar sized, whales. However, since only nine animals were present and 32 coda types were recorded, at least one animal must have made more than one coda type.

My assumption that the true IPI of the clicks I measured did not change during any given coda makes a big impact on the conclusions of this study; how justified is it? Consider a click with a 4ms IPI (i.e. in the middle of my range of estimates), and assume that the spermaceti is at 33°C as measured from a recently killed sperm whale by Clarke (1978). Using Goold's (1996) empirically derived equations relating sound velocity to temperature and pressure in spermaceti oil, a 4ms IPI at 33°C and one atmosphere gives a 5.59m travel distance for the sound pulse (sound velocity  $1397\text{cms}^{-1}$ ), equating to a head size of 2.79m since each pulse is thought to travel twice through the spermaceti before leaving the head (Norris & Harvey 1972). Increasing the pressure to ten atmospheres - representing a dive to 100m - results in a decrease of 0.011ms in the travel time (and hence IPI). Maximum observed dive rates for sperm whale are  $4\text{ms}^{-1}$  (Watkins et al. 1993), so it would take at least 25s for an animal to reach that depth. Since the longest coda of the 94 selected lasted 3.4s, and since I made all the present recordings while the group were socialising at the surface, it seems unlikely that variation in IPI due to pressure would be a significant factor here. Temperature also affects sound transmission in spermaceti. However, this would have to fall 1.5°C from 33°C at atmospheric pressure in order to produce a 0.02ms change in the IPI, again using Goold's (1996) equations; it is impossible that this could occur in the 1-3s it takes to produce a coda (see Clarke

1978). One further potential source of within-coda IPI variation is alteration of the shape of the spermaceti sac using the maxillonasalis muscle, a possibility outlined by Goold (1996). If sperm whales did use this muscle in this way, then IPIs from the same whale could vary unpredictably; evidence that they do not is provided by studies using acoustic tags (Madsen et al. 2002) that showed within-coda IPI variation of less than  $\pm 0.02$ ms for codas recorded in the upper 250m of the water column (P. Madsen, pers. comm.), and studies of solitary male sperm whales that show IPIs in regular clicks remaining stable over periods of minutes (Rhineland 2001). Hence I am confident in the assumption that large variation in within-coda IPI values were due to measurement error and not changes in the true IPI of the clicks. It is unfortunate that I was forced to reject large numbers of codas from the original dataset, probably because the recordings in the present study suffered overloading problems. While I do have other recordings made with better equipment and without overloading that have yielded much higher proportions of usable IPI estimates ( $>30\%$ , unpublished data), I used the recordings of unit T because they were made from a clearly defined set of animals, crucial for the present study.

Variation between codas made by the same animal is another possible source of confound; since the animals were always at the surface, pressure due to depth is an unlikely source of variation. However, I can be less confident as regards temperature, mainly because we do not know how the spermaceti temperature in a sperm whale's head may vary over periods of days – it may not vary at all, but likely does at least to some extent. Sea surface temperature was measured every three hours while at sea; the temperatures nearest to each recording were between  $26.0^{\circ}\text{C}$  and  $31.8^{\circ}\text{C}$ , a range of  $5.8^{\circ}\text{C}$ . Taking a conservative approach by assuming that the spermaceti temperature in the recorded animals oscillated as much as the sea-water temperature (i.e.  $5.8^{\circ}\text{C}$ ) around a mean of  $33^{\circ}\text{C}$  (i.e. up to  $2.9^{\circ}\text{C}$  either side of  $33^{\circ}\text{C}$ ) would result in a maximum change in IPI of  $0.06$ ms between the coolest and warmest conditions according to Goold's (1996) equations. This could account for some of the spread in my data, but is not of sufficient magnitude to significantly alter my conclusions since the gap between most of the clusters in Figure 4.5 is greater than  $0.06$ ms. In addition, it is unlikely that spermaceti

temperature varies as freely as this; given that the primary function of the spermaceti organ is thought to be sound transmission (see e.g. Cranford 1999) it seems reasonable to expect the temperature to be maintained around some optimum for this function, perhaps 33°C as measured by Clarke (1978). Finally, the elimination of codas with variable IPI estimates could introduce bias if it meant only codas from one or two recordings were retained. However this is not the case here – the highly accurate measurements came from 17 different recordings on 10 different days and represent an essentially random sample of the group's total output (Table 4.1).

This study also characterises the coda repertoire of a single social unit. The discovery curve of coda types (Figure 4.2) gives some confidence that, with 32 coda types identified, most of the repertoire diversity has been captured. Most of the diversity was present in the first ~500 codas recorded, giving a useful cue for future studies that seek to characterise unit coda repertoires in sperm whales. However, these patterns may themselves be group-specific, and so care should be taken in generalising. Codas were recorded in very similar behavioural contexts (socialising or resting at the surface), but then codas are generally heard from sperm whales in those contexts (Whitehead & Weilgart 1991); given that the present recordings spanned one month, I am confident that the repertoire of this unit has been well characterised. It is noteworthy that relatively few types dominate the coda output, particularly 2+2 and 3R codas (Figure 4.3); these types may be a 'unit signature' similar to the discrete calls of killer whales (see Ford 1991), but more work is needed on the repertoires of other known social units before conclusions can be drawn (see Chapter 6). Some have suggested that coda types may function as individual signatures (Tyack 1999; Watkins *et al.* 1985; Watkins & Schevill 1977); if this were the case then one would expect nine coda types to be prevalent in the repertoire of these nine animals, but there is no indication of this (Figure 4.3).

The five genotyped individuals show no close relations, and incorporate two mtDNA haplotypes; therefore this unit is not a strict matriline. Given that I only sampled five individuals, there is some chance that first order relationships (sibling, or mother-

offspring) existed in unit T and were not sampled. The most extreme case possible would be that the four individuals not sampled were all first order relatives of one of the five that were sampled. I simulated sampling, without replacement, five individuals at random from nine animals with four, three, two and one first order relationships present; the percentages of 10,000 samples that contained no relationships were 12.9, 28.3, 47.5 and 72.8 respectively; it is therefore quite possible that one or two close genetic relationships were missed, but rather unlikely that more were present. Given that coda types were shared within this unit, and given that the unit members appear largely unrelated, the most parsimonious explanation for these patterns is that coda sharing is a result of social learning rather than common genetic descent. This could take the form of contextual learning, where the context of producing sounds is learned and not the sounds themselves (i.e. learning the timing of clicks in a coda), or production (vocal) learning, where the form of the sound itself is learnt (i.e. the entire coda is learned as a single unit) (see Janik & Slater 2000). The difference depends critically on what the minimum unit of production is for sperm whale social sounds, which remains unknown (Janik & Slater 2000).

The initial impetus for this study was given by Freeberg's (2001) and Tyack's (2001) suggestions that what Weilgart & Whitehead (1997) had labelled group dialects could equally have been difference between individuals in those groups; these suggestions also presumably apply to my description of vocal clans (Chapter 3). Here I have shown that coda types are shared within a social unit, and that several whales produced codas during social periods. Whether this holds true on a wider basis remains to be seen, but the implication is clear – that repertoire differences between recordings of different units represent real differences in the repertoires and not the result of individuals biasing the unit output, provided that the unit has been sufficiently sampled. Similar studies of other units are clearly desirable so we can move forward to study how this communication system fits into the wider context of group-specific signals in social animals as regards the relationship between coda dialect and social structure. We still need to know how coda usage patterns vary between groups, social units, and individuals,

how they vary geographically, how codas are used and whether clan dialects are functional.

## CHAPTER FIVE

### *Coda playbacks to sperm whales in Chilean waters*

## INTRODUCTION

Long-term social units of female and immature sperm whales show consistent variation in their use of ‘codas’, short, stereotyped patterns of clicks generally heard in social contexts; in the Eastern Tropical Pacific units belong to one of five large scale vocal ‘clans’ each with a distinctive pattern of coda usage (Chapter 3). This leads naturally to asking whether these dialects serve an adaptive function, whether in the context of mate choice (e.g. Grant & Grant 1996) or social interaction (e.g. Boughman & Wilkinson 1998; Farabaugh et al. 1994). We still understand virtually nothing about the function of codas in general, let alone clan dialects in particular. In birds, even after decades of study, there is still debate over the functional significance of dialects in bird-song; some consider them to be functionless epiphenomena, others that they are important in mate choice to maintain or control levels of outbreeding in relation to local adaptation (Baker & Cunningham 1985; Slater 1986). In cetaceans, Ford (1991; Ford & Fisher 1982) suggests that discrete call repertoires in killer whales serve to co-ordinate pod activities, maintain pod integrity and indicate pod affiliation; they may also play a role in mate choice, since most matings appear to be between rather than within clans (Barrett-Lennard 2000). In Chapter 3, I suggest that sperm whale clan dialects may serve as markers for altruistic interactions. These are attractive hypotheses for group living species such as killer and sperm whales; however, they have never been tested, mostly because of the difficulty of doing so. The major experimental method in studies of vocal functionality is the playback experiment (Catchpole & Slater 1995, p16).

Playback experiments to study marine mammal vocal communication are relatively few, which is not surprising given the difficulties involved even with coastal and/or captive animals (but see the notable exceptions of Deecke et al. 2002; Richards *et al.* 1984; Sayigh *et al.* 1998; Tyack 1983). Due to the logistical difficulty of getting playback apparatus to sperm whale habitat and the unfeasibility of even temporary captivity in this species, it is even less surprising that ‘playback’ studies on sperm whales



are very rare, and none of them have been systematic. Watkins (1985) reports a single incident of a group of whales ceasing to vocalise after the ‘playback’ of an artificial coda – made by hammering a piece of metal that extended below the water. André *et al.* (1997) report an ‘acoustic reaction’, defined as one or more whales ceasing to make clicks, to seven of 39 playbacks of a single artificial coda type, again produced by hammering two pieces of metal. Few substantial conclusions can be drawn from these studies; one possible exception is that in both cases reactions were reported within a few seconds of ‘playback’. Such methodology will likely not be as effective as playing back actual recordings of codas, and the potential for playback experiments to reveal elements of functionality in codas and coda dialects remains largely unexplored.

In this study I wanted to assess (1) the vocal response of female and immature sperm whale groups to codas in general and, opportunistically (2) whether sperm whales responded vocally to codas that identify their own clan differently to codas that identify other clans. This latter was opportunistic because I had no knowledge of the clan variation in coda production during the planning and execution of the study, only during the analysis phase. In the first case the null hypothesis was that there would be no response to coda playbacks, and in the second that playbacks to codas characteristic of the clan of a particular group would induce a similar response to playbacks of codas from a different clan.

## **METHODS**

Sperm whale groups were detected, tracked and photo-identified from a 12m auxiliary sailing vessel during a nine-month study of sperm whale ecology, social structure and acoustics in northern Chile using methods previously described (Whitehead & Weilgart 2000). In order to conduct a playback experiment I waited for a combination of conditions to be met: Firstly, I only conducted playbacks when whales were collected at the surface during social or resting periods (Whitehead & Weilgart 1991), as this was when their movement was minimal and so I could expect to remain reasonably close to the group while drifting (since deploying the playback system and the ability to make

decent quality recordings both required the vessel be stopped with the diesel engine off). Secondly, I could only conduct playbacks in very calm conditions (Beaufort force 3 or less), as sails were used to stabilise the vessel during playbacks, so increased wind speed resulted in the vessel being rapidly blown away from the whales. These restrictions led to playbacks being conducted on only 5 of 64 days spent with sperm whales during the study.

Playback stimuli were constructed using recordings previously made of codas; these recordings were digitised at 44.1kHz, and then the waveform between clicks in the coda of interest was zeroed using CoolEdit 96 digital audio manipulation software. For each coda type (e.g. 5R) I selected three different examples, and cycled through these during playbacks, such that conclusions drawn would have validity concerning the type as a whole rather than any given exemplar (Kroodsma 1990; Kroodsma et al. 2001). To broadcast sound underwater I used a system called BATS (Broadband Acoustic Transmission System), based on a Class III barrel-stave transducer developed by the Defence Research Establishment Atlantic, DREA (Jones & Rendell 2000; Jones & Reithmeier 1996). Sounds were played into this system using a Toshiba laptop PC. Visual estimates of range to the nearest visible whale were recorded at the start of each playback. The BATS transducer emits a maximum source level without distortion of 165dB//1 $\mu$ Pa-m at a resonant frequency of 5.3kHz (D. Jones, personal communication). Madsen *et al.* (2002) report levels of coda clicks recorded from tagged sperm whales as averaging 165dB//1 $\mu$ Pa peak-to-peak. Using this source level and estimated ranges to the whales I calculated maximum received levels in the 5-6kHz (the band of maximum energy in the stimulus clicks used (Goold & Jones 1995) assuming spherical spreading and frequency dependent absorption (Urick 1983)). I recorded the whale's acoustic responses using a Benthos AQ17 hydrophone connected to a Nagra IV-SJ recorder via Ithaca 453 pre-amplifiers.

I compared photo-identification records from days on which playbacks were performed, and assigned those days to the same group if

$$m_{AB} > 0.25 \cdot \min(n_A, n_B)$$

where  $n_A$  animals were photographically identified on the first day,  $n_B$  on the second, and  $m_{AB}$  were photographed on both days (see Weilgart & Whitehead 1997).

I digitised all recordings made during the study onto a desktop PC at a sample rate of 44.1kHz, and extracted the timing of clicks from both playback and sperm whale codas using software especially written for the task (Gillespie 1997), with a maximum resolution of 0.02ms (from a 44.1kHz sample rate). Codas recorded on each day of playbacks but before playbacks had commenced were used to classify focal groups into clans using data presented in Chapter 3. Using the codas underlying Figure 3.2 in Chapter 3, I considered all the codas recorded from groups assigned to a given clan as representative ‘clan repertoires’, and then assigned the groups in the present study according to which of these clans each group’s repertoire was most similar to, where similarity was measured between coda repertoires using

$$S_{AB} = \frac{\sum_{i=1}^{n_A} \sum_{\substack{j=1 \\ l_j=l_i}}^{n_B} \frac{0.001}{0.001 + d_{ij}}}{n_A \cdot n_B}$$

where  $S_{AB}$  denotes the similarity between coda sets A and B,  $l_i$  is the number of clicks in coda  $i$  of set A,  $l_j$  is the number of clicks in coda  $j$  of set B and  $d_{ij}$  the maximum absolute distance (or infinity-norm) between the vectors containing the standardised inter-click-intervals of the codas  $x_i$  and  $x_j$  (see Chapter 2). Groups were assigned to clans as the final part of the acoustic analysis, such that I was blind to the conditions during both playback and all the previous stages of acoustic analysis.

Playbacks were organised into ‘bouts’ each separated by at least 30 seconds; for each bout, codas played back were assigned to a clan if the coda type in question was a

‘clan defining’ coda (see Chapter 3): any regular coda (e.g. 5R) would be assigned to the ‘regular’ clan, any plus-one coda (e.g. 4+1) to the ‘plus-one’ clan and any short coda (e.g. 3R) to the ‘short’ clan. Bouts were then classified as ‘clan match’ if the playback codas and codas recorded from the focal group were of the same clan, ‘clan mismatch’ if the clans were different, and null in the event that codas from more than one clan were played back in the same bout.

Given the immediate responses observed by Watkins (1985) and André *et al.* (1997), I decided to look for effects over a short time-scale, namely 15 seconds after playback onset. I counted the number of real codas that started in 15-second bins for two such bins (i.e. 30 seconds) before playback start and one after, so for each bout I counted the number of codas in the following time bins (relative to playback start): [-30s:-15s], [-15s:0s] and [0s:+15s]. For brevity I shall refer to these counts as  $n_1$  through  $n_3$  respectively. I used these data to calculate two measure of response. The first was simply the number of codas heard in the 15s after playback start minus the number of codas heard in the 15s prior to playback ( $n_3 - n_2$ ), or simple difference. The expectation for response in this case is straightforward – high positive or negative values indicate signify increased or reduced coda production respectively.

I calculated a second measure by subtracting the absolute *change* in number of codas heard between the time bins [-30s:-15s] and [-15s:0s] from the absolute *change* in number of codas heard between the time bins [-15s:0s] and [0s:+15s] - more formally,  $|n_1 - n_2| - |n_2 - n_3|$ , termed here ‘co-varied difference’. Such an approach attempts to control for the (likely huge) natural variation in coda production by sperm whale groups over time. Here, the expectation for response is slightly more complex; only negative values indicate a change in coda production after playback that is large relative to changes in coda production prior to playback; values near zero indicate little change, while positive values suggest that the change in coda production on playback was small relative to any changes prior to playback.

