Agenda Item 3.7.3

Review of New Information on Threats to Small Cetaceans

Emerging Issues

Conservation Implications of Cetacean Culture

Information Document 3.7.3.b

Report of the CMS Scientific Council Workshop on the Conservation Implications of Cetacean Culture

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CONVENTION ON MIGRATORY SPECIES

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Agenda Item 23.2.4

REPORT OF THE CMS SCIENTIFIC COUNCIL WORKSHOP ON THE CONSERVATION IMPLICATIONS OF CETACEAN CULTURE

4-9 NOV 2014
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UNEP

Convention on the Conservation of Migratory Species of Wild Animals

Scientific Council

Aquatic Mammals Working Group

Distr: General

UNEP/CMS/AMWG/
WS-2014

London, United Kingdom, 15-16 April 2014

CMS Scientific Council Workshop on the Conservation Implications of Cetacean Culture

REPORT OF THE MEETING

A. Opening

The meeting opened with welcoming remarks from Heidrun Frisch, Marine Mammals Officer, CMS Secretariat. She thanked the representatives of Whale and Dolphin Conservation for their help in the organization and financing of the meeting, including providing the excellent venue.

In his introductory remarks Fernando Spina, Chair of the CMS Scientific Council, commented that this was a very timely meeting on an important subject. He noted that one of the challenges was to report to Scientific Council on the discussion. He informed the group that the Steering Committee had selected Giuseppe Notarbartolo di Sciara as the chair for the workshop.

1. CMS Background

1.1 Institutional framework and context of the workshop, Terms of Reference
(Heidrun Frisch, CMS Secretariat)

The CMS Secretariat provided an overview of CMS, its institutional framework and the context for the workshop. She explained that the mandate for this workshop arises from CMS Resolution 10.15, the Global Programme of Work for Cetaceans. This instructed the Aquatic Mammals Working Group (AMWG) of the Scientific Council to *"host a workshop to review and provide advice on the impact of the emergent science of cetacean social complexity and culture, as it relates to regional populations and to inform forward decisions about CMS conservation priorities"*. Accordingly, the recommendations coming from this workshop would be reported to the Scientific Council, which would then consider how this work area could be taken forward.

1.1 CMS Scientific Council and Species Appendices
(Fernando Spina, CMS Scientific Council)

The CMS Scientific Council Chair provided more detail on the structure and role of the Scientific Council. He also pointed out the definition of migratory species in the text of the Convention, which he noted was a geo-political perspective of a natural phenomenon:

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> *"Migratory species" means the entire population or any geographically separate part of the population of any species or lower taxon of wild animals, a significant proportion of whose members cyclically and predictably cross one or more national jurisdictional boundaries;*

He observed that animal culture was seldom taken into account in conservation actions, yet this concept might help provide resilience to populations if incorporated into management. On the other hand it had also been suggested that culture could sometimes lead to animal dependence on humans.

He also noted that countries had made commitments to preserve biodiversity, which included phenotypic variation and could be due to genetic, environmental and cultural factors. No matter what the cause of the phenotypic diversity, the goal of preserving this variety stayed the same.

B. Presentations – Background, Case Studies and Questions

The Chair called on experts to present on the topics listed below. The abstracts submitted are provided in Annex 1.

2. **Social Complexity, Culture and Modern Conservation Efforts**
   (Philippa Brakes, Whale and Dolphin Conservation)

   (LINK TO ABSTRACT: Page 12)

3. **What is Culture: Social, Group and Population Level Consequences**
   (Luke Rendell, University of St. Andrews)

   (LINK TO ABSTRACT: Page 12)

4. **Consideration of Genetics and Culture in Great Ape and Cetacean Conservation**
   (Michael Krützen, University of Zurich)

   (LINK TO ABSTRACT: Page 13)

5. **Genes and Culture: Loss of Migratory Cultural Memory and Recolonisation**
   (Emma Carroll, University of St. Andrews)

   (LINK TO ABSTRACT: Page 14)

6. **Individual Foraging Specializations in Marine and Terrestrial Mammals**
   (Richard Connor, University of Massachusetts Dartmouth)

   (LINK TO ABSTRACT: Page 14)

7. **Implications for Conservation Efforts for Socially Complex Mammals: Culture and the Great Apes?**
   (James Moore, University of California San Diego)

   (LINK TO ABSTRACT: Page 15)

8. **Elephant Matriarchs as Repositories of Knowledge**
(Karen McComb, University of Sussex)

(LINK TO ABSTRACT: Page 15)

9. **Threats to Cetaceans in the Modern Marine Environment**
(Mark Peter Simmonds, Humane Society International)

(LINK TO ABSTRACT: Page 16)

10. **Killer Whale Ecotypes in British Columbia: the Role Culture has Played in Identification, Definition and Protection**
(John Ford, Fisheries and Oceans Canada)

(LINK TO ABSTRACT: Page 17)

11. **Social and Behavioural Factors in Cetacean Responses to Over-exploitation: Are Odontocetes Less 'Resilient' than Mysticetes?**
(Paul Wade, NOAA Fisheries)

(LINK TO ABSTRACT: Page 17)

12. **Learning on line: The spread of a novel foraging behavior among sperm whales (*Physeter macrocephalus*) in the Gulf of Alaska: exploring models of social learning**
(Sarah M. Mesnick, NOAA Fisheries Service)

(LINK TO ABSTRACT: Page 18)

13. **Identifying Demographically-Independent Populations of False Killer Whales and Bottlenose Dolphins in Hawaiian Waters**
(Robin W. Baird, Cascadia Research Collective)

(LINK TO ABSTRACT: Page 18)

14. **Ecologically and/or Culturally Significant Units (ESUs and CSUs)**
(Hal Whitehead, Dalhousie University)

(LINK TO ABSTRACT: Page 19)

15. **Towards a 'Taxonomy' of Cetacean Culture**
(Luke Rendell, University of St. Andrews, and Hal Whitehead, Dalhousie University)

(LINK TO ABSTRACT: Page 20)

C. Identifying the Implications of Culture for Cetacean Conservation Management

The workshop agreed to use, for the purposes of its deliberations, as definition for culture *information or behaviours that are shared by a community and acquired through social learning from conspecifics*. Having differentiated between culture and other aspects of social complexity and considered a wide range of examples for culture in a range of species, the Chair noted that now it was time to look into the implications of such behaviours for conservation efforts.

