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REPORT OF THE CMS WORKSHOP ON CONSERVATION IMPLICATIONS OF ANIMAL CULTURE AND SOCIAL COMPLEXITY

(Submitted by the Secretariat)

Convention on the Conservation of Migratory Species of Wild Animals

CMS

1ST CMS WORKSHOP ON CONSERVATION IMPLICATIONS OF ANIMAL CULTURE AND SOCIAL COMPLEXITY

Parma, Italy, 12-14 April 2018

REPORT

The Government of the Principality of Monaco were recognized as *Champion Plus* for their generous support and commitment towards marine species conservation for the period 2018–2020. This workshop has been co-funded with the contribution granted by Monaco under the Migratory Species Champion Programme.

Summary of Recommendations

Overarching Recommendations:

- Conserving cultural repositories and capacities (e.g. cultural inheritance systems) should be integrated into the development of IUCN, CMS and other conservation and management strategies, including but not limited to assessing populations and designating units to conserve, *in situ* monitoring, human-wildlife conflict, reintroduction programmes, etc.
- Education and raising awareness about the value of conserving cultural diversity should be a priority of the CMS initiative on culture and social complexity in animals.
- Empirical evidence of behavioural diversity, social learning networks and migratory behaviour and connections should be collected for taxa of relevance to CMS.
- Theoretical models of social transmission and population level effects should be developed to inform mitigation and investigate future scenarios for conservation issues for taxa of relevance to CMS.
- It was further recommended that cataloguing the dimensions of cultural diversity in animals may be important to assist in:
  - identifying and conserving cultural capacities and repositories
  - driving conservation actions and strategies.

Potential key dimensions of cultural traits of note:

- What is the domain of trait? foraging, tool use, migration, habitat utilization, communication, social interactions, etc.
- Who performs the behaviour? Is it specific to a particular age/sex class, aspects of age-structure populations (demography), social status within social units, social connectedness?
- What is the spatial occurrence of the trait? E.g., is it a proportion of the range of population /sub-species.
- What is the temporal nature of the trait or the information it conveys? Does the trait have temporal variables, what is its frequency of occurrence and does it show long-term persistence, does the trait convey long-term (e.g., migratory destination) or ephemeral (e.g., food source) information.
- What is the function of the trait? Does it relate to reproduction, growth/maintenance, social relationships, etc. – or no obvious adaptive value?
- Patterns of transmission: evidence of form or forms of cultural transmission, e.g. observational learning, teaching; vertical or horizontal transmission.

Further recommendations arising from sub-group discussions:

- Enhance communication around animal culture and social complexity, especially in areas with human-wildlife conflict (HWC)
- Utilize animal – and human – social learning to facilitate better conservation outcomes in HWC and other conservation management strategies.
- Move beyond counting numbers of individuals when assessing the conservation status of highly social species and the outcomes of conservation actions
- Cultural units should now be considered as potentially meriting conservation efforts, contrasting with the traditional focus on species, and on genetics (Table 3 provides suggestions for criteria that may be used to consider conservation strategies in culturally defined units)
- Consider the overall age and social structure of populations to maintain cultural capacity.