I tested for differences using two approaches. The first using an individual playback bout as an independent unit; however, it could be argued that this introduces pseudo-replication (Kroodsma 1990) into the study if responses of the same *group* of animals to different playback bouts are not independent. Hence in a second approach I also tested for responses using each focal group as an independent unit, with the measures in the latter case being the mean response for each group to ‘clan match’ and ‘clan mismatch’ bouts. I used both parametric *t*-tests and non-parametric sign tests (Sokal & Rohlf 1995) as follows:

- (1) For the ‘simple difference’ measure assuming independent bouts I used a two-tailed *t*-test to test whether the mean of  $n_3 - n_2$  was different from zero, for ‘clan match’, ‘clan mismatch’ and all playback bouts combined. I also used a two-tailed sign test to test the probability that the number of positive and negative values of  $n_3 - n_2$  followed a binomial distribution with probability of success = 0.5.
- (2) For the ‘simple difference’ measure assuming independent *groups* I used a two-tailed paired *t*-test to test whether group means were consistently different between ‘clan match’ and ‘clan mismatch’ bouts. I used a two-tailed sign test on the same group data. I also used a two-tailed *t*-test to test whether the group means of  $n_3 - n_2$ , pooled across ‘clan match’ and ‘clan mismatch’ bouts, were different from zero, and again a sign test on the same data.
- (3) For the ‘co-varied difference’ measure assuming independent bouts I used a one-tailed *t*-test to test whether change in coda production after playback was large relative to changes in coda production prior to playback, that is, whether the measure was less than zero, for ‘clan match’, ‘clan mismatch’ and all playback bouts combined. I also used a one-tailed sign test on the same data.
- (4) For the ‘co-varied difference’ measure assuming independent *groups* I used a two-tailed paired *t*-test to test whether groups means were consistently different between ‘clan match’ and ‘clan mismatch’ bouts, and a two-tailed sign test on the same data; I also used a one-tailed *t*-test to test whether the group means pooled across ‘clan match’ and ‘clan mismatch’ bouts were less than zero, and a one-

tailed sign test on the same data.

These procedures resulted in a total of 20 hypothesis tests, so for the resultant  $p$ -values to be significant with experiment-wise  $\alpha = 0.05$  they had to be less than  $(0.05/20) = 0.0025$ .

## RESULTS

Playbacks were conducted on five days (3<sup>rd</sup> June, 29<sup>th</sup> September, 30<sup>th</sup> September, 31<sup>st</sup> October and 6<sup>th</sup> November 2000); comparison of photo-identification records from those days resulted in the 29<sup>th</sup> and 30<sup>th</sup> of September being assigned the same group (they were also consecutive days of the same encounter, with acoustic contact having been maintained with the group overnight). Hence playbacks were to four groups over five days. I analysed a total of 70 playback bouts, separated by at least 30 seconds. Each bout had between one and eight (mean three) codas played back, with a mean playback duration of 17 seconds. Of these 70 bouts, 45 were ‘clan match’, 21 were ‘clan mismatch’ and 4 bouts played back codas from more than one clan; these latter were excluded from further analysis, leaving a total of 66 bouts included (Table 1). The closest estimated range to a visible whale at playback start was 50m, giving a maximum estimated received level in the 5-6kHz band of 131dB//1 $\mu$ Pa-m. This is some 30dB less than the estimated received levels reported by André *et al.* (1997)

None of the statistical tests gave significant results (Tables 2-5). Box plots of the data by playback bouts show that playback of codas of the same clan produced more extreme values in both the ‘simple’ and ‘co-varied’ response measure, but in neither case was the effect consistently directional (Figures 1 & 2). Plots of the data pooled across groups similarly show little consistent response (Figures 3 & 4), although the ‘co-varied’ measure shows that 3 of the four groups had a lower mean value when played back codas of the same clan, indicating a greater change in coda output after playback compared to before playback; this test also had the lowest (although still non-significant)  $p$ -value of 0.16.

Table 5.1: Details of playback bouts.

<b>Playback start time</b>	<b>Group</b>	<b>#Codas played back</b>	<b>Played clan</b>	<b>Group clan</b>	<b>Clan match?</b>	$n_1$	$n_2$	$n_3$
03-Jun-2000 11:39:05	1	5	Short	Short	Y	0	0	0
03-Jun-2000 11:41:22	1	3	Short	Short	Y	0	0	0
03-Jun-2000 11:42:23	1	3	Short	Short	Y	0	0	0
03-Jun-2000 11:43:19	1	3	Reg.	Short	N	0	0	0
03-Jun-2000 11:44:26	1	4	Reg.	Short	N	0	0	0
03-Jun-2000 11:54:19	1	1	+1	Short	N	0	0	0
29-Sep-2000 15:53:32	2	4	Short	Short	Y	0	0	0
29-Sep-2000 15:55:19	2	3	Short	Short	Y	0	0	0
29-Sep-2000 15:56:00	2	6	Short	Short	Y	0	0	0
29-Sep-2000 15:57:17	2	3	Short	Short	Y	0	0	0
29-Sep-2000 15:59:09	2	3	Reg.	Short	N	0	1	3
29-Sep-2000 16:00:17	2	3	Short	Short	Y	5	5	0
29-Sep-2000 17:42:25	2	4	Short	Short	Y	0	0	0
29-Sep-2000 17:43:45	2	1	Short	Short	Y	0	0	0
29-Sep-2000 17:44:38	2	3	Short	Short	Y	0	0	0
29-Sep-2000 17:46:01	2	2	Short	Short	Y	0	0	2
29-Sep-2000 17:46:55	2	2	Short	Short	Y	0	1	2
29-Sep-2000 17:48:27	2	2	Short	Short	Y	5	11	5
29-Sep-2000 17:50:03	2	1	Short	Short	Y	4	5	2
29-Sep-2000 17:50:37	2	1	Short	Short	Y	2	7	4
29-Sep-2000 17:54:11	2	1	Reg.	Short	N	7	2	7
29-Sep-2000 17:54:51	2	1	Short	Short	Y	2	0	1
30-Sep-2000 09:16:30	2	1	Reg.	Short	N	3	1	0
30-Sep-2000 09:22:46	2	4	Short	Short	Y	0	3	4
30-Sep-2000 09:24:20	2	8	Short	Short	Y	5	0	0
30-Sep-2000 09:30:10	2	1	Short	Short	Y	0	0	0
30-Sep-2000 09:32:30	2	1	Reg.	Short	N	3	0	0
30-Sep-2000 09:36:14	2	1	Reg.	Short	N	4	1	3
30-Sep-2000 09:37:43	2	1	Short	Short	Y	2	4	5
30-Sep-2000 09:40:05	2	3	Short	Short	Y	3	1	0
30-Sep-2000 09:42:00	2	1	Reg.	Short	N	4	2	6
30-Sep-2000 09:42:44	2	3	Short	Short	Y	0	0	0
30-Sep-2000 09:44:28	2	7	Short	Short	Y	0	0	1
30-Sep-2000 09:46:03	2	3	Short	Short	Y	5	2	3
30-Sep-2000 09:47:04	2	3	Short	Short	Y	3	7	7
30-Sep-2000 09:49:05	2	2	Short	Short	Y	3	0	1
30-Sep-2000 09:52:51	2	6	Short	Short	Y	0	0	3
31-Oct-2000 12:58:49	3	3	Reg.	Reg.	Y	3	0	0
31-Oct-2000 12:59:38	3	3	Reg.	Reg.	Y	0	0	0
31-Oct-2000 13:05:20	3	1	Reg.	Reg.	Y	0	1	1
31-Oct-2000 13:06:13	3	3	+1	Reg.	N	0	0	0

Table 5.1 (Contd.)

Playback start time	Group	#Codas played back	Played clan	Group clan	Clan match?	$n_1$	$n_2$	$n_3$
31-Oct-2000 13:09:04	3	3	Reg.	Reg.	Y	0	0	0
31-Oct-2000 13:12:13	3	3	+1	Reg.	N	2	1	0
31-Oct-2000 13:14:24	3	3	Short	Reg.	N	2	0	1
31-Oct-2000 13:17:02	3	3	Reg.	Reg.	Y	0	1	0
31-Oct-2000 14:20:28	3	3	Short	Reg.	N	0	4	4
31-Oct-2000 14:23:53	3	3	Short	Reg.	N	2	1	0
31-Oct-2000 15:25:44	3	3	Reg.	Reg.	Y	0	0	0
31-Oct-2000 15:27:18	3	3	Reg.	Reg.	Y	0	0	0
31-Oct-2000 15:29:18	3	3	Reg.	Reg.	Y	0	0	0
31-Oct-2000 15:32:12	3	3	Reg.	Reg.	Y	0	0	0
31-Oct-2000 15:34:14	3	3	+1	Reg.	N	0	0	0
31-Oct-2000 15:36:24	3	3	+1	Reg.	N	4	1	0
31-Oct-2000 15:37:24	3	3	Reg.	Reg.	Y	0	1	5
31-Oct-2000 16:38:24	3	3	Reg.	Reg.	Y	8	10	8
31-Oct-2000 16:40:47	3	3	+1	Reg.	N	10	9	7
31-Oct-2000 16:42:45	3	3	+1	Reg.	N	8	7	0
31-Oct-2000 16:44:31	3	3	Reg.	Reg.	Y	1	1	0
06-Nov-2000 09:59:19	4	3	Reg.	Reg.	Y	2	5	3
06-Nov-2000 10:05:04	4	3	+1	Reg.	N	8	8	6
06-Nov-2000 10:07:23	4	3	Reg.	Reg.	Y	2	0	0
06-Nov-2000 10:09:22	4	5	Reg.	Reg.	Y	0	0	0
06-Nov-2000 10:47:44	4	3	+1	Reg.	N	8	5	9
06-Nov-2000 10:49:39	4	3	+1	Reg.	N	2	0	0
06-Nov-2000 10:51:36	4	3	Reg.	Reg.	Y	2	2	8
06-Nov-2000 10:53:36	4	2	Reg.	Reg.	Y	2	2	0

Table 5.2: *T*-tests on playback bout data.

Test type	Mean difference	<i>t</i>	d.f.	<i>p</i>
<b>SIMPLE DIFFERENCE</b>				(2-tail)
Clan match	-0.16	-0.469	44	0.64
Clan mismatch	0.19	0.580	20	0.57
All	-0.05	-0.183	65	0.86
<b>CO-VARIED DIFFERENCE</b>				(1-tail)
Clan match	-0.11	-0.346	44	0.37
Clan mismatch	-0.11	1.350	20	0.90
All	0.09	0.360	65	0.64



Table 5.3: Sign tests on playback bout data.

Test type	Signed rank	<i>p</i>
SIMPLE DIFFERENCE		(2-tail)
Clan match	9	0.82
Clan mismatch	5	0.58
All	16	1.00
<i>CO-VARIED DIFFERENCE</i>		(1-tail)
Clan match	10	0.50
Clan mismatch	5	0.29
All	15	0.30

Table 5.4: *T*-tests on bout data pooled by group.

Test type	Mean difference	<i>t</i>	d.f.	<i>p</i>
SIMPLE DIFFERENCE				(2-tail)
By groups	-0.39	-1.049	3	0.37
Overall	0.17	0.397	3	0.72
<i>CO-VARIED DIFFERENCE</i>				
By groups	-0.86	-1.874	3	0.16
Overall	0.04	0.405	3	0.64 (1-tail)

Table 5.5: Sign tests on bout data pooled by group.

Test type	Signed rank	<i>p</i>
SIMPLE DIFFERENCE		(2-tail)
By groups	1	1.00
Overall	1	1.00
<i>CO-VARIED DIFFERENCE</i>		
By groups	0	0.25
Overall	1	0.75 (1-tail)

Figure 5.1: Box plots of 'simple difference' by playback bouts

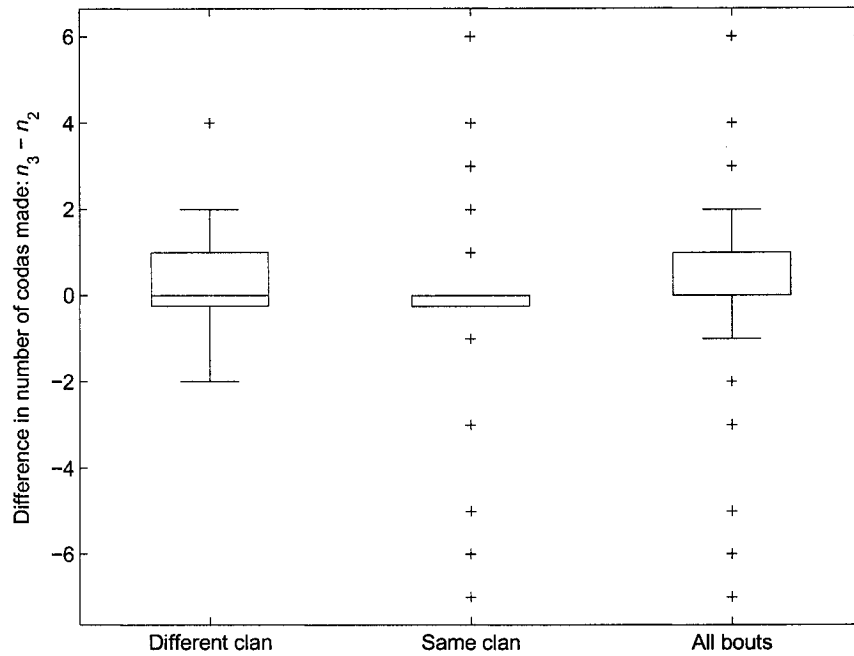


Figure 5.2: Box plots of 'co-varied difference' by playback bouts

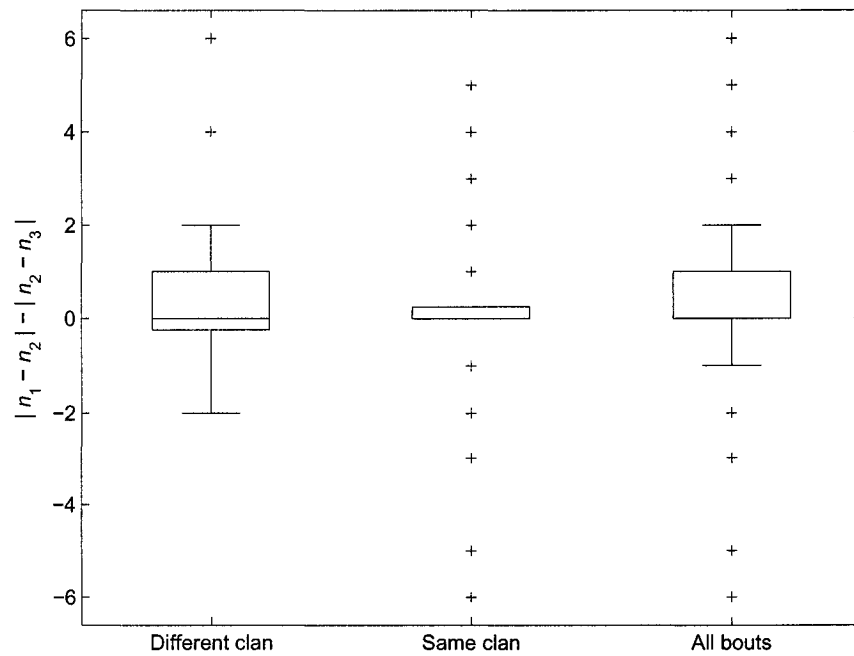
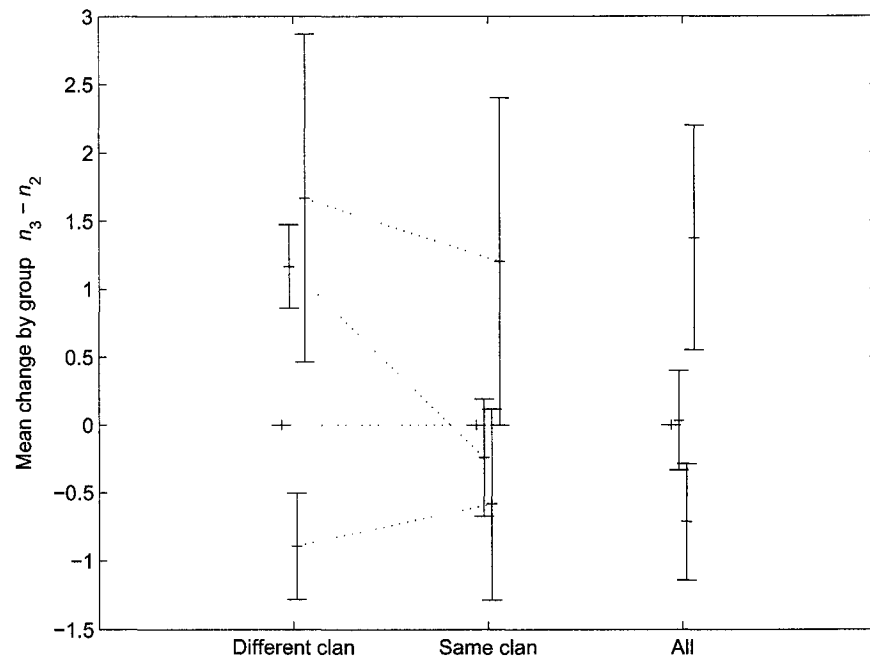
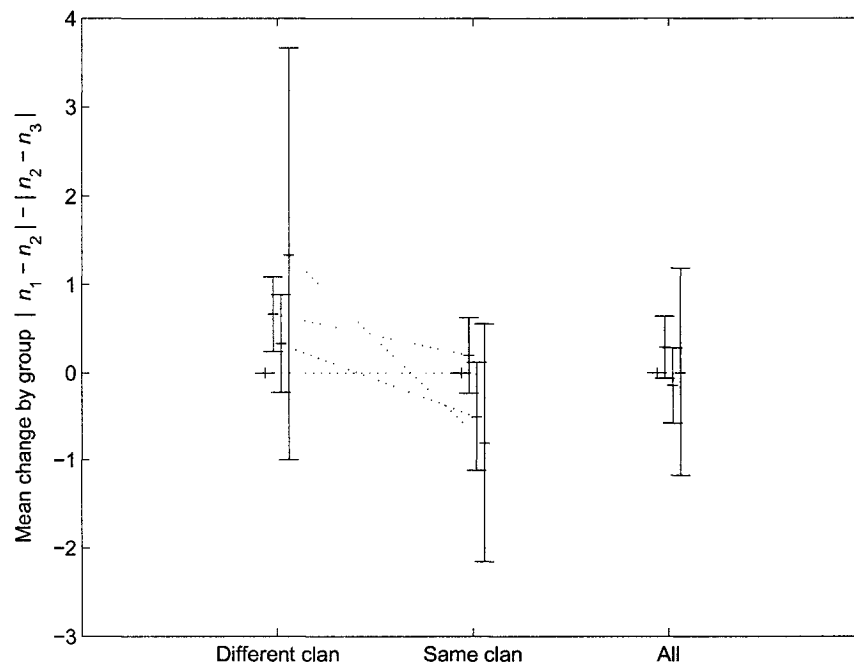