In discussion, it was remarked that both managers and scientists might have concerns relating to the practicality of basing management decisions on culture, as lack of data should not be a reason to delay action. The group agreed that the number of cases in which the consideration of cultural aspects would make a significant difference to the advice given on management decisions may be relatively rare. However, for species or populations where such data were available, the information could provide important insights relating to the delineation of units to conserve and should be taken into account, while not neglecting other lines of evidence such as genetic differentiation. It was agreed that for many geographic areas and species there had been insufficient research on culture and social complexity, or the data had not yet been analysed with a focus on these aspects. However, the distribution of these features – cultural behaviour and social complexity – is almost certainly wider than currently appreciated. More specifically, poorly-known species may have unsuspected cultural variation in behaviour, and some poorly-known populations of species that are known to show significant cultural variations in behaviours may have particular behavioural variants that are particularly significant for the viability of that population. Management decisions should therefore be precautionary and assume that even in the absence of hard data, populations may contain discrete social elements which have conservation significance warranting further investigation.

The CMS Scientific Council Chair emphasized that the presentations and discussions had clearly shown that culture was widespread in socially complex mammals such as cetaceans, primates and elephants. There was sound science demonstrating not only its existence and manifestations, but also the importance to the animals concerned, including their fitness and the viability of their social groups and populations. It was clear that culture needed to be taken into account more clearly than had been done so far, and therefore he considered the findings and recommendations of this workshop to be of high importance to the further work of CMS. The workshop Chair concurred with this view and reminded participants that while the main focus of their discussion was cetaceans, the recommendations should not be limited to this species group, as the Convention covered many others, too.

It was suggested that it might be useful to compile examples of evidence of culture in different behavioural realms into a table. This would help to illustrate the relevance of the discussions to the Scientific Council, which would receive the report of this workshop.

It was agreed that in looking at the implications of culture for conservation, it was important to distinguish:

a) cultural traits that increase the probability of negative conservation outcomes, or compound the negative influence of anthropogenic threats; and
b) cultural traits that might increase population viability in a changing environment and/or help conservation efforts.

It was noted that culture was a form of behavioural plasticity that allowed a group to develop behavioural adaptations in response to changes in conditions in their habitat; on the other hand, conservatism might prevent such adaptation from occurring. Culture therefore potentially influenced how a social group responds to a pressure, and thus was an important factor determining whether or not certain conservation measures were effective.

A concern repeatedly discussed was that the removal of individuals from a population could represent much more than just a numeric loss to its social group. If, for example, the individual removed was an important repository of cultural knowledge, the long-term success and survival of the whole group might be jeopardised. Important examples discussed were migration to critical habitat through maternally led site-fidelity in some baleen whale species and the potential impacts to fitness from the removal of matriarchs in elephant social units. It was therefore important to protect the social structure of species exhibiting cultural traits. At the same time, the importance of individuals in this context also illustrated why studies on animals, and in particular cetaceans, in artificial social groups, taken out of their natural setting, were not necessarily suited for understanding decision-making and behaviour relevant for conservation management.

Participants also noted that beyond the transmission of knowledge through social learning, there were other aspects of social complexity that might have important implications for conservation. As a result of these discussions, two tables were prepared:

Table 1 shows **Examples of the potential relevance of culture to cetacean conservation efforts**[1]:

Issue	**Example**
Range recovery and/or time lag to recovery	Evidence of mitochondrial DNA segregation between breeding populations in several baleen whale species indicates that calves learn migration routes, and other habitat knowledge, from their mothers during their period of dependency and, crucially, are subsequently conservative about exploring new areas. This can lead to a potential loss of cultural habitat knowledge, meaning that range recovery following extirpation could be impeded (Clapham et al. 2008). There is evidence for this in southern right whales around Australia and New Zealand (Carroll *et al.*, 2011, 2014) and humpback whales (Baker *et al.*, 2013), and there has been suggestion that this may be one factor holding back North Atlantic right whale recovery (Mate *et al.*, 1997).
Anthropo-dependence / loss of 'wild' knowledge	Human activities in cetacean habitat can sometimes lead to novel ecological opportunities, and knowledge of these opportunities can spread quickly in cultural species. If this leads some or all of a population to subsequently specialise on that opportunity, then population viability can become dependent on that human activity – what could be termed anthropo-dependence – and could be threatened should that activity cease. Furthermore, if the population originally depended on cultural knowledge to make a living before the anthropogenic opportunity, then that knowledge could be lost, and difficult to recover. Examples include co-operative fishing (Daura-Jorge *et al.*, 2012) albeit that this opportunity had persisted for generations, provisioning, such as in Shark Bay (Mann and Kemps, 2003), and begging, such as in south-western Australia (Donaldson *et al.*, 2012), and the changing niches in Moreton Bay, eastern Australia associated with the bottom trawl fishery (Chilvers and Corkeron, 2001; Ansmann *et al.*, 2012).

[1] For reviews elaborating on some of these issues, see Whitehead (2010) and Whitehead et al. (2004)