- If particularly important classes of individuals can be identified (e.g. social brokers, matriarchs, individuals with resident knowledge), focus on protecting these individuals and connections.
- Where possible maintain population connections across the species' range.
- Identify important keystone "information source" species within wider species communities, and consider their impact on the conservation of target species.
- For reintroduction programmes:
    - Wherever possible, individuals should be exposed to experienced conspecifics interacting with a range of stimuli that they are likely to encounter in the wild (e.g. conspecifics; foods; predators)
    - Where cultural knowledge has been entirely lost in the wild, human tutors may need to be used to re-establish desired behaviour in the first instance
    - In species that show parental care, intensive support should be provided to achieve breeding in reintroduced populations, so that future generations can learn from the most competent surviving conspecific parental models
    - Programmes should take into account likely social learning biases – e.g. individuals may be more likely to learn from adults, or from resident individuals
    - Programmes should monitor and maintain detailed data encompassing individuals' social interactions (e.g. social affiliations; exposure to human or conspecific models) and exposure to stimuli pre- and post-release
- Recognizing that culture is another aspect of biology that should be considered within existing conservation initiatives, it is recommended that the social learning and culture are integrated into efforts to:
    i. assess populations and designate units to conserve
    ii. assess the impact of introgression and hybridisation
    iii. manage endangered populations and reintroduction schemes
    iv. mitigation planning for environmental change and development
- Develop rapid assessment tools and emerging technologies to provide direct and indirect evidence of social transmission, migration routes, social networks, as well as anthropogenic effects on behaviour, informing conservation and management
    i. Acoustics: passive acoustic monitoring (Wrege et al. 2017); acoustic identification of population units; autonomous recording with identification software (Zimmer 2011 Passive acoustic monitoring of cetaceans, Cambridge University Press)
    ii. Biologging: movement and activity tracking; direct and indirect encounter mapping for social network building (Krause et al. 2013, Tr. Ecol. Evol. 28:541-551; Kays et al. 2015, Science; Hussey et al. 2015, Science)
    iii. Genetic and genomic techniques including eDNA and minimally-invasive sampling to identify kin groups, population structure and migratory connections (Carroll et al. 2018; Arandjelovic and Vigilant 2018)
    iv. Stable isotopes, fatty acids and other biochemical makers to delineate population segments with distinct habitat use, as well as transmission patterns of foraging behaviour
    v. Proxies of culture that can be assessed more easily. For example, in tool-using New Caledonian crows, the idea has been explored to rapidly map possible regional variation in foraging behaviour, using vocal dialects as 'markers' (Bluff et al. 2010, Biol. J. Linn. Soc.). the Pan African Programme: the Cultured Chimpanzee of the Max Planck Institute for Evolutionary Anthropology, is underway using camera traps, quantification of resource availability, and other rapid assessment techniques to survey further diversity of behaviour amongst chimpanzees across 40 African study sites, and has already revealed forms of behaviour previously unknown (Kuhl et al. 2016).

Further, it was noted that whilst the efforts of CMS are focussed on migration across jurisdictions, the migration of some species, where the migration routes are contained within one nation, may warrant special attention. For example, there are some species where migration routes are entirely contained within one jurisdiction that show migratory behaviour that is likely to be influenced by social learning, and where some aspects of migration routes may represent cultural traditions. For example, several species of Australian bird, including but not restricted to Orange-bellied Parrots (*Neophema chrysogaster*) and Swift Parrots (*Lathamus discolor*), exhibit a high degree of sociality in foraging and migration patterns. It was noted that these species could be highlighted for future action by national authorities, and that research on these species could be useful and informative for the broader aims of understanding these process in species that do migrate across international jurisdictions (particularly since the total migration distance of the two examples given are probably of a longer absolute distance than of many migratory species that cross multiple national jurisdictions).

Report of the Workshop

A. Opening and Introductions

The meeting opened with welcoming remarks from Giuseppe Notarbartolo di Sciara, Fernando Spina and Philippa Brakes, expressing gratitude to the hosts and sponsors of the workshop, the Appennino Tosco-Emiliano National Park, the Fondazione Monteparma, and the Principality of Monaco. They also thanked the many workshop participants who had made time in their busy schedules to contribute to the deliberations of the workshop.

B. Background Presentations

1. CMS background

1.1. History, context and mandates for the workshop

Heidrun Frisch-Nwakanma of the CMS Secretariat provided an overview of CMS, its objective, mechanisms, institutional framework and the context for the workshop. She explained that the Convention's interest in the subject had started in 2011, when Resolution 10.15 Global Programme of Work for Cetaceans requested the Scientific Council to investigate relevance of this emerging field of science to cetacean conservation. This had resulted in a workshop focusing mostly on cetaceans in 2014 and a first resolution being adopted on the issue the same year. In October 2017, at the 12th Meeting of the Conference of the Parties to CMS (CMS COP12), this resolution had been revised and was now explicitly referring to animal culture, expanding the scope of work to all taxa covered by CMS.