Figure 5.3: 'Simple difference' group means  $\pm 1$  s.e.; lines link group dataFigure 5.4: 'Co-varied difference' group means  $\pm 1$  s.e.; lines link group data

## DISCUSSION

This first attempt at playing back pre-recorded codas to sperm whale groups has produced inconclusive results for the response measures used, namely subsequent coda output by playback focal groups. There was no consistent reaction to coda playback, groups did not consistently cease vocalising, as reported by Watkins (1985) and André *et al.* (1997), nor did they consistently reduce or increase coda production. The study is also generally inconclusive as regards clan playbacks, although I believe this may be due to lack of power in the tests, as there are indications of an effect when codas of the same clan as the focal group were played. For example, playback of same clan codas produced a higher variance in response (Figs 1 & 2) between different playback bouts. This could in future be tested using maximum likelihood estimation on models with a common mean and different variances versus models with common means and common variances, but is not appropriate here because *post-hoc* models are not a sound basis for analysis (Hilborn & Mangel 1997). Potentially interesting is the apparent effect on the group co-varied differences (Figure 4), where three of four groups tested had lower values (indicating stronger responses) when codas of the same clan were played back versus when codas of different clans were played back. The group that showed no change was a group that did not make a single coda during any playback bout. Parametric power analysis based on the *t*-tests showed that the tests had low power (0.26), but also that for the effect sizes observed, power of 0.8 could be achieved with  $n > 11$ ; this is not an unreasonable target. However, the effect is small, and arguably of little biological significance – it is on the order of one or two codas making the difference in each case.

It is difficult to see how these inconclusive results should be interpreted. On the one hand, they could be superficially read as suggesting that sperm whales react very little to codas made by non-group or -unit members and therefore as evidence that codas are primarily used for within-group communication. However, I believe such a view would be over-optimistic as regards the efficacy of the playback procedures used here. In the absence of consistent responses, there remains very little basis for confidence that the focal animals in this study really ‘believed’ (in whatever sense a sperm whale can

‘believe’) that they were hearing other sperm whales. For example, the resonance patterns of the BATS transducer (Jones & Reithmeier 1996) may have led to unrealistic coda clicks. Hence we are still awaiting evidence of coda playbacks being clearly interpreted as other sperm whales as opposed to a novel environmental sound. However, on the other hand, there are indications that codas identifying the same clan as the focal group do produce different responses in terms of the number of codas produced; over bouts, responses had a greater variance, and over groups, responses were generally more marked for same-clan codas. This study cannot report more than a suggestion of an effect, but it is interesting nonetheless, given the current data vacuum.

Clearly larger sample sizes are needed for greater power in testing potential effects, but given that it took approximately 170 days at sea to produce four opportunities for playbacks, there should be no doubting the difficulty of this task; however, this figure is likely to be a worst-case scenario resulting from a study that was constrained by other research goals and encountered worse than expected weather conditions. Similarly this study was not designed with testing clan effects as the primary goal, in which case a protocol leaning more towards sampling more groups with less bouts per group would likely have been more appropriate.

Pseudo-replication is a primary concern in the design of playback studies (Kroodsma 1990), but it is unlikely that this study would have been severely affected by these issues, primarily because of the range of stimuli used to represent each ‘class’ – clan and non-clan. Although the design was not perfectly balanced in terms of stimulus exemplars, each class was represented by nine different coda types (same-clan stimuli coda types : 3R, 2+1, 1+2, 1+2+1, 4R, 5R, 7R, 8RB, 12R, different clan : 2+1, 1+2+1, 3+1, 4R, 5R, 4+1, 5+1, 10R, 12R; note that same coda types can be clan or non-clan depending on the clan of a given target group) such that if the study had found any significant effects it is unlikely they would have been severely compromised by pseudo-replication. Similarly, the observation that sperm whales apparently do not react consistently to coda playback is not restricted to just one coda type, but to a whole range

of types.

It remains only to draw the somewhat disappointing conclusion that we have learned little from this playback study. I remain convinced that such studies will eventually prove crucial in elucidating the function of codas and coda clans, but that we also need further study of coda usage in natural conditions, especially at the individual level, to allow the formulation of more sophisticated hypotheses. Such studies should be designed to take maximum advantage of the relatively few opportunities that are presented during most field seasons, and unlike this one should incorporate some clear test of whether the stimuli are being perceived as other sperm whales rather than environmental noise. This latter surely requires further study of how codas are used so that we might learn what the 'normal' reaction of a sperm whale is upon hearing codas. Thus, it remains the case that the potential for playback experiments to reveal elements of functionality in codas and coda dialects remains largely unexplored.

## CHAPTER SIX

*Geographic variation, temporal stability and within-type variation in sperm whale codas.*

## INTRODUCTION

In many species vocal output varies over time and space. Factors affecting this variation include random genetic drift, random or directional cultural evolution (Deecke *et al.* 2000; Slater 1986), local adaptation to acoustic environments or ecological niches (e.g. Au *et al.* 1985; Barrett-Lennard *et al.* 1996; Daniel & Blumstein 1998; Nottebohm 1972), the need to recognise certain portions of a population, be it single offspring (e.g. Charrier *et al.* 2001), group-mates (e.g. Boughman & Wilkinson 1998), territorial neighbours (e.g. Catchpole & Slater 1995), co-adapted conspecifics (e.g. Grant & Grant 1996) or entire species. Studying the features of variation in any particular case can help us understand which of these factors might be operating; often, levels of variation are important clues in assessing function and the relationship between social vocalisations and social structure (Tyack & Sayigh 1997). In cultural systems, such as suggested for vocal clans in sperm whales, knowing how rapidly those systems evolve is important in evaluating the possibility of cultural traits interacting with the genetic evolution of the species, particularly in the light of current debate over the role of gene-culture co-evolution in reducing mtDNA diversity levels in matrilineal odontocetes, of which the sperm whale is a prime exemplar (Whitehead 1998).

While the description of vocal clans in sperm whales (Chapter 3) considerably improves our knowledge of vocal variation in this species, it concentrates analysis at the level of the clan. In this chapter, my aim is to use the data available to describe patterns of variation *within* clans, over time and space, as well as variation across clans in the structure of vocalisations as opposed to repertoire patterns. I attempt to answer several specific questions about sperm whale vocal dialects that follow naturally from the discovery of vocal clans.

Firstly, I ask whether social units have characteristic repertoires within clans. There is striking variation in coda usage between social units in that each unit can be assigned to a clan (Chapter 3); however, clans are large and geographically diffuse, and



we currently understand sperm whale social structure at smaller scales, units of on average 11-12 females and their offspring (Christal *et al.* 1998). In the most similar vocal system, that of killer whales, the clan is only one level of variation – pods and even matrilineal units also have distinctive repertoires (Ford 1989; Miller & Bain 2000). Thus the question of unit-specific repertoires in sperm whales is important from a comparative perspective – some have drawn potential links between social structure and vocal variation in cetaceans (Tyack & Sayigh 1997), such that we might expect group-living species to have group (or unit) specific repertoires. Also, behavioural evidence that members of foraging groups tend to associate with members of their own unit over members of other units (Christal & Whitehead 2001) suggests that sperm whales can readily identify unit members in a mixed group, so looking for unit-specific repertoires at the sub-clan level also investigates whether there are vocal mechanisms by which individuals can identify their own unit within clans.

Secondly, I look for evidence that coda usage repertoires change over time using recordings of known social units. Stable cultural traits are probably a pre-requisite for significant interaction between cultural and genetic evolution (Laland 1992), and stability is an important cultural feature for this reason. There is also a fascinating range of stability in vocal cultural traits within the Cetacea, with humpback song changing occasionally very rapidly - complete population-level song replacement in ~2 yrs (Noad *et al.* 2000) - and killer whale dialects changing relatively slowly, such that dialects may reflect recent ancestry rather reliably (Barrett-Lennard 2000; Deecke *et al.* 2000). The sperm whale's taxonomic position is in some debate (see e.g. Milinkovitch *et al.* 1993), but in terms of social structure it is much closer to the killer whale (Baird 2000) than the humpback so it is of obvious interest to know where sperm whale vocal behaviour might lie in a comparative analysis.

Thirdly I look for evidence of geographic variation *within* clans. There are many reasons to expect this; in birds adaptation to local acoustic conditions is likely an important determinant of signal structure (Nottebohm 1972; Nottebohm 1975), and

apparently similar variation has been noted in other cetaceans (Ding et al. 1995; Rendell et al. 1999) and is sometimes demonstrably linked to local acoustic conditions (Lesage et al. 1999). This variation may be facultative in the sense that the animal itself can vary vocal parameters in response to varying conditions; in belugas this evidently is the case (Au et al. 1985; Lesage et al. 1999). Geographic variation can also arise through neutral drift in signal structure in relatively isolated populations, arising through either genetic or cultural drift (see e.g. Slater 1986). However, there is at least one cetacean species that maintains highly homogenous patterns of culturally transmitted behaviour over large geographic areas – the humpback (Cerchio et al. 2000). In sperm whales, previous studies of geographic variation in coda repertoire found a weak pattern overlaid and dominated by what we now know to be clan structure (Rendell & Whitehead 2003, Chapter 3; Weilgart & Whitehead 1997). Here I aim to remove the variance in repertoire attributed to clans and look in more detail at geographic variation within clans.

Finally I focus attention on a single coda type. Culturally-transmitted repertoires can evolve in at least two ways (Lynch 1996); *combinatorial*, where repertoire elements, such as syllables, or in this case, codas, are rearranged or used in differing frequencies in vocal bouts, but remain largely structurally identical, and *mutational* change, where the structure of individual signal elements changes, whether through drift or selection. The questions so far outlined deal with the former, but the latter is also relevant. Therefore it is also of interest to look for variation within coda types over time and space. A distinctive aspect of clan dialects in sperm whales compared to killer whales is that some coda types are ubiquitous – all clans share them – whereas in killer whales, only pods within clans share call types (Ford 1991; Yurk et al. 2002). An example that stands out is the 5R coda, consisting of five regularly spaced clicks. This coda type was heard from all units analysed in Chapter 3, and is by far the most numerous type in my sample – it alone accounts for 29% of the 14,065 codas I have assigned to types, over four times as much as the next most common type (1+2, 7%). Further, it was highlighted by Weilgart & Whitehead (1993) as a type that occurred disproportionately often at the beginning of coda exchanges. Therefore I focus on it here and ask whether structural variation within a

single coda type, 5R, mirrors clan level repertoire variation, and look for detectable evidence of change in five-regular codas over time.

## **METHODS**

The acoustic and photo-identification database used in this chapter is identical to that presented in Chapter 3, with codas being assigned to coda type, unit and group as described therein. For brevity I will not repeat these methodological details here, but start with a database of coda inter-click intervals assigned to coda type, social unit and group. I will retain here the meanings of ‘unit’ and ‘group’ used in Chapter 3.

### **Do units have characteristic repertoires within clans?**

I used all recordings that had been assigned to a social unit (at least one member of a unit had to have been identified within 2hrs of the recording start; see Chapter 3) as base data. I calculated pair-wise similarities (using both multivariate similarity and repertoire correlation between usage repertoires as in Chapter 2) between all unit recordings containing more than 25 codas within each clan, and then divided these according to whether the recordings had a unit in common (e.g. A, A2B or J, J&K) or did not. If units have specific repertoires, then recordings with units in common should be more similar than those without. To test this I constructed a similarity matrix between all recordings of units of a given clan, and a 1/0 matrix of equal size that contained 1 if two recordings shared a unit, and 0 if not. I then tested for correlation between the elements of these matrices using Mantel tests (Mantel 1967) within clans, employing the permutation technique with 10,000 permutations (Schnell et al. 1985). If units did have distinctive repertoires within clans, then the expectation is of a significant positive correlation between these matrices.

### **Do unit repertoires change consistently over time?**

I calculated the similarities between the first and last days each unit was recorded (i.e. unit members were photographed within 2 hours of the recording start time, as in Chapter 3), provided 25 or more codas were recorded on both days, using both multivariate

similarities and repertoire correlations. I estimated bootstrap standard errors for these similarities as the standard deviation of the similarities between 1,000 bootstrap resamples of the codas recorded on each day. I then plotted these similarities against the number of days between the first and last recordings. If repertoires are evolving over the timescales for which data are available, such a plot should show a trend with similarity declining over longer time intervals. I calculated the Spearman rank correlation between similarity and days between recordings and performed a linear regression analysis on the same data.

I also calculated ‘trajectories’ for each unit for which 25 or more codas had been recorded on more than one day. For this analysis I compared the repertoire on any given day with the repertoire recorded on the first day, and plotted the similarity between the first and  $n$ th dates against the number of days between the two dates. Each line on the graph thus shows how each unit’s repertoire varied in relation to the repertoire on the first day it was recorded. Again, consistent repertoire change would result in unit ‘trajectories’ that declined steadily over time.

### **Is there evidence of geographic variation *within* clans?**

To look for evidence of geographic variation in vocal output within clans, I first selected all days on which the group recorded had been assigned to a clan (see Chapter 3). Then, within each clan, I calculated the similarities between repertoires recorded on pairs of days having no photo-identified animals in common (to be as sure as possible that different groups were recorded) and the geographic distance between the midday positions on those days. If there were geographic variation within clans then one would expect these data to be related – as distance increases, repertoire similarity should decrease. To test for this, I calculated Spearman rank correlation coefficients for each clan independently, and then performed a one-tailed  $t$ -test assuming that each correlation coefficient was an independent estimate of a single ‘true’ value, to determine the probability that this ‘true’ value was negative.

**Does structural variation within a single coda type, 5R, mirror clan level repertoire variation?**

To view data on 5R codas I plotted by clan the first two principal components (see Chapter 2) calculated from a dataset containing only 5R codas (assigned to clan according to the 'groups' analysis in Chapter 3; only groups assigned to clan were included). I repeated the analyses in Chapter 3 comparing repertoires between units and groups, except I restricted the analyses to just one coda type, 5R. Because of the reduced dataset, I set a minimum of ten 5R codas to have been recorded for the unit to be included (as opposed to 25 for the full analysis). The data-dependence of the clustering was tested using 100 bootstrap resamples, as in Chapter 3.

**Is there detectable evidence of change in five-regular codas over time, and of geographic variation in five-regular codas within clans?**

I repeated the analyses for repertoire evolution but restricted the input data to codas assigned to the 5R class (as assigned in Chapters 2 & 3). In this way I hoped to see whether there was consistent detectable change in the structure of the 5R coda vocalisation over time. Here, because of the restricted dataset the minimum number of codas required for a day to be included was reduced to 10. As in the test for complete repertoire change over time, I calculated the Spearman rank correlation between similarity and days between recordings and performed a linear regression analysis on the same data.

To look for geographic variation in five-regular coda structure, I repeated the geographic analyses within clan as described above but restricted input data to five-regular codas only, and again dropping the minimum coda requirement to 10. As in the full analysis I used a one-tailed *t*-test to determine the probability that the 'true' correlation between distance and similarity was negative.

**RESULTS**

### Do units have characteristic repertoires within clans?

Data were available for 52 recordings on 29 different days, from 19 social units (as per Christal *et al.* 1998) belonging to three clans (Chapter 3). 12 units were from the Regular clan, six from the +1 clan, and a single unit, T (as in Chapter 3), from the Short clan (hence there were no recordings without units in common for this clan). In the other two clans there is an apparent clan effect - +1 similarities are all lower than in Regular clan comparisons (Figures 6.1 & 6.2), although this possibly reflects differing similarity index response to structurally different coda types, namely regular spaced codas and the plus-one variety (see Chapter 2). The differing repertoire similarity measures, multivariate similarity (infinity-norm and Euclidean distance measures produce similar patterns) and repertoire correlation (Chapter 2) give divergent results (Figures 6.1 & 6.2); in the former there is a significant Mantel test result indicating that groups sharing units do tend to have higher similarities, but for the regular clan only, and only when using the multivariate similarity measure (Table 6.1).