Issue	**Example**
Population vulnerability due to specialisation	Reliance on cultural knowledge for hunting prey that require skill, complex behavioural sequences, or cooperation, can lead populations or sub-populations down paths of increasing specialisation. With specialisation on a given resource comes vulnerability – if the resource is depleted, potentially by the specialist themselves, then they have no alternative knowledge base to turn to. This risk seems most obvious in orca ecotypes (Whitehead *et al.*, 2004).
Interaction with climate change	The rapid environmental changes predicted by climate scientists could outstrip the ability of culturally conservative populations to adapt. This seems most likely to be a problem at high latitudes where there is little or no opportunity to move to higher latitudes to compensate. A relevant example is the changing habitat of beluga whales in Baffin Bay (Colbeck *et al.*, 2013), and potentially the bowhead whale's close relationship with sea-ice makes this consideration relevant for them also.
Influence on population structure	Population structure has important management implications, especially for understanding how population segments are connected. In several cetacean species population structure and cultural behaviour are significantly related, in ways that are often not fully understood. Examples include the vocal dialects of fish-eating orcas (Deecke *et al.*, 2000), sperm whales (Rendell *et al.*, 2012), and the songs of a number of baleen whale species (McDonald *et al.*, 2009; Garland *et al.*, 2011; Tervo *et al.*, 2011), all of which indicate some level of population structuring that would be difficult to detect without reference to the behaviours themselves. In some cases, perhaps including orcas and sperm whales, the whales may use the cultural behaviours themselves to structure their social relationships, and so populations, by means of symbolic marking (Whitehead and Rendell 2014). Fidelity to learned migration routes generates or strengthens population structure (Carroll *et al.*, 2011; Baker *et al.*, 2013). Finally, foraging specialisations produce heterogeneity in the ecological interactions of a population that could represent cryptic genetic sub-structuring (Mann and Sargeant, 2003; Mann *et al.*, 2005; Sargeant *et al.*, 2005).
Conflict with human activities	Many fisheries have the side-effect of creating a new foraging opportunity or niche for marine mammals. In social species that learn quickly and from each other, the exploitation of these opportunities can quickly reach problematic levels. It is typically social cetaceans for which there is independent evidence for cultural processes that become problematic. Examples of depredation are widespread (Hucke-Gaete *et al.*, 2004; Gilman *et al.*, 2006; Sigler *et al.*, 2008), and on balance it is highly likely cultural transmission has resulted in them spreading through populations (Whitehead *et al.*, 2004) in a similar way to the spread of a 'natural' foraging innovation in humpbacks (Allen *et al.*, 2013).

Issue	**Example**
Increased ecological resilience	The flip side of the rapid spread of innovations is that some cultural species can be more resilient to ecological change because they are able to exploit a wider diversity of resources. One good example of this in cetaceans is the case of bottlenose dolphins feeding from trawler discards in Moreton Bay, Australia – one section of the population had for decades fed on these discards, but when the fishery closed, were able to revert to pre-trawling foraging and also rebuild social bonds with dolphins that had never fed in this way (Ansmann *et al.*, 2012). This resilience acts as a behavioural buffer to ecological change, but comes with risks – adaptation through behaviour can mask growing problems within an ecosystem or habitat, so, as resource bases are changing then the animals switch primary prey, but once that buffer is exhausted, the consequences for the cultural population could be more severe and more rapid, and so give managers less time in which to respond.
Complication of determining anthropogenic influence versus maladaptive culture	Mass stranding in some species (for example pilot whales) may be linked to conformist cultures (Rendell and Whitehead, 2001) – the drive to stay with the group overrides short term behavioural payoff assessments by individuals, and while broadly adaptive, can be locally maladaptive when entire groups end up stranded. However, strandings can also result from anthropogenic factors, such as noise (Frantzis, 1998) and so understanding human-induced impacts on cultural populations may at times be difficult to separate from naturally occurring stranding events, because sometimes cultural behaviour can be maladaptive.
Seeking human interaction behaviour	While not necessarily a culturally transmitted behaviour, individuals in some social cetaceans actively solicit interactions with humans. This can be apparently misdirected social drives (Simmonds and Stansfield, 2007; Eisfeld *et al*., 2010) or looking for food by begging (Mann and Kemps, 2003; Samuels and Bejder, 2004; Donaldson *et al.*, 2012). In the latter case, such interactions are, when studied, almost universally detrimental.
No obvious significance for conservation in some cases	Not all cultural behaviour will have conservation implications. This is particularly true for behaviours that appear to be play, or that take arbitrary form. So for example, the spread of tail-walking in bottlenose dolphins (Bossley & Rendell in prep), or salmon carrying in orcas (Whitehead *et al.*, 2004), currently have no known conservation significance. However, this could potentially change over time if behaviours spread to large proportions of a population.

Table 1: Potential relevance of culture to cetacean conservations efforts: some examples (note that examples of cultural behaviour can have implications for more than one conservation issue)

References can be found in Annex 4.

In addition to issues associated with social learning, Table 2 shows **Examples of unique conservation concerns for highly social cetaceans associated with their complex social systems**:

Issue	**Examples**
Social disruption from hunting/killing of key individuals	Loss of foraging knowledge, for example of timing/variability of fish runs (Southern Resident orcas, US and Canada) Increased survival of sons linked to survival of their post-reproductive mothers (Resident orcas, US and Canada) Loss of risk avoidance knowledge (avoidance of ice entrapment by beluga and narwhal) Increased predation risk due to loss of social connection and "babysitting" by relatives and non-relatives (sperm whales) Existence of post-reproductive female pilot whales implies an important role for them, perhaps similar to post-reproductive mothers in orcas
Atypical stranding of entire social groups as a result of human activity	Potentially the result of mal-adaptive social pressures or group cohesion (beaked whales, Canaries, Mediterranean; common dolphins, UK; melon-headed whales, Madagascar; pilot whales)
Fragmentation/fission/dispersal of social groups from hunting, chasing, or other harassment, leading to lower survival and/or fecundity	Separation of mother and calves (Eastern Tropical Pacific dolphins)
Sex-biased human-caused mortality leading to decreased survival or fecundity from a skewed sex ratio	Insufficient males or females for mating (Eastern Tropical Pacific sperm whales)
Greater risk of extirpation from existence in smaller population or subpopulations units	

Table 2: Conservation concerns for highly social cetaceans associated with their complex social systems

The experts noted that the presentations at the workshop had shown clearly that there was a vast array of examples of cultural behaviours. Regrettably, however, there was limited literature on the subject. It was suggested that the information presented over the two days of the workshop was worthy of being developed further into a scientific paper, which should focus on the conservation importance of considering culture in cetaceans. It was agreed that the paper would take a wide view of culture and include various aspects of social complexity that the discussions had also touched upon. Luke Rendell kindly offered to produce a first draft, which could include a range of examples, such as cooperative fishing between dolphins and humans, and the issue of how removing key individuals could have an effect on the whole population, as had been seen from the elephant case study. In addition, Mark Peter Simmonds was encouraged to write a new review paper on solitary dolphins.