The Expert Working Group on Animal Culture and Social Complexity, established in 2015 and working through an online workspace, was directed by CMS COP12 to "[d]evelop a list of priority species listed on the CMS Appendices for a comprehensive investigation of culture and social structure and commence more detailed analysis as appropriate, including for example developing a list of key factors that should be taken into consideration for effective conservation" (Decision 12.75 b.). To assist the Expert Working Group, the Secretariat was requested to convene this workshop, specifically with the aims of developing a list of key factors for identifying priority species and populations listed under CMS where social learning may influence their conservation, and to explore the opportunities for engagement across the CMS daughter agreements (Decision 12.76). The outputs of this workshop would accordingly go to the Expert Working Group, who would use them to fulfil their mandates, and report their findings to the Scientific Council, which would be responsible to make recommendations to the 13th Meeting of the Conference of the Parties (Decision 12.77).

1.2. CMS Scientific Council, species appendices and progress to date

The Chair of the CMS Scientific Council, Fernando Spina, provided more detail on the role of the Scientific Council in this process to date and highlighted the definition of migratory species within the context of the Convention text which defines migration thus:

"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 noted that the Convention's definition provides a geo-political perspective of a natural phenomenon, which includes cyclical dispersal across national jurisdictions, hence the inclusion of species such as gorillas on the appendices.

2. Social learning and conservation across taxa: definitions, methods and relevance

Philippa Brakes noted the challenges and opportunities associated with moving this work across taxa and provided some orientation for efforts to date. She highlighted the definitions used by the CMS Expert Working Group on culture and their use of the exclusionary process for assessing the plausibility that social learning, rather than ecological or genetic factors may be driving specific behaviour within a social group. As a starting point she suggested a number of factors which could be important for considering the conservation implications of various aspects of sociality including, ontogeny, social structure, social role and social learning mechanism.

C. Conservation Priorities for CMS-listed Species

Sub-group discussions

Facilitated by Mark Simmonds, participants then worked in four sub-groups to explore the following issues as they related to CMS:

- Worlds that collide: Human-wildlife conflict (HWC) and anthropo-dependence
- Wildlife sages: Conserving valuable cultural diversity in wildlife
- Socio-geography: Social learning, range recovery and migration, island populations
- Socio-vulnerability: Specialization versus ecological resilience

The groups recorded the outcome of their discussions in the following reports from each sub-group. More generally it was agreed that the goals of conservation were to (1) determine which aspects of biodiversity were in need of conservation; (2) identify and evaluate threats to biodiversity; and (3) establish means of mitigating these threats with the overarching aim of maintaining evolutionary or adaptive potential, which was the ability of species/populations to respond to selection by means of phenotypic or molecular changes (Eizaguirre and Baltazar-Soares, 2014). Animal culture and the use and transfer of social information were highly relevant to each of these aims (Greggor et al. 2016).

Social learning of behavioural variants and potential resultant culture generated phenotypic diversity and influenced population viability, demography and evolutionary or adaptive potential by allowing adaptive information to spread through groups and between parents and offspring. Thus, cultural variation could be considered a crucial element of biodiversity to be conserved. In addition, cultural traits in some behavioural domains might be used as a proxy for assessing cultural traits in other domains that might be more challenging to measure in the wild (for example, measuring song or vocalizations mighty be easier or more efficient than measuring tool use). Culture could also lead to the promotion of isolation between groups, for example, between those that had distinct acoustic, migratory or foraging traditions.

In addition, an often-overlooked threat to biodiversity resulted from perturbations to patterns of cultural transmission that limit the acquisition of fitness-related knowledge and skills. Finally, by implementing protocols that maintained or in some circumstances even re-created channels for cultural transmission, we might help to maintain healthy populations or re-establish populations that had declined or even gone extinct in the wild.