Table 6.1: Results of Mantel tests on repertoire similarity and unit presence data, by clan.

Clan	Method:	
	<i>Multivariate similarity</i> ( $b = 0.001$ )	<i>Repertoire correlation</i>
Regular	$r_m = 0.21, p = \mathbf{0.019}$	$r_m = 0.09, p = 0.11$
+1	$r_m = -0.08, p = 0.303$	$r_m = -0.04, p = 0.42$

### Do unit repertoires change consistently over time?

Data were available for 17 days, incorporating codas assigned to 10 different social units from three clans (Regular clan: A, A2B, C, I, J, K, P, +1 clan: F, G, Short clan: T). There was no statistical evidence for consistent unit repertoire changes over time in the timescales for which data were available (up to 2203 days,  $\sim 6$  years; Figures 6.3-6.6) using either multivariate similarity (Infinity-norm,  $b = 0.001$ :  $r_S = -0.04, p = 0.45$ ; Linear regression :  $r^2 = 0.006, F_{1,9} = 0.046, p = 0.84$ ) or repertoire correlation ( $r_S = -0.09, p = 0.40$ ; Linear regression :  $r^2 = 0.004, F_{1,9} = 0.033, p = 0.86$ ). Neither is there a general pattern of decline in unit similarities when tracked over time (Figures 6.4 & 6.6); this result is particularly clear with the plots of usage correlation.

Figure 6.1: Similarities (infinity-norm,  $b = 0.001$ ) between recordings of the same clan that share and do not share units, plotted by clan. Green and red lines indicate mean ( $\pm 1$  s.e.) unit similarities within and between clan respectively (from Chapter 3). Figures in brackets are numbers of recording pairs.

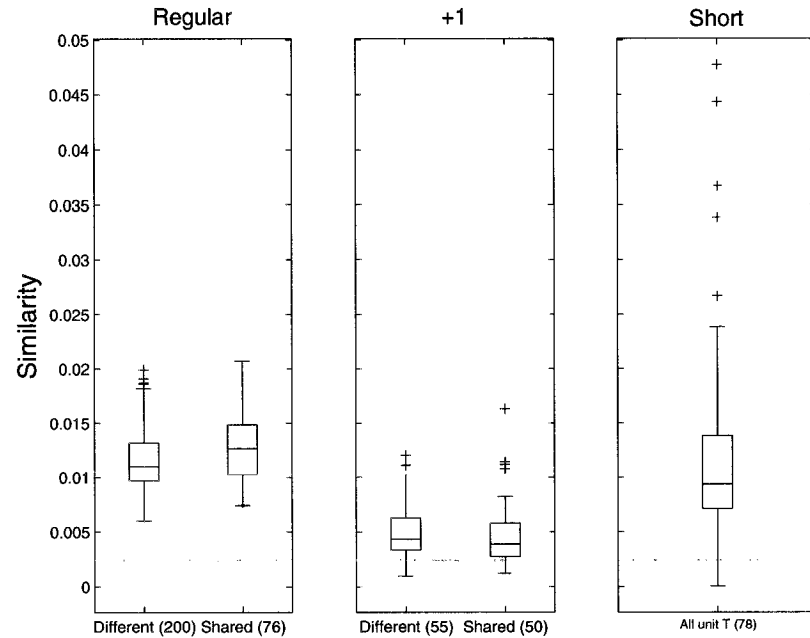


Figure 6.2: Repertoire correlations between recordings of the same clan that share and do not share units, plotted by clan. Green and red lines indicate mean ( $\pm 1$  s.e.) unit correlations within and between clan respectively. Figures in brackets are numbers of recording pairs.

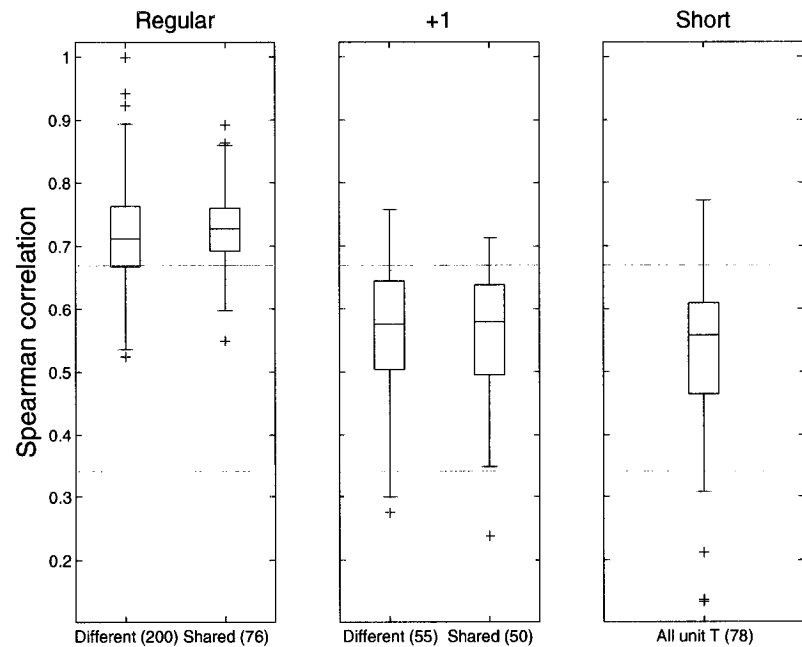


Figure 6.3: Similarities (infinity-norm,  $b = 0.001$ ) between first and last days each unit recorded against the number of days between dates. Error bars are bootstrap standard errors from 1,000 bootstrap resamples; green and red lines indicate mean ( $\pm 1$  s.e.) unit similarities within and between clan respectively.

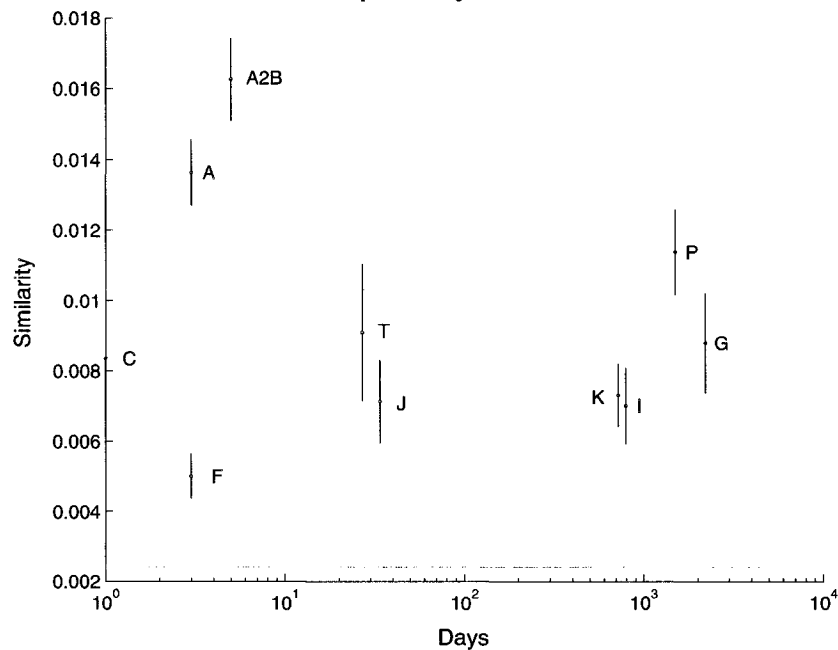


Figure 6.4: Unit similarity 'trajectories' calculated using multivariate similarities (infinity-norm,  $b = 0.001$ ) between repertoires. Error bars are bootstrap standard errors from 1,000 bootstrap resamples; green and red lines are mean similarities as above.

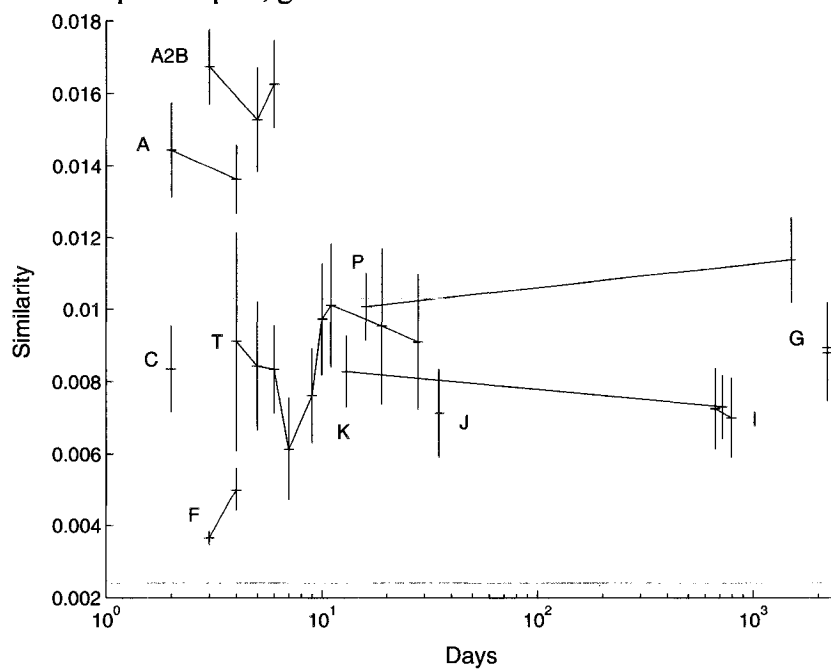




Figure 6.5: Rank correlations between first and last days each unit recorded against the number of days between dates. Error bars are bootstrap standard errors from 1,000 bootstrap resamples; green and red lines are mean similarities as in Figure 6.3.

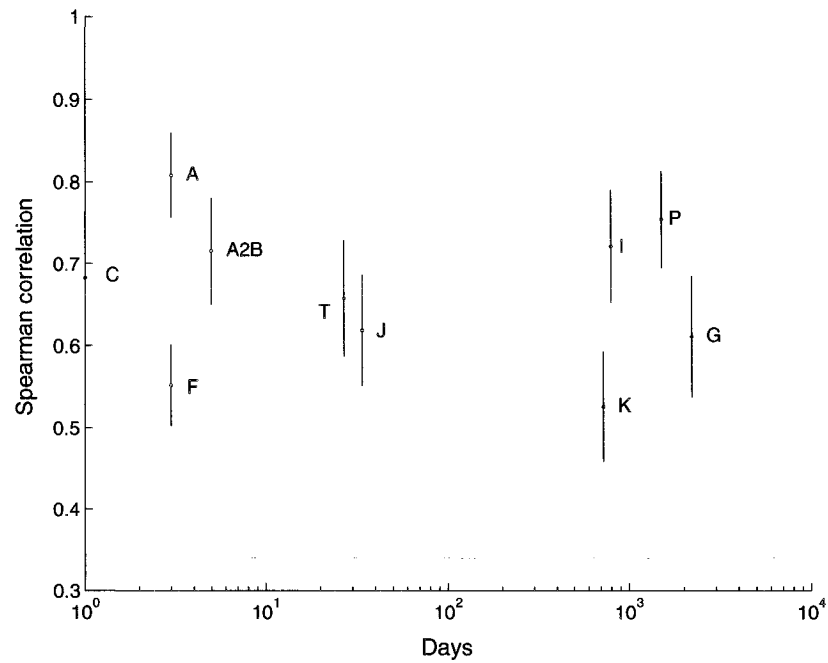
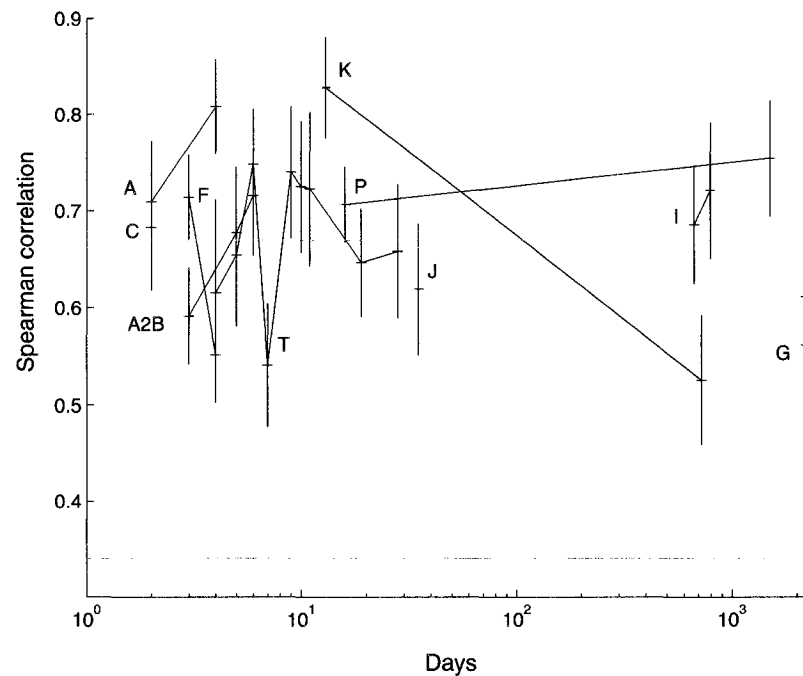


Figure 6.6: Unit similarity 'trajectories' calculated using Spearman rank correlations between repertoires. Error bars are bootstrap standard errors from 1,000 bootstrap resamples; green and red lines are mean similarities as in Figure 6.3.



**Is there evidence of geographic variation *within* clans?**

There is evidence of geographic variation within clans (Figures 6.7 & 6.8) based on data from 87 different days and five clans. Pairs closer than ~100 nautical miles have elevated similarity, but this drops off between 100 and 500 miles. Two of the clans had large negative correlations between distance and similarity - +1 and 4+ - and *t*-tests of the combined geographic distance vs. repertoire similarity correlation values for each clan (Table 6.2) returned significant results for both similarity methods (Multivariate similarity:  $t = -3.7646$ , 3 d.f.,  $p$  (one-tail) = 0.016; Repertoire correlation:  $t = -2.5385$ , 3 d.f.,  $p$  (one-tail) = 0.042).

Table 6.2: Correlations between repertoire similarity measures and geographic distance across groups.

Method:	<i>Multivariate similarity</i> ( $b = 0.001$ )	<i>Repertoire correlation</i>	
Clan	$r_s$	$r_s$	<i>Number of pairs</i>
Regular	-0.14	-0.58	540
+1	-0.33	-0.22	37
Short	-0.17	-0.08	461
4+	-0.45	-0.21	27
ALL	-0.37	-0.58	1066

Assuming the clan coefficients are normally distributed and estimate a common value, the maximum likelihood estimators for the common correlation coefficient are -0.27 (95% C.I. = [-0.41 -0.14]) and -0.27 (95% C.I. = [-0.56 0.02]) for the multivariate similarity and repertoire correlation measures respectively.

Figure 6.7: Similarities (infinity-norm,  $b = 0.001$ ) between repertoires of groups sharing clan but no individuals (according to photo-identification records) plotted pair-wise against geographic distance between midday positions; green and red lines are mean ( $\pm 1$  s.e.) unit similarities, within and between clans respectively. Linear smoother added to illustrate trend.