Given that some governments had already included cultural factors in their management practice, it was agreed that an overview of these examples should be included in this report, as shown in Table 3:

Population / Cultural Unit	**Nation**	**Details**
Southern Resident orcas, *Orcinus orca*	Canada and USA	Southern Resident orcas: Canadian Government: • Reviewed by COSEWIC (Committee on the Status of Endangered Wildlife in Canada) in 1999 and 2001 • Listed under Species at Risk Act as Endangered in 2001 – Southern Residents separate Designatable Unit – "acoustically, genetically and culturally distinct" US Government (Endangered Species Act): • Reversal of 2002 decision by NMFS (National Marine Fisheries Service) in 2004/2005 – Southern Residents recognized as "Distinct Population Segment" in 2004 and listed as Endangered in 2005 – "differences in cultural traditions, and the Southern Residents may have unique knowledge of the timing and location of salmon runs"
Southern Right whales, *Eubalaena australis*	Australia	Southern right whales show maternally-directed fidelity to migratory destinations, which can be viewed as a type of cultural memory (Carroll *et al*. 2011). This cultural memory appears to have contributed to the development of distinct matrilineal genetic stocks in southeast and southwest Australia, identified by significant differences in maternally-inherited mitochondrial DNA. Demographic independence of the two Australian stocks is highlighted by dramatically different recovery rates and they are considered distinct management units in the Australian Government Conservation Management Plan for the Southern Right Whale 2011-2021 (Department of Sustainability, Environment, Water, Population and Communities 2012 http://www.environment.gov.au/resource/conservation-management-plan-southern-right-whale-recovery-plan-under-environment) and the International Whaling Commission.

Population / Cultural Unit	**Nation**	**Details**
Southern Right whales, *Eubalaena australis*	New Zealand	Southern right whales show maternally-directed fidelity to migratory destinations, which can be viewed as a type of cultural memory. This fidelity appears to isolate the New Zealand (NZ) population on an evolutionary timescale, as shown by the differentiation in maternally-inherited mitochondrial DNA haplotype frequencies between Australia and NZ, and on a generational timescale, as shown by paternity analyses indicating the population is relatively demographically closed (Carroll *et al.* 2012). It also contributes to the patchy nature of recovery in NZ, with large concentrations of whales in the sub-Antarctic but infrequent sightings of the species around mainland NZ (Carroll *et al* 2014). The NZ population is recognised as a distinct stock by the International Whaling Commission and the NZ Department of Conservation (http://www.doc.govt.nz/conservation/native-animals/marine-mammals/whales/southern-right-whales-tohora/facts/).
False killer whales, *Pseudorca crassidens*,	USA, Hawaiian Islands	Status review in 2010 under the U.S. Endangered Species Act (ESA) for the insular population of false killer whales around the main Hawaiian Islands (Baird 2009; Oleson *et al.* 2010) involved assessing whether the population qualified as a Distinct Population Segment (DPS) under the ESA and whether the DPS met a variety of "significance criteria". One criterion evaluated was cultural diversity. The status review concluded that "Hawaiian insular false killer whales represent a significant cultural unit independent of other false killer whale populations" (Oleson *et al.* 2010), and along with genetic and ecological evidence the population thus qualified as a DPS under the ESA and was considered significant to the taxon. This population was listed as endangered under the ESA in 2012.

Table 3: Examples of management decisions made on the basis of cultural units

References can be found in Annex 4.

16. Recommendations on How Conservation Policies and Actions Should be Affected by Data on Cetacean Culture

The group discussed which recommendations should be forwarded to the CMS Scientific Council. Given the strong evidence for the importance of taking culture and social complexity into consideration in conservation efforts for such species, the participants concluded that while biologists studying elephants, primates and cetaceans were becoming more and more aware of these issues, there was a need to get the message out to the conservation management community. It was therefore agreed that not only should the Council be encouraged to continue work on this issue, but there would also be merit in suggesting the development of a draft resolution for submission to COP11.

The recommendations of the workshop can be found in Annex 2.

D. Concluding Remarks

The Chair, Giuseppe Notarbartolo di Sciara, thanked CMS for inviting all the experts to this forum, and expressed his hope that it would have a positive outcome for the species whose cultural attributes had been discussed.

Fernando Spina, Chair of the CMS Scientific Council, noted in closing that while he had expected it to be a very stimulating meeting, it had greatly exceeded his expectations. He concluded that this was exactly the kind of initiative that CMS needed, providing a basis for conservation decisions to be made based on sound science.

Annex 1

Abstracts: Background Presentations

Social Complexity, Culture and Modern Conservation Efforts

Philippa Brakes, Whale and Dolphin Conservation

Competition is no longer regarded as the single biggest driving force for evolution. There is growing evidence that cooperation and other positive social interactions play an important role in influencing evolutionary development (Sussman and Cloninger, 2011). Silk (2007) argues that sociality can be beneficial for mammals for a range of reasons including providing: protection from predators, access to resources; mating opportunities; or reducing vulnerability to infanticide. However, sociality can also incur costs; it can increase competition over some resources, may increase competition between mates, potentially increases exposure to infection and conspicuousness to predators.

There is now strong evidence for a range of species that the quality and nature of social relationships has measureable fitness consequences. One aspect of social complexity which may have particular significance for conservation efforts is culture. Since culture may influence how a particular social group, or cultural unit responds to specific anthropogenic threats, or conservation measures, it is important that for groups exhibiting culture this aspect of their lifecycle be taken into consideration when evaluating conservation management options.

Whitehead et al. (2004) noted that '…*non-human culture should be integrated into conservation biology when considering populations*…'and further that '…*culture can affect behavioral and population biology, and thus conservation issues, in ways that are importantly different from those traditionally expected from a model that only includes genetic inheritance*'. Whilst further evidence within the scientific literature on the importance of culture has been emerging within the last decade, there has been very little advance in conservation policy in response to this new knowledge.

Current international and domestic efforts to conserve biodiversity focus almost exclusively on maintaining genotypic diversity, whereas sociality and behavioural diversity may also constitute an important aspect of the viability of individuals, social groups, populations and species. It is now timely to turn attention towards also maintaining phenotypic diversity, particularly for some of the socially complex mammalian species.

Silk , J.B. 2007.The adaptive value of sociality in mammalian groups, *Phil. Trans. R. Soc. B* 362: 539–559

Sussman, R. W. and Cloninger, C. R. (Eds.) 2011. Origins of altruism and cooperation, Dordrecht: Springer.

What is culture? Social, Group and Population Level Consequences

Luke Rendell, University of St. Andrews, and Hal Whitehead, Dalhousie University

Biologists and theoreticians use definitions of culture like: behaviour or information transmitted through some form of social learning and shared among members of a community. Thus culture is a flow of information among organisms, a flow that may affect phenotypes and can be a force in evolution not only of cultural variants themselves, but also of genes.