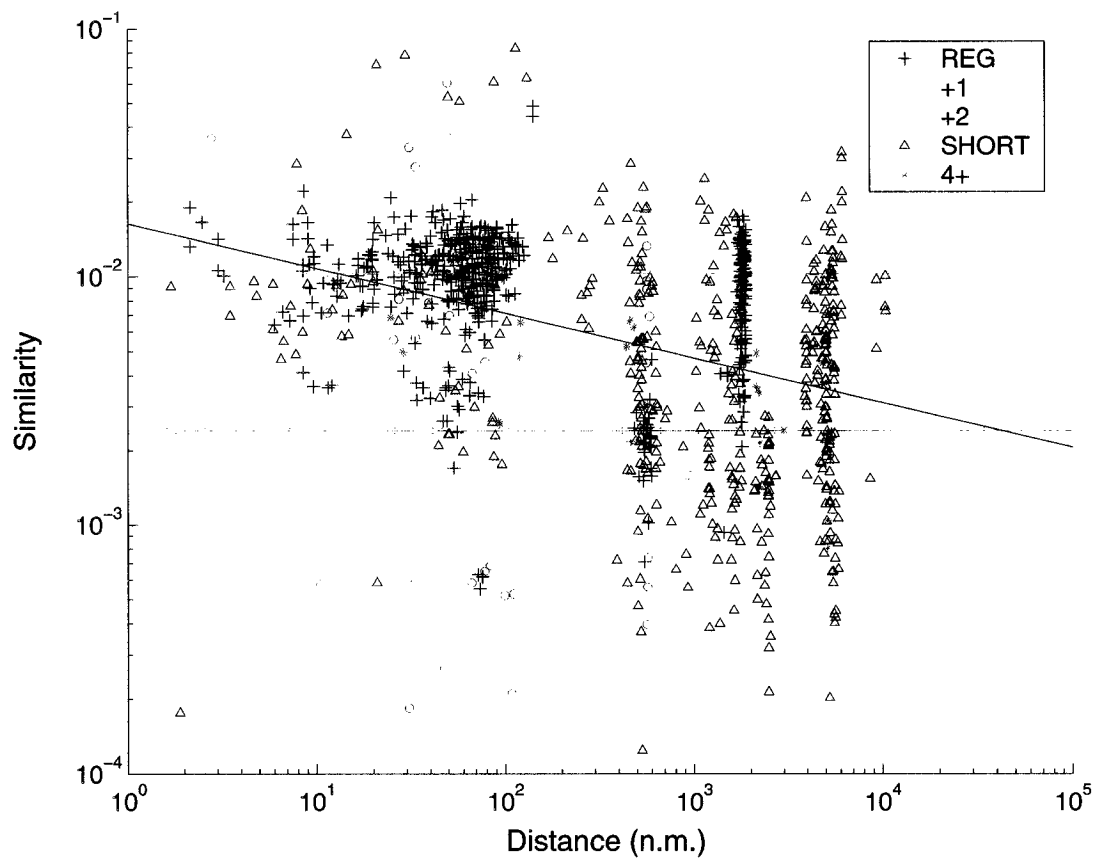
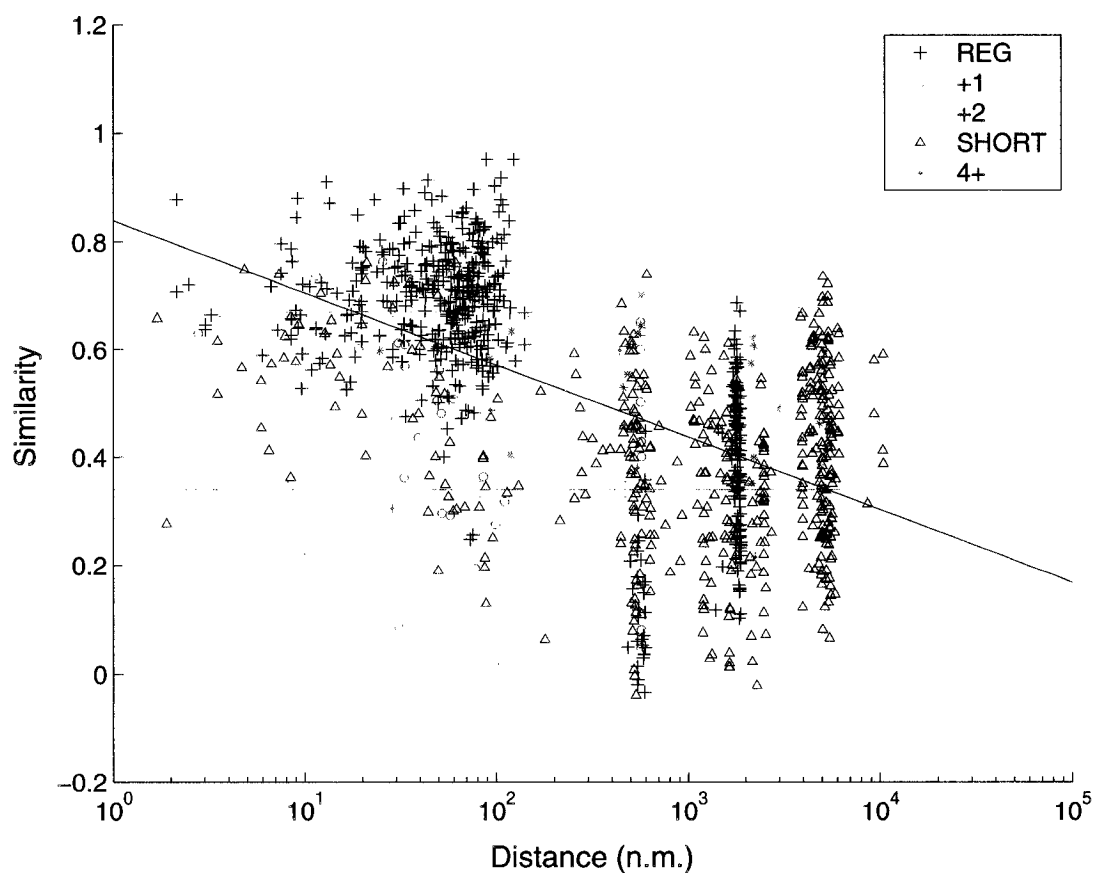


Figure 6.8: Rank correlations between repertoires of groups sharing clan but no individuals (according to photo-identification records) plotted pair-wise against geographic distance between midday positions; green and red lines are mean ( $\pm 1$  s.e.) unit similarities, within and between clans respectively. Linear smoother added to illustrate trend.



**Does structural variation within a single coda type, 5R, mirror clan level repertoire variation?**

Sufficient data were available for 15 units and 30 groups, originally assigned to three clans. There is evidence that different clans make 5R codas in different ways, although there is considerable overlap between clans in the elements of coda structure we have measured here (Figure 6.9). The dendrograms reproduce clan structure well at the level of unit, with bootstrap support values high at the clan defining nodes (Figure 6.10); at the group level, clans *tend* to cluster together, but the overall analysis does not reproduce clan structure as well (Figure 6.11).

Figure 6.9: Principal components 1 and 2 of all 5R codas assigned to clan, plotted by clan. First two principal components are shown, accounting for 77% of the variation present in the original data.

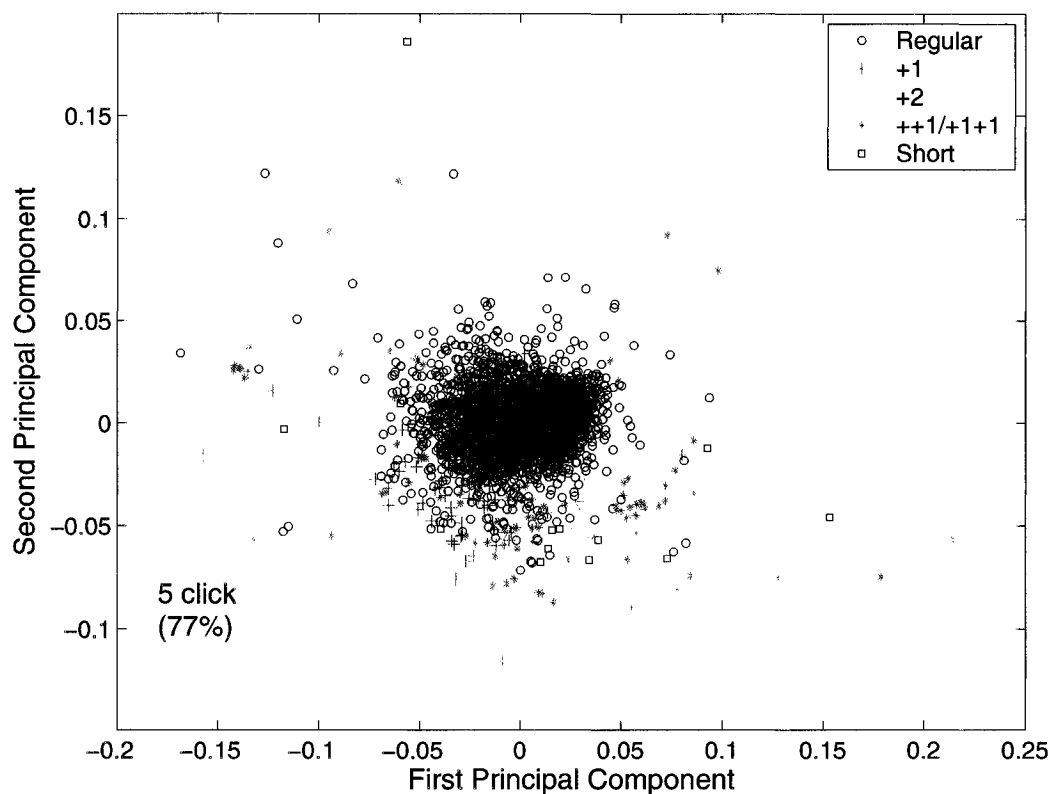


Figure 6.10: Dendrogram of similarities between units based on 5R codas only. Numbers beside branches show how many times in 100 bootstrap resamples that branch was reproduced with the same units as the real data. Node data indicates clan (REG = Regular, SHO = Short), and bracketed are unit name and number of codas recorded from that unit.

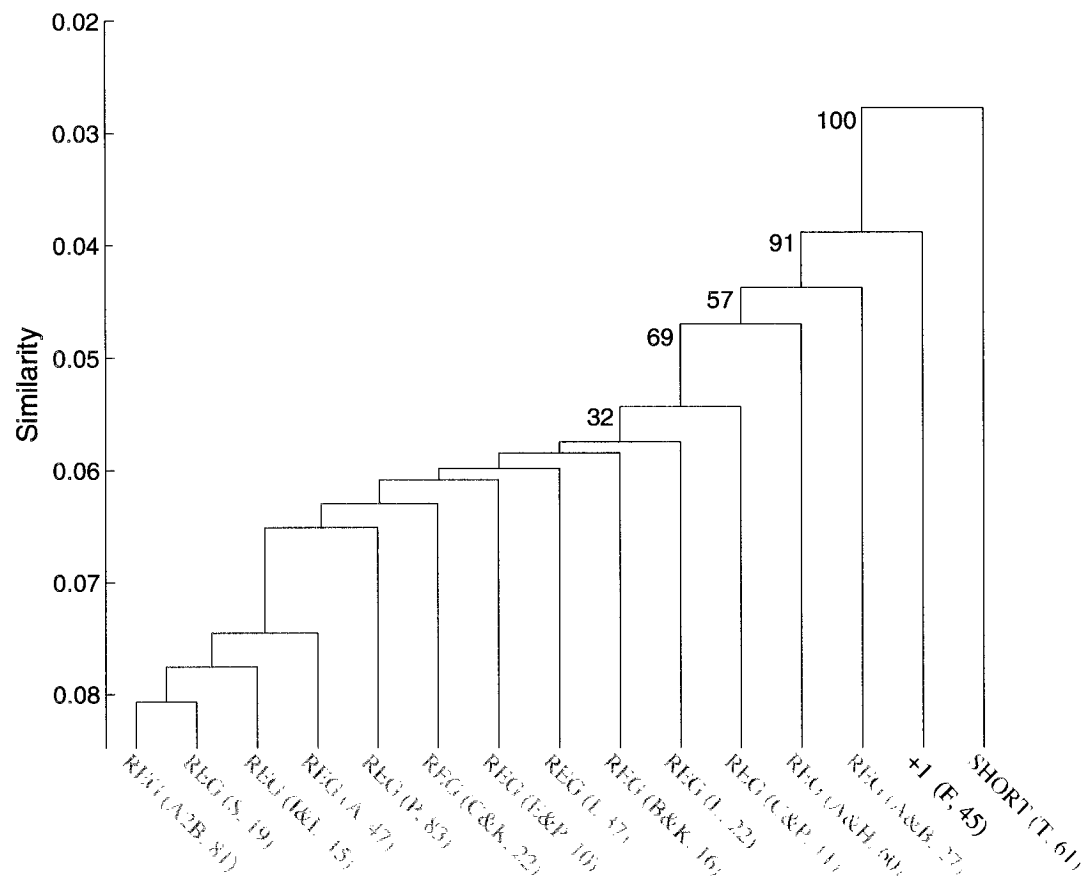
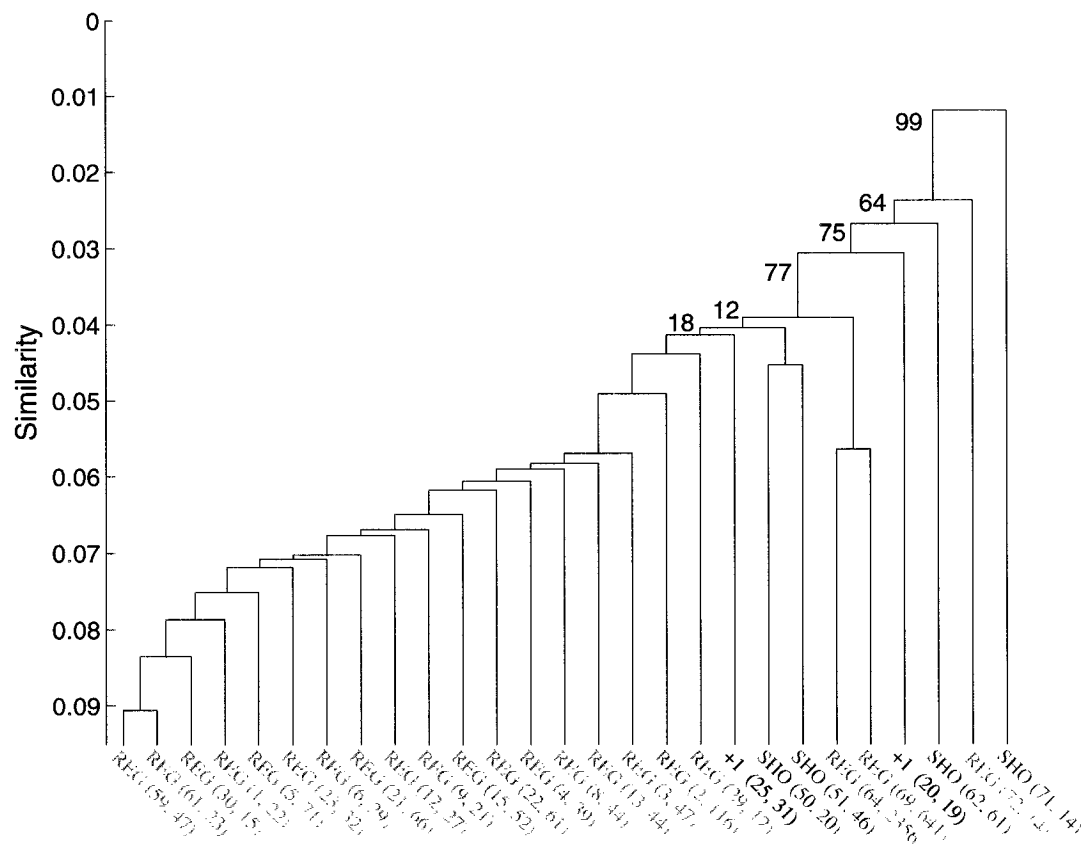


Figure 6.11: Dendrogram of similarities between groups based on 5R codas only. Numbers beside branches show how many times in 100 bootstrap resamples that branch was reproduced with the same units as the real data. Node data indicates clan (REG = Regular, SHO = Short), and bracketed figures are group code and number of codas recorded from that group.



**Is there detectable evidence of change in five-regular codas over time, and of geographic variation in five-regular codas within clans?**

There was little obvious change in 5R codas over time (Figure 6.12 & 6.13) based on data from eight units recorded on 14 different days, over a maximum timescale of 1497 days, ~4 years, although all the unit trajectories available showed decreases in similarity (Figure 6.13). However, there was no statistical evidence of systematic changes in the structure of 5R codas within units over time whether from correlation (Infinity-norm,  $b = 0.001$ ,  $r_s = -0.07$ ,  $p = 0.43$ ) or a linear regression model ( $r^2 = 0.141$ ,  $F_{1,11} = 2.139$ ,  $p = 0.17$ ).

I did find some evidence for geographic variation in 5R codas, paralleling that found in the same analysis on overall repertoires, based on data from 40 days and three clans. Two of the clans had large negative correlations between distance and similarity (Table 6.3), and a  $t$ -test on clan correlation coefficients against mean of zero returned a marginally significant result ( $0.10 > p > 0.05$ ):  $t = -2.1257$ , 2 d.f.,  $p = 0.084$ .

Table 6.3: Correlations between multivariate similarity (infinity norm,  $b = 0.001$ ) and geographic distance across groups.

<b>Clan</b>	$r_s$	<i>Number of pairs</i>
Regular	-0.47	430
Short	-0.02	14
4+	-0.5	3
ALL	-0.50	447



Figure 6.12: Similarities (infinity-norm,  $b = 0.001$ ) between first and last days each unit recorded against the number of days between dates, for 5R codas only. Error bars are bootstrap standard errors from 1,000 bootstrap resamples; green and red lines are mean ( $\pm 1$  s.e.) unit similarities, restricted to 5R codas, within and between clans respectively.

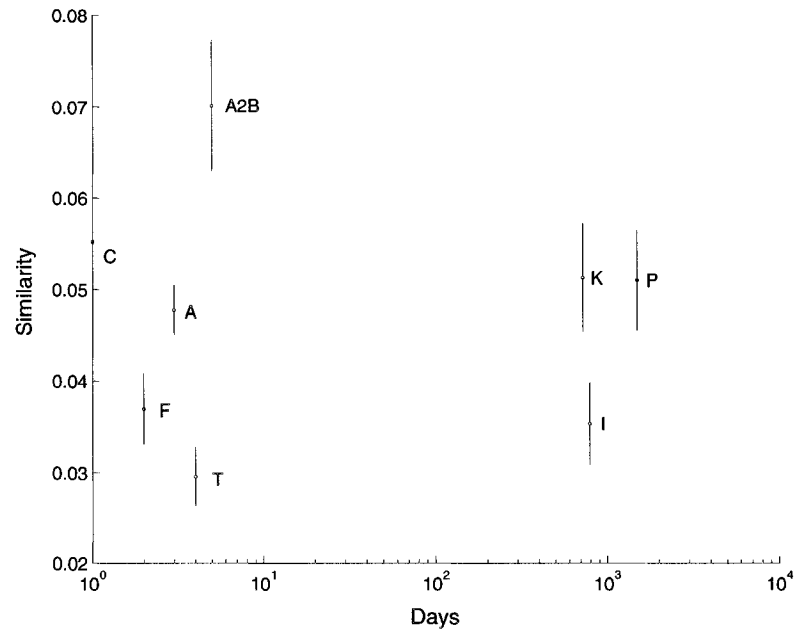


Figure 6.13: Unit similarity 'trajectories' calculated using multivariate similarities (infinity-norm,  $b = 0.001$ ) between repertoires, for 5R codas only. Error bars are bootstrap standard errors from 1,000 bootstrap resamples; green and red lines are mean similarities as in Figure 6.12.