The study of non-human culture has traditionally used the "method of exclusion" by which culture was inferred as behind a behavioural pattern if genetic causation, ontogeny, and individual learning in different environments could be excluded. Excluding causes is logically and practically troublesome, and cultural variants are bound up with genetic patterns in matrilineal societies, and with ecological variation for foraging behaviour. Thus new methods that apportion behavioural variation to genes, environment and culture are being developed and used.

The best evidence for culture in cetaceans includes songs and migration patterns of baleen whales, foraging techniques of bottlenose dolphins, and the calls, foraging techniques, and "play behaviour" of killer whales, as well as the coda dialects and movement patterns of sperm whales. Cetacean cultures include both stable elements largely transmitted through the maternal line, including dialects of sperm and killer whales and foraging techniques of bottlenose dolphins and killer whales, as well as horizontally-transmitted labile elements such as the songs of some baleen whales and "fads" in killer whales. Culture is most conclusive when norms of behaviour change over time periods less than lifetimes, or when ecological and genetic measures are explicitly included in quantitative analyses. Culture allows cetaceans to efficiently utilize oceanic resources that have very considerable variability over large spatial and temporal scales. It also intensifies their interactions with humans for good—ability to adapt to anthropogenic change—and ill—depredation. Culture seems an important determinant of a wide range of behaviour for all the best studied species. In comparison with non-human primates, cetacean culture includes little tool-use, but more vocal behaviour. Bird song is also partially cultural, but culture seems to affect a wider range of behaviour in cetaceans. There are suggestions that cultural processes in cetaceans include symbolic marking, affect fitness, and lead to gene-culture coevolution, all attributes previously believed to be unique to humans.

Consideration of Genetics and Culture in Great Ape and Cetacean Conservation

Michael Krützen, University of Zurich

In general, geographic variation in an organism's traits is often seen as a consequence of selection on locally adaptive genotypes. However, developmental plasticity may also play a role, especially in behaviour. Behavioural plasticity includes social learning of local innovations (''culture''). Cultural plasticity is the undisputed and dominant explanation for geographic variation in human behaviour. I present long-term data documenting extensive geographic variation in behavioural ecology, social organization, and putative culture of orang-utans. I show that genetic differences among orang-utan populations explain only very little of the geographic variation in behaviour, whereas environmental differences explain much more. Moreover, variation in putative cultural variants is explained by neither genetic nor environmental differences, corroborating the cultural interpretation.

I also present data on ecological consequences of culturally transmitted tool use. In Shark Bay, particular bottlenose dolphins ('spongers') use marine sponges during foraging. To date, evidence of whether this foraging tactic actually provides access to novel food items is lacking. I present used fatty acid (FA) signature analysis that identified long-term dietary differences between spongers and non-spongers, as revealed by both univariate and multivariate. Furthermore, culturally transmitted tool use leads to fine-scale genetic structure within this population, as I will show for maternally transmitted (mtDNA) genetic markers. Due to cultural hitchhiking, there is a significant mtDNA/habitat correlation, which cannot be explained by standard genetic models. Thus, it appears that cultural transmission of tool use in dolphins, as with humans, allows the exploitation of an otherwise unused niche and can lead, on a modest scale, to the change of genetic structure.

Although historically it has been good scientific practice to assume canalized development as the null model, we might now have to question its adequacy for long-lived animals that rely on extensive external inputs, including social ones, during development. First, long-lived animals are likely to be confronted with variation over time in environmental conditions, and being usually large-bodied also tend to roam so widely that they may encounter many different conditions. Second, these animals may not have the demographic potential to respond rapidly to selection for local adaptation, forcing them to rely more on plasticity to maintain locally adaptive phenotypes. The indications for extensive social learning and cultural variation in other long-lived organisms such as dolphins, whales, elephants, monkeys, and some birds support the idea that cultural plasticity is an important pathway to local adaptation.

Genes and Culture: Loss of Migratory Cultural Memory and Recolonisation

Emma Carroll PhD, University of St Andrews

Migratory fidelity can be viewed as a 'cultural memory' of suitable migratory destinations, which can be extirpated along with the whales that formerly inhabited an area. In southern right whales (SRW), there is evidence that cultural transmission of migratory destinations is mediated through maternally-directed learning of such habitats. Here I focus on SRWs around New Zealand and Australia, where historically the species was found in large aggregations during the austral winter. Today there is spatially variable recovery, with the New Zealand sub-Antarctic (NZSA) and southwest Australia (SWA) wintering grounds showing strong signs of recovery, while the mainland New Zealand (MNZ) and southeast Australia (SEA) wintering grounds show little increase in the past few decades. We used DNA profiles, comprising genetically identified sex, multilocus microsatellite genotype and maternally-inherited mitochondrial DNA (mtDNA) haplotype, from over 800 whales to examine individual movement, population structure and paternity. There was no significant genetic differentiation and evidence of direct movement between MNZ and NZSA. Given the current and historical evidence, we hypothesise that individuals from the NZ sub-Antarctic are slowly recolonising MNZ, where a former calving ground was extirpated. In contrast, we suggest that the SEA population is distinct from SWA based on significant differentiation in mtDNA haplotype frequencies and the contrasting patterns of recovery. Paternity analysis, based on data from NZSA, was consistent with the hypothesis of local mating, suggesting this wintering ground is a reproductively isolated population. Taken together, it seems that while maternally-directed fidelity isolates SRW populations on an evolutionary timescale, male fidelity acts as an isolating mechanism on a generational timescale. The cultural traditions to migratory destinations, demonstrated in both males and females, appears to be a strong driver in the patterns of recovery and recolonisation we see in the SRW today.

Individual Foraging Specializations in Marine and Terrestrial Mammals

Richard C. Connor, University of Massachusetts Dartmouth

Connor (2001) suggested that individual foraging specializations were more common in marine than terrestrial mammals, possibly owing to habitat differences in one or more of five ecological parameters: prey diversity, prey biomass and replacement rate, predator mobility, practice rewards and seasonality. Subsequently, an influential review by Bolnick et al. (2003) indicated that individual foraging specializations were widespread in many taxa, including terrestrial mammals. However, the majority of terrestrial mammals listed in their table were characterized by dietary differences among spatially separate individuals, as occurs when individuals on different territories experience different resource abundances. It is striking that nothing has been described from terrestrial mammal studies that is comparable to the multiple specialized foraging tactics found among individuals with overlapping ranges in marine mammals as disparate as bottlenose dolphins and sea otters. A review of recent sea otter work points to dependability (which might combine reduced seasonality and a high biomass/replacement rate in the marine habitat) and learning (including practice rewards) as key factors in resource specialization. Predator mobility (associated with low cost of locomotion and large day ranges) is likely not a key factor in the sea otter case but may be important in marine mammal taxa with low costs of locomotion. A recent possible terrestrial example is instructive with respect to resource diversity. Orangutan diet overlap is not predicted by range overlap and maternal transmission is implicated. The range of food items consumed in the orangutan population is very high as is dietary overlap. Thus, striking prey specializations may be associated with some minimal amount of prey diversity (so long as they are sufficiently abundant) such as can be maintained by top-down predation (as in the sea-otters) or other mechanisms. Conservation strategies will improve with a better understanding of the ecology of foraging specializations.

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Implications for Conservation Efforts for Socially Complex Mammals: Culture and the Great Apes?

Jim Moore, University of California San Diego

By nearly any definition, chimpanzees are cultural animals (less is known about the other apes), and socially-mediated learning is (nearly?) ubiquitous in primates. It is unclear whether "joining the culture club" adds anything to popular perception of which species are worth conserving (over and above apes' profound behavioral and physical similarities to humans), and expanding membership may dilute its PR value; both are empirical questions.

For translocations and reintroductions, social learning/culture must be considered; this is expensive (e.g., US$ > 50,000 per individual chimpanzee reintroduced). It is less clear how culture is to be used in deciding which animals to conserve, because primates are tied to place; the adaptive potential of a variant is tied to the location where it is found until proven otherwise, and that proof is likely to be hard to obtain. Thus, prioritizing one ape community over another (elsewhere) based on cultural variation is problematic. This is likely to be different when considering migratory/wide-ranging taxa.

Any loss of cultural variants/social knowledge may prove problematic. For example, Goosens et al. (2005 Biol Conserv. 123: 461) report that reintroduced female chimpanzees who joined wild communities tended to return to the reintroduced group after some months, perhaps due to harassment from resident females (transfer is usually permanent among wild chimpanzees, despite such harassment). It is plausible that reintroduced females were less likely to overcome harassment because they are less socially skilled than wild females. van Schaik (2002 Int. J. Primatol. 23: 527) notes that loss of resources that require complex processing may lead to loss of the ability to exploit the resource (unless methods are independently rediscovered). Such effects are likely to be subtle. Whether that means they are likely survivable, or conversely that they won't be noticed until it is too late, is difficult (for me) to predict.

Elephant Matriarchs as Repositories of Knowledge

Karen McComb & Graeme Shannon, University of Sussex

Like many cetaceans, African elephants have large brains, long lifespans and live in tight-knit kin-based units within complex fission-fusion societies. Family groups of related adult females and their offspring are the primary social units in elephant societies and within these the oldest female or matriarch plays an important co-ordinating role. I will present the results from a range of our playback studies showing that these matriarchs act as repositories of knowledge, not only in relation to determining the level of threat posed by other elephants around them but also by predators in the wider environment. Matriarch age was consistently the key factor in determining sensitivity to level of threat, groups with older matriarchs being more adept at focusing their defensive reactions on the genuinely threatening situations – encounters with strange conspecifics and male lions. Even in dealing with human predators there are indications that older matriarchs may have superior discriminatory abilities. The matriarch also appears key in determining the nature of the response, which is very specifically tailored to the threat in hand - playbacks of lion roars are mobbed but rapid defense and retreat is the common reaction to voices of Maasai men. As well as highlighting the importance of conserving these oldest individuals, I will use our studies to illustrate how disruption to the social fabric through human activities can have severe impacts on this crucial knowledge base in long-lived, cognitively advanced mammals such as elephants and whales.

Threats to Cetaceans in the Modern Marine Environment

Mark Peter Simmonds, Humane Society International

All cetacean populations are affected by human activities. Many are affected simultaneously, or over the course of their migrations or life-times, by many different activities. The primary threats can be divided into those where the animals are deliberately targeted (whaling, removals for captivity, whale watching and anti-predator actions) or where impacts are incidental (which is not the same thing as unknown or accidental) to the primary purpose of the activity (noise pollution, chemical pollution, marine debris, climate change, bycatch and prey depletion).

The intensity and significance of these threats vary for each population and, whilst it might be expected that animals living closest to our major conurbations will be most affected, our fishing and other activities are now conducted far from land, including fossil fuel prospecting and extraction which has moved into ever deeper waters. Retreating polar ice is opening up waters to such activities, as well as allowing more ship movements generally. The vulnerability of ice-associated cetaceans to their changing environment, including increasing human activities, is unclear.

New threats to cetaceans have emerged in recent years. Noise – whilst its significance is often hotly disputed – is now being addressed through a number of international bodies, and much the same thing could be said for boat-strikes, marine debris and whale watching. Amongst these bodies, the International Whaling Commission has emerged as a forum where both scientific aspects of these matters and management and mitigation are increasingly considered. The Convention for Migratory Species and its daughter agreements are also important.

Attempts to mitigate or manage threats typically refer to population parameters (principally population size) and management areas. This provides at least the temptation to calculate sustainable removal rates from such units. However, the elaboration of even nominal ‘safe removal’ levels as a reference (if not a target), requires several key factors to be known with a high level of certainty, including the actual level of removal and the unit of conservation concerned. The significance of cultural units to such approaches requires urgent elaboration.