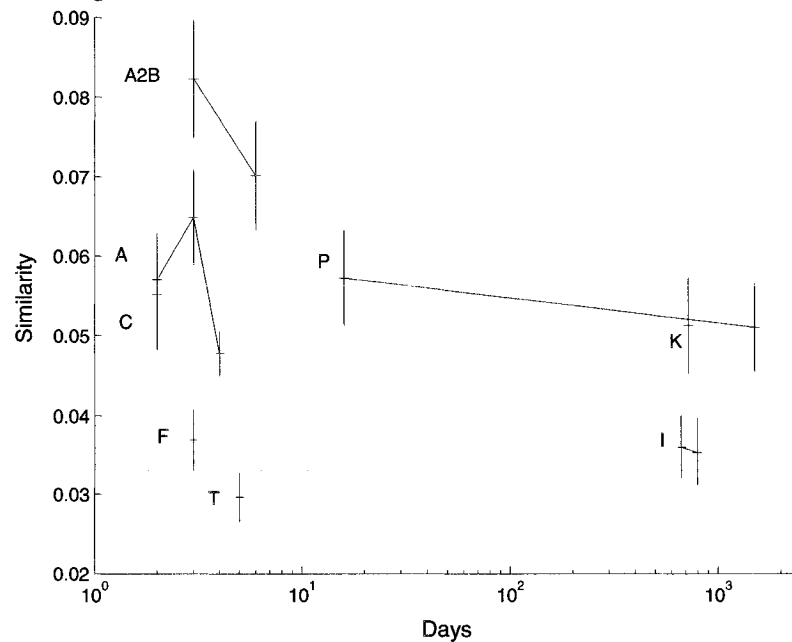
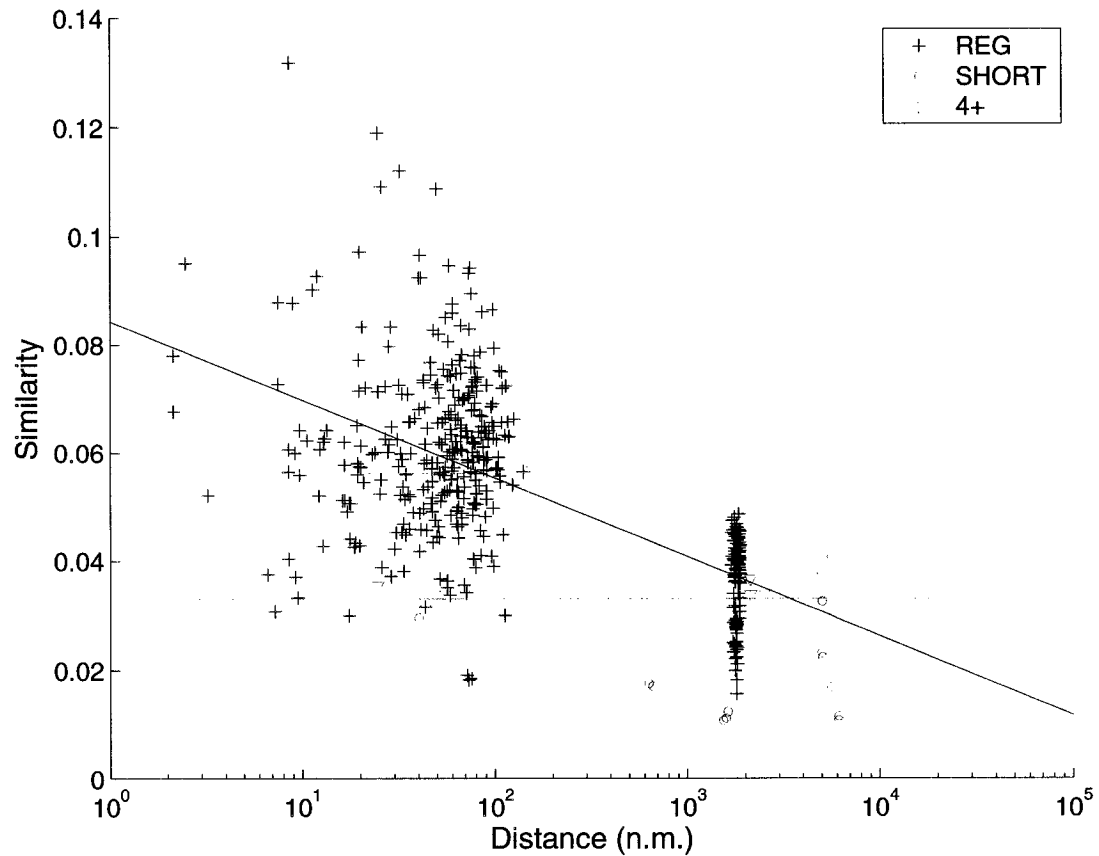


Figure 6.14: Similarities (infinity-norm,  $b = 0.001$ ) between repertoires, restricted to 5R codas, of groups sharing clan but no individuals (according to photo-identification records) plotted pair-wise against geographic distance between midday positions; green and red lines are mean ( $\pm 1$  s.e.) unit similarities, within and between clans respectively. Linear smoother added to illustrate trend.



## DISCUSSION

The most significant findings of this chapter are in the analysis of geographic variation within clans, which produced evidence that groups within the same clan have elevated repertoire similarities up to ranges of ~3-500 n.m., even though they have no individual animals in common, and the finding that clans make a certain coda type – 5R – in distinctive ways.

I found little evidence that units have characteristic repertoires within clans, at

least in terms of the timing of clicks within codas, and that which did emerge was of only a small effect relative to that of the clan. If Tyack & Sayigh's (1997) suggested relationship between social structure and vocal variation in cetaceans holds, it suggests that the clan may in fact be the primary level of social structure in sperm whales. Alternatively, it may suggest that we need data for more than three or four of the ~80 cetacean species before we can fully appreciate such comparative perspectives, since a *prima facie* reading of these social-vocal links would suggest that sperm whales, living in social units (Christal *et al.* 1998), might be expected to have unit-specific repertoires. This result also marks a further point of contrast with the similar killer whale clan dialect system; in killer whales, pods within clans have distinctive, although not exclusive, repertoires (Ford 1991). One implication is that the mechanism sperm whales use to recognise unit members is *not* vocal (unless of course it depends on some vocal characteristics not so far measured), unless there is important variation at the individual level; the latter issue urgently requires investigation.

Neither did I find any evidence that unit repertoires change consistently over time. However, an important caveat to this result is that data are only available for a very limited timescale relative to the lifespan of a sperm whale. The maximum time between recordings in this analysis was ~6 years (Unit G; Figures 6.3 & 6.5), one tenth of a female sperm whales lifespan of ~60 years (Rice 1989). Hence while the best data available on this question tells us that repertoires are essentially stable over periods of ~6 years, we remain ignorant of rates of change over longer, and arguably more relevant, timescales. Still, these data provide an important foundation to investigate this issue further in the future; for comparison, Deecke *et al.* (2000) used a dataset spanning 12 years to detect fine scale structural evolution of discrete calls in killer whales, although these calls remain easily recognisable over periods of >30 years (Ford 1991). More longitudinal data are the only remedy for our ignorance in this case.

I did however find good evidence of geographic variation within clans, with groups of the same clan that shared no individuals having markedly higher repertoire

similarities at ranges of <300 n.m. (Figures 6.7 & 6.8). This result is in accordance with previous studies that found some evidence of geographic variation, albeit weak relative to clan variation (Weilgart & Whitehead 1997), although the present study is novel in that it can separate geographic effects due to varying clan distributions and those that occur within clans. This variation could occur in two ways – animals staying in one area and developing local vocal patterns (as in geographically based bird song dialects), or animals moving into a given area adopting the vocal patterns of that area, perhaps in response to local ecological conditions, in the light of some cetaceans species ability to facultatively adjust vocal parameters (Au *et al.* 1985); in mobile species like cetaceans either is possible. Female sperm whales are known to range over thousands of nautical miles (Jaquet *et al.* in press), but the average displacement over periods of ~5yrs is nearer 400 n.m. (Whitehead 2001a) – this latter distance matches the distance below which repertoire similarities are elevated (Figures 6.7 & 6.8), although the extent to which large scale movements (i.e. >1,000n.m.) are a regular occurrence for individual sperm whales is still largely unknown (e.g. Dufault & Whitehead 1995). Because of these potential movements, I cannot differentiate between the possibility that the observed variation represents some form of geographic within-clan ‘accent’ and the possibility that the variations described here represent coda output being altered according to local conditions, ecological, physical or otherwise: do individual sperm whales off Chile always sound the same wherever they are, or do they sound different if they are off, say, Ecuador? Given the apparent stability of unit repertoires (Chapter 3, Figures 6.3-6.6) the former seems more likely. Whether local ‘accents’ are permanent or facultative, I consider this geographic variation unlikely to take the form of direct acoustic adaptation to local sound propagation conditions, referred to as ‘habitat matching’ in birds (Catchpole & Slater 1995), given the structural homogeneity of the sperm whale’s deep ocean habitat. Autocorrelation in oceanic ecosystems breaks down on the order of 500km (~260 n.m) according to fisheries data analysed by Myers *et al.* (1997), and it is notable that the elevated repertoire similarities in Figures 6.7 & 6.8 also fall within this range. At lower trophic levels oceans can be divided into bio-geographic ‘provinces’ with distinct primary production properties (Platt & Sathyendranath 1999; Sathyendranath *et al.* 1995);

in the Atlantic, these can be ~1,000 n.m. across (Sathyendranath *et al.* 1995), larger than the average ranges of sperm whales (Whitehead 2003a); while I am aware of no such similar formal partition of the Pacific ocean - although a biome level approach was taken by Longhurst (1998) - and we remain ignorant of the relationships between primary productivity, fish populations, and cephalopod ecological dynamics, it seems that geographic variation of coda repertoires is broadly congruent with what we know of the spatial structure of ocean systems. An interesting future study would relate repertoire variation within a group of known animals (e.g. unit T; Chapter 3) to concurrent ecologically relevant data such as defecation rate and scattering layers, and with physical oceanographic parameters – if vocal patterns change according to local conditions, this should also be detectable longitudinally. However, a pattern of local ‘accents’ would be closer to what is observed in other cetacean species (see e.g. Ding *et al.* 1995); we need to know more about sperm whale movements to clarify this issue – there will be an upper limit to the rate of permanent range shifts for geographic variation to become established.

Repeating the clan level analysis of Chapter 3 on a single coda type, 5R, produced interesting results. There are structural differences in this coda type as made by different clans (Figures 6.9), such that codas from units of the same clan cluster together (Figure 6.10), and at the group level, codas from groups of the same clan *tend* to cluster together (Figure 6.11). However, there is considerable overlap within this, such that within-5R variation is unlikely to be sufficiently reliable to allow clan identification, and therefore I suggest that this variation is most likely due to random drift through within-clan cultural processes (Slater 2001) rather than a functionally driven feature, although there may be other acoustic cues undocumented here that do lend a unique clan ‘accent’ to each coda type, and that sperm whales can use to pick up clan identity cues. Random drift likely operates over time-scales far greater than the data currently available to us, since the analyses of temporal change in the 5R coda type over ~3 years returned little evidence for systematic change. This latter result comes with an important caveat – data here are sparse, and more is needed before a robust negative conclusion can be drawn. In addition, insight would be greatly improved were we able to remove individual level variation in

5R coda production from this analysis; such data require new field techniques to assign codas to individuals, such as multi-element localising hydrophone arrays (Møhl et al. 2001). The analysis of geographic variation in 5R codas showed a similar pattern to that of the overall repertoire analysis, suggesting that the structure of single coda types is also subject to geographic variation; this is harder to explain by facultative responses to local ecological conditions than type usage variation, since it is very difficult to envisage ecological factors that could lead to subtle variations in click timing such as represented here. It is easy however to envisage that drift in isolation could produce such within-type variation, as in geographic variation in birdsong (e.g. Catchpole & Slater 1995).

## **CHAPTER SEVEN**

### ***General Discussion***

Here I summarise the key findings of this thesis, and outline what I see as the priorities for future research. I also defend a broad comparative approach to the study of culture in animals, and to this end briefly compare what we know of culture in other taxa. When comparing sperm whale and primate culture, I also discuss some key elements of anthropological notions of culture such as symbolism, meaning and identity, and how they related to my findings. I conclude with an optimistic outlook for a cultural cetology.

### **KEY RESULTS AND FUTURE RESEARCH DIRECTIONS**

In Chapter 1 I summarised the evidence for culture in cetaceans, and concluded that some cetacean species do have culture under the definition adopted. This suggestion is a point of controversy in the ongoing interdisciplinary debate on non-human culture (see commentaries on Rendell & Whitehead 2001). A middle ground position in the spectrum of responses to this position is summarised by Dunbar (2001):

*Rendell and Whitehead provide a convincing case for the claim that whatever it is that can be classed as culture in primates (notably great apes) must necessarily apply to cetaceans.*

Thus there is little doubt that cetaceans have a previously under-appreciated but important place in this ongoing debate. I continue to believe that our increased understanding of culture in non-humans, and humans too, depends critically on continuing this type of exchange and on a broad-based, comparative study of cultural processes across many taxa, including birds (West et al. 2003), bats (Boughman 1998) and primates (Whiten *et al.* 1999).

Coda data are challenging to visualize and analyse. One especially vexing issue is whether to characterize repertoires as continuous gradients (Murray *et al.* 1998; Taruski 1979) or as categorical entities, as used for example in studies of killer whale discrete calls (Ford 1989), or bottlenose dolphin signature whistles (Caldwell et al. 1990). Given this uncertainty, the most secure way forward must then be to take a multiple methods approach, as I have attempted in Chapter 2, using both continuous measures and



classification based approaches. This broader methodological approach is also being employed in recent studies of killer whales and bottlenose dolphin vocal patterns (Deecke *et al.* 2000; McCowan & Reiss 2001).

Previously, some have also queried the existence of stable, culturally transmitted vocal dialects in sperm whales, since the groups recorded were unstable, being temporary aggregations of long-term social units (Christal *et al.* 1998). How can these unstable groups support stable cultural variants (Mesnick 2001; Tyack 2001)? They can if the primary level of cultural vocal variation is the clan structure I described in Chapter 3. The discovery and description of sperm whale vocal clans is perhaps the most important contribution of this thesis; I have described sympatric vocal variation on an oceanic scale, unique outside humans. If there are indeed only five clans in the South Pacific (Chapter 3), then each must contain on the order of ~10,000 individuals<sup>1</sup>. These results raise the fascinating possibility that sperm whale populations are structured primarily along cultural lines, and have potentially profound consequences for our understanding and management of these populations. Inevitably, these results also raise many more questions than they answer, and point the way to fascinating questions about sperm whale social structure, population structure and culture. We still do not understand the genetic relationships between the clans, and hence whether clans are important factors in genetic population structure; the gene-dialect question has occupied ornithologists for decades (Baker & Cunningham 1985) and unravelling the relationship in sperm whales will be a challenge, requiring cooperation between research groups.

One important question is whether clans are distinct enough to be considered management units. They are certainly not monophyletic, but to what extent are they differentiated, and could they act as rides for neutral mtDNA hitchhikers (as in Whitehead 1998)? Studies of birds have shown that dialect structure can be associated

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1. As the global sperm whale population is about 360,000 (Whitehead 2002), of which perhaps one quarter (90,000) are in the South Pacific, which contains 5 clans, this may be a conservative estimate that also assumes clans to be of roughly equal numerical size.

with population structure (e.g. MacDougall-Shackleton & MacDougall-Shackleton 2001), and we need to know whether the same is true of sperm whales. We also need to know if there are any other aspects of sperm whale behaviour that vary along clan lines – for example, foraging is one area of behaviour that appears regularly in social learning literature (Boesch *et al.* 1994; Lee & Moss 1999; Lefebvre & Palameta 1988; Mann & Sargeant 2003; Weinrich *et al.* 1992; Wilkinson & Boughman 1999) – do sperm whale clans have distinctive foraging behaviour? There is some evidence that they do (Whitehead & Rendell in review), and if they do, this would lend credence to Whitehead's (1998) 'cultural hitch-hiking' hypothesis. Another important question is whether clan structure is unique to the Pacific, or whether it is ubiquitous in sperm whales, since not all segments of cetacean populations have similar vocal or social patterns (see e.g. Baird 2000); only longitudinal studies in other geographic areas can answer this. Finally, what are clans for? Do they have a biological function, or are they epiphenomena, adaptively neutral, the result of neutral drift processes (Slater 1986; Slater 2001)? Do clans form social barriers, as in human dialect groups, mating barriers, as in killer whales (Barrett-Lennard 2000), or do sperm whales see all clans as the same colour? Answers to these last questions will be hard won; detailed observations of coda interactions, preferably at the level of individual, and playback experiments are the most likely routes to success.