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Killer Whale Ecotypes in British Columbia: the Role Culture has Played in Identification, Definition and Protection

John K.B. Ford, Fisheries and Oceans Canada

Killer whales are high trophic-level social predators that have a cosmopolitan distribution in the world's oceans. Only a single species, *Orcinus orca*, is currently recognized globally but there are multiple genetically and socially discrete regional populations that differ in morphology and ecology and often co-occur in sympatry. Some of these distinct ecotypes have been suggested to warrant status as separate species. The ecological specialisations and related foraging tactics within killer whale populations appear to be learned behavioural traditions that are passed across generations by cultural transmission. The same is true of various other aspects of their behaviour, such as population- or group-specific vocal patterns. Life history parameters and social structure of killer whales facilitate the development and maintenance of multi-generation cultural traditions. Killer whales are slow to mature, long lived and remain with close matrilineal kin for extended periods, sometimes for life. Some of the best known killer whale ecotypes are found in coastal waters of British Columbia, where on-going annual field studies have been conducted for over four decades. Three sympatric but socially-isolated ecotypes occur sympatrically in the region – Residents, which specialize on salmon prey, Transients (or Bigg's), which specialize on marine mammals, and Offshores, which appear to specialize on sharks. The Resident ecotype is further divided into two distinct subpopulations, the Northern and Southern Residents, which have overlapping ranges but also maintain social isolation from each other. All four of these discrete populations are considered to be separate Designatable Units (DUs) in Canada for conservation and management purposes based on genetic (mtDNA) and cultural distinctiveness. Each is listed as either Endangered or Threatened under Canada's Species At Risk Act and recovery strategies have been developed that explicitly recognize the importance of maintaining cultural identity and continuity of these DUs.

Social and Behavioural Factors in Cetacean Responses to Over-exploitation: Are Odontocetes Less 'Resilient' than Mysticetes?

Paul R. Wade, NOAA Fisheries

Many severely depleted populations of baleen whales (Mysticeti) have exhibited clear signs of recovery from exploitation whereas there are few examples of recovery of severely depleted populations of toothed cetaceans, or odontocetes (Odontoceti). We have hypothesized that odontocetes are less resilient to intensive exploitation than mysticetes and that this difference is due, at least in part, to social and behavioural factors. Clearly, a part of the lack of resilience to exploitation stems from the life history of odontocetes, particularly their relatively old ages at first reproduction and low calving rates. However, an additional factor that may contribute to this lack of resilience is that odontocetes exhibit a diverse array of social systems, ranging from the relatively hierarchical and stable pattern of killer whales and sperm whales, to the classic fission-fusion pattern of many dolphins. In at least some odontocetes, survival and reproductive success may depend on such things as: (a) social cohesion and social organization, (b) mutual aid in defence against predators and possible alloparental care such as 'babysitting' and communal nursing, (c) sufficient opportunities for transfer of 'knowledge' (learned behaviour) from one generation to the next, and (d) leadership by older individuals that know where and when to find scarce prey resources and how to avoid high-risk circumstances (e.g. ice-entrapment, stranding, predation). We found little evidence of strong recovery in any of the depleted populations examined, even when decades had passed since the phase of intense exploitation ended. Their relatively low population potential rates of increase mean that odontocete populations can be over-exploited with take rates of only a few percent per year. In several species of highly social odontocetes, there is evidence that exploitation could have effects beyond the simple dynamics of individual removals. Four species showed evidence of a decrease in birth rates following exploitation, from mechanisms hypothesized to include a deficit of adult females, a deficit of adult males, and disruption of mating systems involving dominance by a few individuals. The evidence for a lack of strong recovery by many heavily exploited odontocete populations indicates that future management of exploitation should be more precautionary.

Learning on line: The spread of a novel foraging behavior among sperm whales (*Physeter macrocephalus*) in the Gulf of Alaska: exploring models of social learning

Sarah Mesnick, NOAA Fisheries Service

Fishing, farming and ranching provide opportunities for wild animals to prey on resources concentrated by humans, a behavior termed depredation. In the Gulf of Alaska, observations of sperm whales depredating on fish caught on demersal longline gear dates back to the 1970s, with reports increasing in the mid 1990s. Sperm whale depredation provides a unique opportunity to study the temporal and spatial spread of a novel foraging behavior within a population. Data were collected during National Marine Fisheries Service longline surveys using hook-and-line gear in waters off Alaska from 1998 to 2010. We evaluated whether observations of depredation fit predications of social learning by using two models of social transmission in tandem: the Diffusion Curve and Wave of Advance. We found that the data were consistent with social learning for both models, and provide circumstantial evidence for social transmission of depredation, yet we provide caveats in both methods and models. We discuss how changes in human activities (fishing methods and regulations) in the region have created a situation in which there is spatial-temporal overlap with foraging sperm whales, likely influencing how the behavior spread among the population. We describe various insights learned about mitigation and human-animal coexistence in order to improve management and conservation of highly social marine mammals.

Identifying Demographically-Independent Populations of False Killer Whales and Bottlenose Dolphins in Hawaiian Waters

Robin W. Baird, Cascadia Research Collective

False killer whales and bottlenose dolphins have been studied around the main Hawaiian Islands since the mid 1980s and 2000, respectively. Fisheries interactions in Hawaiian waters have been documented for both species. False killer whales are the species most frequently recorded as bycatch in the U.S.-based longline fishery, and levels of serious injury and mortality have exceeded the Potential Biological Removal level since abundance estimates for false killer whales first became available for Hawaiian waters. Three independent lines of evidence are used to assess social organization, population structure and movements of both false killer whales and bottlenose dolphins in Hawaiian waters: 1) satellite tagging, providing information over periods of weeks to months; 2) photo-identification, providing information over periods of months to years; and 3) genetic analyses of biopsy samples, providing information over generations. For bottlenose dolphins, data are available for four different island areas: Kaua‘i and Ni‘ihau, O‘ahu, the “4-island area”, and Hawai‘i Island. Photo-identification data indicate high site fidelity to specific island areas, with analyses of dispersal among island areas estimated at less than 1% per year (Baird et al. 2009). Analyses of genetic data indicated genetic differentiation and low dispersal rates for bottlenose dolphins among the main Hawaiian Islands (Martien et al. 2011). Limited satellite tagging data available for individuals from Kaua‘i, Lana‘i, and Hawai‘i Island also indicate high site fidelity. Combined evidence suggests there are four demographically independent populations of bottlenose dolphins among the main Hawaiian Islands, which have been recognized by the

National Marine Fisheries Service as distinct stocks. For false killer whales, satellite tagging, photo-identification and genetic data indicate the existence of three different populations: insular populations in the main Hawaiian Islands and in the northwestern Hawaiian Islands, and a pelagic population (Chivers et al. 2007; Baird et al. 2008, 2010, 2012, 2013; Martien et al. in press), with substantial overlap among the populations. Individuals from the pelagic population are known to use both U.S. and high-seas areas. The main Hawaiian Islands insular population was recognized as a Distinct Population Segment under the U.S. Endangered Species Act, and the Biological Review Team noted the population represents "a significant cultural unit independent of other false killer whale populations" (Oleson et al. 2010). This population was listed as endangered in the U.S. in 2012. Analyses of association patterns revealed the existence of three distinct social clusters within the main Hawaiian Islands population, and satellite tag data from two of the three social clusters indicate differences in habitat use and high density areas among the clusters (Baird et al. 2012). An assessment of fisheries-related dorsal fin injuries indicate that the proportion of individuals with evidence of fisheries interactions varies among social clusters. The proportion of individuals with evidence of fisheries interactions ranged from approximately 4% to 13% of the individuals in the different social clusters (Baird et al. 2014). Females are disproportionately documented with evidence of fisheries interactions. Differences in habitat use and the rates of fisheries interactions among social clusters are evidence of group-specific behaviors consistent with cultural transmission.