In documenting group-specific vocal patterns, care is necessary to ensure that vocal output ascribed to the group really is a group attribute rather than, for example, the output of one dominant individual. For this reason, some have voiced concern about descriptions of group variation in vocal output in sperm whales, specifically group-specific coda usage repertoires (as in Weilgart & Whitehead 1997), and their interpretation as the result of cultural transmission (by Rendell & Whitehead 2001; Weilgart & Whitehead 1997; Whitehead *et al.* 1998), based on a restrictive limitation of that data (Freeberg 2001; Tyack 2001): Recording sperm whales on one hydrophone does not allow the attribution of single codas to the individual whales, so we cannot know how much variance in output can be attributed to that individual level. The inter-pulse-interval

(IPI) in sperm whale clicks - apparently a stronger signal in coda clicks than 'usual', probably echolocation, clicks (Madsen 2002) - and its relation to body size provide a partial solution to this problem in Chapter 4. The data here, though limited to one unit, are inconsistent with the idea that one or two whales in unit T (nine animals) dominated the recordings of that unit. However, the picture provided is limited – it cannot differentiate between similar sized individuals. Hence ongoing efforts and successes to record sperm whale vocalisations at the individual level (Møhl *et al.* 2001) are important, and the application of these techniques to socialising sperm whale groups is likely to lead to a rich vein of data.

I was unable to find any evidence for differential response to codas from different clans during a playback study, as reported in Chapter 5. However, the study was limited in power, and based on a fairly simplistic hypothesis – that repetition of any 'clan defining' coda type (e.g. 4R, 5R, 6R for Regular, 4+1, 3+1 for +1) would be a signal of clan membership. This is simplistic because we know that coda types are widely shared across clans, and it is the *usage patterns* of those types that provides the clan signal detected in Chapter 3. Hence we need more understanding of how this clan signal is built up over coda bouts – are the 'clan defining' codas heard together, and if so where, or are they randomly distributed in a bout. Again, individual level studies of social vocalisation periods will likely be essential in understanding this, and in developing more elegant playback hypotheses (e.g. Deecke *et al.* 2002). In Chapter 3 I suggested that vocal clans may serve as barriers to altruism within sperm whale groups, since within-group altruism seems to be crucial to sperm whales in communal defence (Pitman *et al.* 2001) and care of young (Whitehead 1996a). One problem with this suggestions is that group badges in such a system should, in theory, be somehow costly to acquire, since only then would signals be honest and so evolutionarily stable – the 'handicap principle' (Grafen 1990; Zahavi 1975). However, sperm whale clans clearly share coda types (Chapter 3; Figure 3.1 & 3.2), so how can a clan-specific signal be costly to acquire in such circumstances? It could be that other features – such as within-type 'accents' (Chapter 6), which might require more exposure to acquire, or other parameters not measured here – are also

important in perception of clan membership.

Another potential problem is that sperm whale vocal variation does not fit with current expectations for signals important in mediating altruism. These expectations currently focus on signals that either (i) give cues to kinship, under kin-selection for altruism (e.g. Beecher 1982) or (ii) give cues to individual identity, for individual-level monitoring of social interactions (e.g. Janik 1999a), but (i) there are significant numbers of non-kin in sperm whale social groups (Christal 1998; Mesnick 2001; Mesnick *et al.* 2003) and (ii) there is little evidence of preferred dyadic relationships within units (Christal & Whitehead 2001), but there is evidence of widespread coda type sharing (Chapter 4; Moore *et al.* 1993), which would limit individual level recognition, leaving us with a conundrum. Alternatively, there is clearly a relationship between culture and altruism in human affairs, both in the sense of altruistic norms being culturally determined and also of altruism, or social commitment, being available principally to those of the same linguistic or dialectal group (Ehrlich 2000; Milroy 1987; Nettle 1999; Wilson 1978), an element of cultural group-selection (Boyd & Richerson 1985). Rendell & Whitehead (2001) have suggested that cultural group-selection may also be acting in cetaceans. If clans are indeed boundaries to altruism, then vocal dialects in sperm whales would directly parallel the human variety, but not current models of animal signal evolution.

In Chapter 6 I explored the characteristics of the clan dialect system in more detail, and also expanded the scope of my analysis to the level of an individual repertoire element (the 5R coda type). Firstly, I found little evidence of unit-specific dialects in coda repertoires, a surprising result that apparently requires that we re-assess either (i) our understanding of the relationship between social structure and vocal variation in cetaceans (Tyack & Sayigh 1997) or (ii) our understanding of what the primary sperm whale social element is. Before such drastic measures, however, this result should be explored by measuring other aspects of coda production, which may yet reveal unit-specific cues undetected here. Perhaps differentiating social units requires extensive

experience of the local social environment, as in elephants (McComb et al. 2001). Secondly I found no evidence of dialect change over time, but data were only available for timescales that are short compared to the lifespan of female sperm whales, such that while I can say that repertoires do not change *very* rapidly, the stability of coda dialects over longer timescales remains as inference, albeit strong inference (Whitehead *et al.* 1998). Thirdly, I did find geographic variation in coda repertoire within clans, suggesting some kind of local effect; this could be either genetic or cultural, and selected or the result of neutral drift. Given the existing evidence that coda repertoire is culturally acquired (Chapter 3; Whitehead *et al.* 1998), and the lack of plausible selective mechanisms that would favour say a 5R coda over a 4+1, I suggest that these patterns are not genetically based, but the result of neutral cultural drift (Slater 2001). This pattern of vocal variation is thus likely indicative of underlying population structure, especially since it fits well with what is known of sperm whale movements (Jaquet *et al.* in press; Whitehead 2001a). However, we still need to know more about the movements of individuals and within-ocean genetic variation before we can understand how this vocal pattern reflects other forms of population structure and any implications for management, and also whether these geographic variations may have functional roles for sperm whale social interactions, since variation between animals that never meet is unlikely to have such a role (Searcy et al. 2002). Finally, I found that there is also variation within a single coda type – 5R, the most common – that broadly reflects the patterns found by comparing entire repertoires. This shows that there is both structural and combinatorial (Lynch 1996) variation in sperm whale vocal output.

### **SPERM WHALE CULTURE: A COMPARATIVE PERSPECTIVE**

I believe that a broad comparative approach to the study of culture will prove to be the most productive in terms of understanding the forces affecting the evolution of and ecological correlations with both cultural transmission itself and the cultures that are transmitted (Box & Gibson 1999; Boyd & Richerson 1996; Lefebvre & Palameta 1988). I therefore conclude by comparing what I have found in sperm whales with related phenomena in other cetaceans, birds, bats, elephants and primates, including humans; I

do not pretend to be exhaustive, but rather provide an outline sketch of how phenomena compare across taxa.

### **Sperm whales and the diversity of cetacean culture**

I discussed what is known of cetacean cultural diversity in Chapter 1, and it is clear that there is much work still to be done before we can adequately describe this diversity. Hence there are only three species that I can discuss here – the humpback whale, the bottlenose dolphin and the killer whale.

It is clear that there are important differences between humpback and sperm whale vocal cultures; humpback song is characterised by cultural evolution in isolation (Cerchio *et al.* 2000), with all animals in a given breeding population maintaining a homogeneous song, hence sympatric cultural variants are not present. Indeed, when different cultural variants do encounter each other, the results are a dramatic increase in the rate of cultural change, but not the sympatric co-existence of cultural variants (Noad *et al.* 2000). Humpback vocal culture has low stability, relative to that observed (Chapter 6) or inferred (Whitehead *et al.* 1998) in sperm whales. Pronounced annual migrations and an apparent lack of long-term social bonds (Clapham 2000; but see Sharpe *et al.* 2001) are features of humpback life that contrast sharply with sperm whales.

Studies of social learning in bottlenose dolphins have concentrated on individual ‘signature’ whistles (Caldwell *et al.* 1990) at the individual level, and so the study of behaviour shared by more than one animal such as characterises culture has been under-emphasised. Still, these animals are clearly excellent social learners and likely acquire a large proportion of their life skills in this way, most likely through vertical transmission (Chapter 1; Mann & Sargeant 2003). There is documentation of sympatric cultural variants for this species (e.g. Chilvers & Corkeron 2001; Mann 2001; Mann & Sargeant 2003) but the geographic scale is apparently limited relative to sperm whales. Bottlenose dolphin societies are organised around geographically based ‘communities’ within which individual relationships are maintained in a fission-fusion context (Connor *et al.* 2000); it

is entirely possible that these communities each develop their own distinctive cultures, but research at this scale is extremely rare. One striking example are the generations-old fishing cooperatives between humans and bottlenose dolphins (Pryor *et al.* 1990; Simões-Lopes *et al.* 1998), which involve large portions of the resident dolphin communities (this phenomenon is also mirrored in another delphinid, the Irrwaddy dolphin; Smith *et al.* 1997). In the vocal domain, Ding *et al.* (1995) showed that vocal variation does exist at the population level, but could not exclude genetically-based geographic variation as an explanation. Thus, more work is needed at the ‘community’ level in this species, just as more work is needed at the individual level in sperm whales.

The closest known parallel to sperm whale vocal culture has to be that found in killer whales, where groups can be classified into sympatric clans based on vocal traits (Chapter 3; Ford 1991; Yurk *et al.* 2002). However, there are important differences between the species – for example, killer whale clans do not share discrete calls (Ford 1991), while sperm whale clans clearly do share coda types. Why this should be so is a puzzle, but points to a more open, labile vocal system in sperm whales, which is consonant with results on the stability of social structure in the two species (Baird 2000; Whitehead 2003b; see below). In terms of vocal repertoire stability, the species are apparently similar; while Deecke *et al.* (2000) documented changes in one call type over ~12 years in killer whales, restricting these data to the same scale as I was able to examine (~5yrs) would lead to the same conclusion that I draw in Chapter 6 (see Deecke *et al.* 2000, Figure 2). In killer whales, we know that clans have been found to be boundaries to mating (Barrett-Lennard 2000), although this is in a portion of the population notable for the natal philopatry of both sexes (Baird 2000). We do not know whether sperm whale clans are barriers to mating, but it is unlikely that they are absolute barriers given male dispersal (Whitehead & Weilgart 2000) and the sharing of mtDNA haplotypes between clans (Chapter 3). Finally, in killer whales we know that cultural inheritance is not limited to the vocal domain but extends into other behavioural traits in ways that are unique outside humans (Chapter 1; Rendell & Whitehead 2001); there are indications that this is also the case for sperm whales (Whitehead & Rendell in review),

but evidence is much harder to obtain for large oceanic populations of sperm whales than for coastal, relatively small killer whale populations that have been the subject of research by numerous groups and individuals over more than three decades.

Parallels between the cultures of these two species may reflect a level of linkage in their evolutionary trajectories; killer whales are predators of sperm whales (Pitman *et al.* 2001), and Rendell & Whitehead (2001) suggest that an evolutionary arms race between predator and prey may have been a factor in the evolution of culture in both species (whether oceanic killer whales also have vocal clans is unknown, but seems likely). However, they also share a social structure based on matriline, and this has been highlighted as a potentially important factor in the evolution of cetacean culture (Rendell & Whitehead 2001; Whitehead 1998). Hence it is of obvious interest to know whether such a link between matrilinearity and culture continues to other species that are known to be at least partially matrilineal but that are not yet the focus of much behavioural research – these include the pilot whales, two other species with low mtDNA diversity (Whitehead 1998), and the beluga (O'Corry-Crowe *et al.* 1997). I highlight these species in particular since the former is generally oceanic (Bernard & Reilly 1999) while the latter generally coastal or estuarine (Brodie 1989); comparing cultural phenomena in these species could help delineate the relative roles of oceanic habitat and matrilineal social structure in the evolution of culture.

#### **Avian and sperm whale cultures: Birds of a feather?**

The study of the cultural transmission of bird song has been a highly productive field for decades (Slater 2003), has led to convincing descriptions of gene-culture co-evolution outside humans (Grant & Grant 1996), and serves as an excellent general model for the future study of culture in cetaceans. In songbirds (Passeriformes), most vocal learning is done by males and related to sexual selection (Catchpole & Slater 1995), and there has been much research into this phenomenon, but it does not have much in common with what we know about sperm whales. This learning commonly results in geographically-based dialect systems, either through local adaptation (Nottebohm 1972) or cultural drift



in isolation (Slater 1986); while dialect boundaries may be very sharp, this situation is still different from the complete sympatry of sperm whale clans (see e.g. Slater 2001), as well as the most likely agents (females in sperm whales) and functions (unlikely to be sexual selection in sperm whales) of cultural transmission. Some species have apparently flock-specific calls, usually used to defend group territories. One such is the Australian magpie, *Gymnorhina tibicen* (Brown & Farabaugh 1991), although it seems in this case that most apparently flock-specific calls are actually individual-specific - specifically 77% of warble syllables, 'almost all' warble song types, 78% of carol syllables and apparently all carol song types are all unique to one individual, rather than shared (Brown & Farabaugh 1997) - hence without group-level sharing, labelling this as vocal culture is problematic (see Freeberg 2001). Others species use shared vocalisations to defend colonial nest sites, such as the yellow-rumped cacique, *Cacicus cela*, (Feekes 1982; Trainer 1989); the result is geographically based dialects based on convergence through vocal learning of a few, sometimes just one, contact call(s). Similarly, non-breeding chickadees, *Poecile atricapillus*, and finches, *Carduelis* spp. form flocks that converge on a shared contact call through vocal learning, but these groupings appear not to be stable to the extent of sperm whale social units (Ficken & Popp 1995; Mammen & Nowicki 1981; Mundinger 1970; Nowicki 1983).

Among other bird groups, the European starling (*Sturnus vulgaris*) is noted as a particularly adaptable species due to its success in colonising new habitats, and has a complex vocal repertoire (Adret-Hausberger & Güttinger 1984) that contains cues to population, social group and individual identity (Hausberger 1997). While starlings are much better studied than sperm whales, it is still clear that vocal variation in the starling differs from that in sperm whales. In starlings vocalisations can be separated into "universally shared songs" that are species-specific and "more individual structures" such as individual whistle themes (Hausberger 1997); 'group-specific' songs are thus the summed individual-specific song types of the individuals in a group, as in the Australian magpie, and not shared call types as in sperm whales (Chapters 3 & 4), although more work is needed at the individual level with sperm whales before this difference can be

definitively asserted. Another difference is the large horizontal component in starling vocal learning; typically song sharing is mediated by social interaction such that changing social bonds are reflected in changing call repertoires; Hausberger (1997) reports that “*both males and females appeared to show an important repertoire turnover in response to social changes*” (original emphasis). If the same thing happened in sperm whales we would expect to see evidence of unit repertoires changing over the timescales analysed in Chapter 6, given that unit membership transfers do occur over these timescales (Christal *et al.* 1998). I did not find this, so it appears that the stability of sperm whale vocal variation is robust to changing social circumstances, perhaps due to relatively higher levels of vertical rather than horizontal transmission (e.g. Feldman & Laland 1996). One other important lesson from studies of starlings is that vocal repertoires vary dramatically between captive and field conditions, another example of the dangers involved in relying to heavily on data from captive experiments; at the end of her review of vocal sharing in starlings, Hausberger (1997) stresses that “*captive studies have to have field validations when possible*”, and further, that when examining social learning, “*only studies of birds raised in a group can really inform us about social influences*” (see also West *et al.* 2003).

The other major group of avian vocal learners are the Psittaciformes (Bradbury 2003). In this group is one of the most adept avian social learners, the African grey parrot, *Psittacus erithacus* (Moore 1992b; Moore 1996; Pepperberg 1999). There is also impressive evidence of the importance of social learning in the wild provided by naturally occurring cross-fostering: for example, galah (*Cacatua roesicapilla*) chicks cross-fostered by Major Mitchell cockatoos (*Cacatua leadbeateri*) developed vocal characters, food preferences and food handling techniques typical of the foster-parent (Rowley & Chapman 1986). Such observations lead Bradbury (2003) to refer to a ‘habitat lore’ that individual birds must learn in order to survive and prosper in any given habitat. In the wild, the fundamental unit of parrot society is the mated pair, but these pairs generally form groups or flocks that are not closed or stable, but that do converge upon group-specific contact calls, usually only a single call type; these groups are highly mobile, and regularly share foraging sites with other groups over large ranges (Bradbury

2003; Farabaugh & Dooling 1996); hence here we find truly sympatric behavioural variants. Bradbury (2003) draws parallels with bottlenose dolphins in that parrots appear to have individual signatures that also convey group affiliation, and this helps provide a contrast with the relatively stable, group-specific *repertoires* of sperm whales. One of the better studied species in this group, the budgerigar, *Melopsittacus undulates*, provides a typical picture of groupings that converge on a single shared contact call (Brown & Farabaugh 1997; Farabaugh & Dooling 1996; Farabaugh *et al.* 1994). Again, however, it appears that most cultural transmission is horizontal – group mates converge on a common call by altering their own in response to stimuli from other group members; given the general lack of kin relations and apparently extensive dispersal (Bradbury 2003), I therefore question whether this form of vocal variation really represents a heritable cultural ‘institution’ (Mundinger 1980) in the sense that I suggest is the case for sperm whale clans. However, I do think there is more to be learnt from parrots; like sperm whales, they are difficult to study in the wild, but more information on the behavioural variation of larger parrots such as the African grey in the wild is needed before we can fully appreciate the role that cultural transmission plays in the lives of these birds (Bradbury 2003).

The study of song learning is a model for similar work on cetaceans. In particular, these studies have made the link between social interaction and social learning particularly clear, showing how “social knowledge is earned by organisms acting on their particular social surroundings to probe its properties” (West *et al.* 2003), and promoting a view of social learning as an active process by which an individual animal learns appropriate behaviour (see also Hausberger 1997). However, social learning in birds is not restricted to the vocal domain – there is also evidence of the social transmission of foraging information (e.g. Lefebvre 1995b; Lefebvre 2000; Lefebvre & Palameta 1988) and of motor-imitative abilities in the Grey parrot (Moore 1992b; Moore 1996). The relationship between these abilities and the evolution of vocal learning remains to be established, since research on bird culture has sometimes been restricted by ‘the compartmentalized way in which culture has been studied’ (West *et al.* 2003), although

Moore (1992b; 1996) hypothesises an evolutionary trajectory that involved incremental evolution from song learning through vocal imitation to motor imitation. This hypothesis could equally apply to cetaceans such as the bottlenose dolphin (Moore 1996), killer whales, and potentially sperm whales too (Rendell & Whitehead 2001).

There is much still to be learned about culture from birds (West *et al.* 2003). However, I would still argue that there is no phenomenon of which I am aware that compares with sperm whale vocal clans. In general, bird vocal cultures tend to be geographically based, to vary according to current social environment, to have a large horizontal transmission component, and appear not to give rise to ‘institutions’ such as clans. The closest parallels are seen in the sympatric flock-specific contact calls of parrots; future studies of parrots in the wild may close this gap even more. However, dialect sharing in birds is apparently restricted to those animals in direct contact (e.g. Hausberger 1997), whereas in sperm whales, units that have likely never interacted share vocal patterns (Chapter 3), suggesting a very high level of persistence (Whitehead *et al.* 1998).

#### **Culture in bats *and* sperm whales?**

Evidence is also growing for social learning in bats (Chiroptera), and like cetaceans evidence is mostly from studies of vocal behaviour; this is particularly intriguing given that echolocation is common to both orders. Another rare trait common to both is alloparental care (Boughman 1998). In group living bats, social structure generally centres on groups of individuals that roost together, defend food patches, and share information about food sources (Kerth & Reckhardt 2002; Wilkinson & Boughman 1999). There are three examples known so far of vocal learning in this order (Wilkinson 2003); one is of echolocation calls, one is of infant isolation calls, and the third gives rise to group-specific vocal traits, specifically the contact calls of greater spear-nosed bats, *Phyllostomus hastatus* (Boughman 1998). This species is group living, with social structure based on groups of females that roost together and cooperatively defend food and roosts; both sexes disperse from the natal group, so opportunities for vertical cultural

transmission are limited, but females can go on to remain together in groups for up to 10 years (Wilkinson 2003). Group-mates converge on a common contact call, and this variation can be sympatric since several groups can share large roosting sites such as caves (Boughman 1997; Boughman 1998); Group mates can discriminate between group and non-group members based on this call (Boughman & Wilkinson 1998). As groups contain multiple age cohorts (McCracken & Bradbury 1977) then they may be loci of oblique cultural transmission of the contact call, but transmitting a single call type across generations is not as complex as the patterns that differentiate clans in sperm whales. However, there are some bat species that show female social philopatry, like sperm whales: Common vampire bats (*Desmodus rotundus*), Bechstein's bats (*Myotis bechsteini*) and little free-tailed bats (*Tadarida pumila*). In these species matrilineal kin are present in the same, stable, social groups; given the relationships that have been suggested between matrilineal social structure and stable, vertical, cultural transmission (Rendell & Whitehead 2001; Whitehead 1998), more data on behavioural variation and candidate cultural behaviours in these species is highly desirable – perhaps there we will find more parallels with sperm (and killer) whale cultures.

I would interrupt the taxonomic roll-call to briefly highlight an interesting factor common to the groups discussed thus far: mobility (see Janik & Slater 1997; Tyack & Sayigh 1997; Chapter 1). Cetaceans are particularly mobile animals - for instance, the mean monthly displacement of a female South Pacific sperm whale - ~350km - is roughly ten times that of members of a particularly mobile population of a particularly mobile terrestrial, flightless, mammal: the savannah elephant, *Loxodonta africana*, (Thouless 1995; Whitehead 2001a). However, *flying* terrestrial animals are also potentially at least highly mobile, so it is interesting that Bradbury (2003) and Hausberger (1997) highlight movement and the resultant high variation in social environment as important factors leading to social learning of group-specific vocal signals in parrots and starling respectively. Tyack & Sayigh (1997) proposed a similar relationship in the evolution of cetacean vocal learning, and the fluidity of sperm whale groups would certainly lead to predictions of dialects under this proposal, since although the underlying units stay stable,

these unit join and leave larger groups regularly (Christal 1998; Whitehead *et al.* 1991). However, it is unclear how the dialect system I have described in this thesis could provide useful cues of unit membership (Chapter 6), so the fit to expectations is not perfect. Finally, the efficiency of movements could also be enhanced by cultural transmission of desirable movement strategies, or ‘habitat lore’, vertically from mother to offspring, horizontally among animals in the same region, or, perhaps especially, between generations within stable groups (see also O’Corry-Crowe *et al.* 1997; Whitehead 1996b).

### **Big brains for big noses: A colossal cultural convergence<sup>2</sup>?**

There are obvious parallels between the social lives of elephants (Proboscidea) and sperm whales - both are long-lived, show male dispersal, and females live in generally or strictly matrilineal alloparental (Lee & Moss 1999) social groups (for more details see Whitehead & Weilgart 2000). If the form of culture, or even the presence of social learning itself, depends on a relationship with underlying social structure, then we would expect similar patterns. In a superb playback study, McComb *et al.* (2001) showed very well the value of an experienced matriarch in a long-lived matrilineal society – elephant families with older matriarchs were much more likely to correctly differentiate between the calls of familiar and unfamiliar other families, and respond accordingly, than families with younger matriarchs. This value relates to matriarchal knowledge of the immediate and continuously changing (Lee & Moss 1999) social surroundings and the willingness of the rest of their groups to follow their lead. Is this cultural knowledge? One test might be to observe how relationships between kin groups change over time, especially around the deaths of old matriarchs: If the relationships change sharply, then ‘knowledge’ of groups would be the accumulated experience of whichever individual was dominant, while if relationships only change gradually regardless of matriarch age or death, it is hard to see how this social knowledge could not have been culturally acquired.

The term clan is also used with respect to elephant, to refer to collections of matrilineal kin groups that (probably) share a common ancestry and generally occupy the

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<sup>2</sup> See Weilgart *et al.* (1996), Whitehead & Weilgart (2000).

same area, overlapping ranges and interacting frequently (Payne 2003). However, there is apparently “neither genetic nor behavioural homogeneity” (Payne 2003) within clans; hence it is unlikely that these clans share a common cultural inheritance in the sense I suggest for sperm whales; the focus of cultural inheritance if it exists is thus likely the matrilineal kin group. While there is currently little evidence of group-specific behaviour at this level, it seems likely that young elephants derive local ‘habitat lore’ through following adult kin (Lee & Moss 1999; Payne 2003). One contrast with sperm whales are the geographic properties of clans. In elephants, clans tend to dominate geographical areas (Payne 2003), whereas in sperm whales groups from a given clan sometimes occupy a given area for a number of days, but there is no evidence for longer term residencies (Whitehead & Rendell *in review*), so geographical persistence is low.

#### **Tools, symbols, meanings and identities: Comparing primate and sperm whale culture**

Cultural primatology is an established field (McGrew 1992; Wrangham *et al.* 1994), and attention has long focussed on understanding human evolution by studying our primate cousins, looking for evidence of “elementary complex culture” in non-humans (Richerson & Boyd 2000). This intensity of study has born the fruit of exhaustive catalogues of cultural diversity in chimpanzees and orangutans (van Schaik *et al.* 2003; Whiten *et al.* 1999). These studies describe entire suites of culturally transmitted behaviours, to a breadth not previously known outside humans; perhaps the closest parallels are the combined vocal and motor cultures of killer whales. However, in other respects, ‘cetaceans do things that no ape has been seen to do’ (McGrew 2003). This is certainly so in the case of sperm whales – in the non-human primates, there is no such cultural institution as the sperm whale vocal clan (Chapter 3).

Primate culture has a strong geographical basis, with communities in one place having cultural complexes distinct from those in other localities, and often geographical barriers prevent diffusion (McGrew *et al.* 1997; Whiten *et al.* 1999), in contrast with sperm whale clans. We also see material culture in primates, where tool manufacture and

use is culturally transmitted (McGrew 1994); while there is no direct parallel in cetaceans (Whiten 2001), bottlenose dolphins do use sponges, albeit unmodified, in what is apparently a culturally transmitted foraging technique (Mann & Sargeant 2003). There are however few materials available to sperm whales, and so unsurprisingly, sperm whale culture seems to lack any material aspect. Generally, vocal variation is not a striking aspect of primate culture; while some vocal patterns are clearly affected by social influences (Marshall et al. 1999; Mitani et al. 1992), there is little evidence for anything approaching the scale of bird, bat or cetacean vocal sharing; perhaps this is related to a relatively constant inter-group social environment due to the geographic structuring of populations, reducing the need for ready cues to social affiliation.

In humans culture takes a startlingly unique form, especially with regard to vocal variation; there are currently 4,000-6,000 extant languages (Ehrlich 2000). This level of variation contrasts sharply with other primates, but killer whales and sperm whales may provide a closer parallel than other non-humans. Nowhere else do we see such large scale, sympatric, cultural institutions as killer and sperm whale vocal clans than in dialect and language groups in humans. In humans too, vocal variation has been linked to mobility, with the need for ready recognition of an individual's in-group (Nettle 1999). Ehrlich (2000) states that 'we can assume that languages varied from group-to-group of hunter-gatherers' in human ancestry, and there is evidence that those pre-industrial groups interacted with each other, exchanging goods and individuals, yet maintained clear ethnolinguistic boundaries (Nettle 1999); in modern humans sympatric cultural variants are the norm. Thus in humans culture is an important factor in population structure; killer and sperm whale vocal clans show obvious parallels. In these two species populations are well structured on cultural lines, but overlap significantly in geographic ranges. Despite contact between clans, and in the case of sperm whales, transfer of individuals between them, boundaries remain sharply defined. In humans, dialect boundaries are often important social boundaries, and may also be barriers to altruistic acts, despite occasional or regular exchange of individuals (Nettle 1999). *If* clan dialect boundaries are also barriers to altruism in sperm whales, then we may draw very close



parallels with the evolution of human linguistic variation (Nettle 1999). The adaptive value of human linguistic variation remains unclear; some have suggested that variation facilitates effective cultural adaptation to local conditions (interestingly, this suggestion was prompted by a comparison with birds, (Labov 1973), showing again the value of comparative perspectives), others suggest that the prime function of linguistic variation is to provide ethnic markers for in-group identification (Nettle 1999). We remain ignorant of the function of sperm whale clan dialects, but given the prominence of clan variation over geographic variation, the former seems unlikely.

To what extent does this discussion relate to deeper anthropological concepts of culture that include symbols and meanings, considered by social scientists to be fundamental to human culture? If meaning is defined as the attribution assigned to cultural knowledge by minds (McGrew 1998), then there appears little hope for overlap. Meanings are inaccessible to students of all non-human cultures, and they are really only partly accessible to students of human cultures – specifically, that part of an interview where the interviewee is telling the truth. While bottlenose dolphins have enough cognitive capacity to be taught artificial ‘languages’ (Herman *et al.* 1993), this tells us no more about the ‘meanings’ dolphins assign to gestures than it does about the ‘meanings’ assigned to owner’s gestures by their dogs. More interestingly, bottlenose dolphins are known to engage in whistle matching in the wild, and Janik (2000) suggests that these whistles may be used to refer to individuals – so in that sense the whistles used may be said to have meaning. This overlap between meaning and identity perhaps provides a link to notions of meaning in culture. Do the dialect variations that define cultural groupings in sperm whales hold meanings for the animals themselves? If they do, that meaning likely concerns *identity* – the identity of the caller’s group, with respect to the listener’s group. Whether this would qualify as a *system of meanings* for anthropologists is perhaps for anthropologists to answer. In the meantime, I am more interested in the concept of *cultural identity* (McGrew 2003); populations of killer and sperm whales are so strongly structured along cultural lines that I suggest the importance of a cultural identity is not something unique to humans.

## CONCLUSIONS – THE PROMISE OF A CULTURAL CETOLOGY

Compared to say, cultural anthropology, or even cultural primatology, cultural cetology is yet an infant, if born at all. In all four well-studied cetacean species we find strong evidence of cultural processes. In the bottlenose dolphin this is coupled with perhaps the most advanced non-human social learning abilities. As I have shown, in the sperm whale the evidence apparently encompasses some of the largest non-human cultural institutions we know. Direct research on cetacean culture has barely started in earnest, and most of our knowledge is restricted to just four of the ~80 cetacean species. While evidence is accumulating ever more rapidly (Chilvers & Corkeron 2001; Deecke *et al.* 2000; Yurk *et al.* 2002), the true cultural richness of cetaceans remains largely unknown. Nevertheless one can point to large geographic scale, a lack of material culture, and, perhaps most interestingly, sympatry of stable cultural variants as general features of cetacean culture that contrast with terrestrial non-human analogues.

I have promoted a broad and inclusive idea of cetacean culture. This is because I believe that comparative analyses of culture will be highly informative, whether comparisons are within or between taxa (such as within or between species, or between higher order taxa, such as Cetacea and Pscattiformes). The sperm whale surely has a fascinating place in such comparisons. The promise of a cultural cetology, over and above a correct understanding of cetacean behaviour, is the comparative potential inherent in such a group; cetaceans have a variety of social structures, inhabit a broad range of ecological niches and have varying cultural systems. More broadly, a fascinating range of evidence exists for birds (Slater 2003; West *et al.* 2003) and primates (de Waal 2001; van Schaik *et al.* 2003; Whiten *et al.* 1999), to which the little data we have on cetaceans stands up well (Dunbar 2001; McGrew 2003; Slater 2001); furthermore, work is in progress on parallel phenomena in bats (Wilkinson 2003) and elephants (Lee & Moss 1999; Payne 2003). Thus we can hold out the hope of a greatly increased understanding of how social and ecological factors impact the evolution of culture, of interest to biologists but also those seeking to understand humanity's own biological and

cultural evolutionary history.

APPENDIX ONE

Data underlying Figures 3.1 and 3.2

TABLE A.1.1: Details of coda repertoire over time for groups recorded more than once with at least one year between first and last recording

Unit / Clan	Recording Date	3R	2+1	4R	3+1	4A	3++1	5R	4+1	4+1	6R	5+1	2+4	4+1+1	7R	6+1	1+6	2+5	5+2B	1+7	8RA	8RB	7+1	8S	7++1	9R	N codas
A&H, Regular	February 25, 1985							1	2						5						7				4	24	
	January 7, 1987							15	2						13					1	4				3	38	
	January 9, 1987							27	10						10						3	13			1	65	
	January 18, 1987							4																		4	
	March 9, 1987							13				2	1	1	1						1			1		21	
G, +1	April 19, 1987								2			3														5	
	April 16, 1989		1				1		1			6								2						12	
	April 26, 1993							3	27			16								1						63	
	April 27, 1993								38			16														75	
I, Regular	March 10, 1985							12			4	1			3						2	4				33	
	January 6, 1987							19	10		10	1			19					1	4	13				10	
	May 12, 1987							6	2		2				2							3				17	
P, Regular	March 6, 1985							7			1				8											16	
	March 30, 1985							5	4						8							4				20	
	April 14, 1985							57	8	1	30	1		1	34					1	17	24				20	
	April 15, 1985							7	2		2				1											11	
	May 5, 1989							12	7		7				9				1		1	5				5	
																										43	







## APPENDIX TWO

### *Publications*

*Chapter 1 draws on material that also appears in:*

Rendell, L. E. & Whitehead, H. (2001) Culture in whales and dolphins. *Behavioral and Brain Sciences* **24**, 309-382.

*The work presented in Chapter 2 will also appear in:*

Rendell, L. E. & Whitehead, H. (in press) Comparing repertoires of sperm whales: A multiple methods approach. *Bioacoustics*.

*The work presented in Chapter 3 also appears in:*

Rendell, L. E. & Whitehead, H. (2003) Vocal clans in sperm whales (*Physeter macrocephalus*). *Proceedings of the Royal Society of London, B - Biological Sciences* **270**, 225-231.

*The work presented in Chapter 4 will also appear in:*

Rendell, L. E. & Whitehead, H. (in press) Do sperm whales share coda vocalizations? Insights into coda usage from acoustic size measurements. *Animal Behaviour*.



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