Ecologically and/or Culturally Significant Units (ESUs and CSUs)

Hal Whitehead, Dalhousie University, and Luke Rendell, University of St. Andrews

One of the more difficult decisions in conservation and wildlife management is defining the populations to be managed and conserved. A consensus is that we should be trying to preserve evolutionarily significant units (ESUs) that contain important, and in some ways unique, biological information. Defining the ESU has proved difficult. It is felt that ESUs should be delineated to preserve both adaptive variation in genes and phenotypes as well as evolutionary divergence caused by spatial and/or temporal isolation. Usually genetic data have been used to distinguish ESUs. However, if important phenotypic variance is culturally determined, then this should also be incorporated. Thus we propose that ESUs should be defined so as to potentially include genes, culture or other methods of information transfer among organisms: " an ESU is a lineage demonstrating highly restricted flow of information that determines phenotypes from other such lineages within the higher organizational level (lineage) of the species" (Whitehead et al. *Biological Conservation* 2004). Alternatively, as proposed by Ryan (*Conservation Biology* 2006) culturally significant units (CSUs) could be considered for species in which culture is an important determinant of phenotype. Cetaceans are perhaps the species where culture is most likely to be relevant when assigning conservation units. Cultural differences were evoked by both Canadian and (eventually) U.S. authorities when assigning the transboundary "southern resident" killer whales to their own conservation unit ("designated unit" in Canada; "distinct population segment" in U.S.A.). Evidence suggests that Pacific sperm whales are more clearly segregated culturally, into clans, than geographically. As the clans respond differently to rises sea temperature, this clan structure should be part of the considerations of the effects of climate change, and other anthropogenic impacts, on the species.

Towards a 'Taxonomy' of Cetacean Culture

Luke Rendell, University of St. Andrews, and Hal Whitehead, Dalhousie University

Defining culture as behaviour or information shared by a group or community that is acquired through some form of social learning, we have classified cetacean cultural behaviour in several dimensions. The strength of evidence varies from definitely culture (the pattern of behavioural variation can be explained no other way), to likely culture (non-cultural explanations are extremely tortuous) to plausibly culture (non-cultural explanations are possible). Lumping forty or so behaviours from these categories, we then classified them taxonomically, by mode of transmission, extent of shared behaviour, behavioural domain, persistence, and conservation implications. Taxonomically, the number of examples roughly follows the number of species at the family level with the majority of examples involving Delphinidae. Vertical transmission of culture from mother to offspring appears particularly important, implying that passing on knowledge is a crucial part of the mother-calf relationship. However, in three of the four most studied species horizontal transmission within generations is implicated, sometimes involving crucial foraging behaviour. Among mysticetes, songs and migration routes are shared at population level, while culture in odontocetes rarely appears to be universal, instead facilitating specialisation and adaptation to new niches at a ranges of scales from large sub-populations down to a tapestry of traits varying at the level of matrilines. Cultural traits are present in communication, foraging, habitat use, migration, and play for both odontocetes and mysticetes. While most recognized cetacean cultural traits persist for multiple generations, some are transient, not lasting beyond a single generation, and a few are highly ephemeral. Cetacean cultures have implications for a range of conservation issues including range recovery following extirpation, generated dependencies on anthropogenic activities, population vulnerability due to specialisation, interactions with climate change, influence on population structure, and increased ecological resilience. Due to lack of information, we did not classify cetacean cultures using transmission mechanisms.

Annex 2

Recommendations of the CMS Scientific Council Workshop on the Conservation Implications of Cetacean Culture

Cetaceans include socially complex species that show evidence of having culture.

The social transmission of knowledge between individuals may increase population viability and provide opportunity for innovation and adaptation to environmental change. However, this transmission of knowledge can also increase the impact of anthropogenic threats or can operate synergistically with anthropogenic threats to compound their impact on a specific social group. Additionally, there are unique conservation concerns facing highly social species.

Based on its deliberations and discussions, the workshop concluded that:

1) The scientific investigation of culture and social complexity in mammals is a rapidly evolving field which is increasingly important for conservation management; and
2) The CMS Family is in a strong position to incorporate this emerging information into species specific agreements and its other work.

As a result, the workshop recommends that the Scientific Council reports to Parties that:

1) Anthropogenic threats to socially complex mammalian species such as but not necessarily restricted to cetaceans, great apes and elephants should be assessed on the basis of their interactions with social structure;
2) The role and dynamics of culturally transmitted behaviours should be taken into consideration when determining conservation measures;
3) Where sufficient data are available CMS should include culture when considering population units to conserve;
4) CMS should consider that the impact of removal of individuals from socially complex species may have consequences beyond simply a reduction in absolute numbers; and
5) For those populations for which the influence of culture and social complexity may be a conservation issue, but for which there are presently insufficient data, a precautionary approach to their conservation management should be applied and the acquisition of necessary data should be prioritised.

The workshop also recommends that:

1) Additional focus is applied to this area in the coming triennium, including:
    a) where possible, comprehensive investigation of culture and social structure across all species that CMS is mandated to consider;
    b) the inclusion of culture in considering the population units to conserve, where data are available;
    c) development of appropriate guidelines for a precautionary approach to the conservation management of culturally and/or socially complex cetacean species, where data are scarce.

An expert group focusing on the conservation implications of culture and social complexity is established under the auspices of the Scientific Council to undertake this work and to report to CMS COP12.

Annex 3

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Annex 4

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