GROUP A
Worlds that collide: Human-wildlife conflict (HWC) and anthropo-dependence

Scope

While the overarching workshop theme was culture and social complexity, the sub-group focused discussions on social structure and social learning, as the substrate for culture to emerge.

The group discussed several ways in which "worlds that collide" occurred and focused on four of these: (a) the impact of socially learnt animal behaviour on human activities, more broadly termed "human wildlife conflict" (HWC), which included interactions such as crop raiding, and depredation of commercial fisheries or livestock; (b) human impacts on animal social structures and cultural traditions, which could have population-level consequences; (c) the influence of climate change on animal social learning and sociality; and (d) a lack of understanding of animal culture and social complexity which could confound conservation efforts.

Examples of these collisions included (see Table 1 for additional examples):

a) Impact of socially learnt animal behaviour on human activities

African elephants commonly foraged on crops wherever they co-occurred with farmers and cultivated food sources are usually preferred by elephants, even when wild food sources were plentiful. Electric fences might deter crop raiding, but they were extremely expensive to deploy and elephants could quickly learn techniques to break them, increasing maintenance costs. All elephants learned from each other, particularly young males which could learn raiding techniques from experienced older males, and which often raided in the company of close associates (Chiyo et al. 2012). While raiding defended farms, male elephants had been observed to guide and protect younger males from farm defenders. Experienced fence breakers served as a repository of knowledge and spread this behaviour among a population, exacerbating human-wildlife conflict. Similarly, in chimpanzees information on which crops were raided might also be socially learned (McLennan and Hocking 2014).

b) Human influences on animal social structure and cultural traditions

During fishing operations for tuna in the eastern tropical Pacific Ocean social disruption caused by repeated chase, encirclement, and release of dolphins might have negative impacts on survival and reproduction, which might impede population recovery, even in the absence of direct mortality (Wade et al. 2012). Pelagic dolphins were thought to live in fission-fusion societies in which small social units (e.g., mother-calf pairs, bonded adult females, nursery groups, juvenile sub-groups, male alliances) aggregated in large, dynamic schools. Tuna-purse seine operations might cause social separation of units or might disrupt the mating system (especially for species where few males controlled most mating opportunities, Perrin and Mesnick 2003);

c) Lack of understanding of animal culture and social complexity confounding conservation efforts

A lack of understanding of animal sociality might actually serve to contradict intended management objectives. Unselective lethal control of wolves had been shown to decrease pack stability and territory persistence, which increased the number of breeding pairs and resulted in compensatory numerical responses (predator density) by surviving wolves (Brainerd et al. 2008, Borg et al. 2014).

d) Influence of climate change on animal social learning and sociality

Global warming was a serious issue for lizards and had already resulted in population-level extinctions in many species (Sinervo et al. 2010). Lizards were capable of social learning (Noble et al., 2014) and their cognitive ability was affected by warming incubation environments (Amiel et al. 2017). Under global warming, lizards had a more restricted daily activity period and less opportunity to learn socially from conspecifics, which could impact on foraging success and information transfer about key environmental variables.

The group noted that such "collisions" generated conservation risk in two senses. First, when animal behaviour generated negative impacts on human activity (as in point (a) above) and second, when human activities generated negative impact on animal populations (points (b) – (d), see also Table 2). The former could include injury to humans or loss of income and could cause unfavourable attitudes towards animals and decrease interest in conservation. The latter mighty, directly or indirectly, disrupt animal social systems with negative impacts on survival and reproduction with resulting population-level consequences. The group determined that climate change issues were beyond the scope of these discussions, but found common issues with the remaining collisions: they highlighted the need for conservation interventions that considered site-specific human and animal context and the need to bring stakeholders together early. The group also discussed the definition of "conflict" including the distinction between "impacts" and "conflict" (see below).

We recognized that many other "worlds that collide" problems existed but were not addressed here. These included issues such as provisioning, in which animals became dependent on humans (such as Bottlenose Dolphins or bears; Foroughirad and Mann 2013; Kirby et al. 2016), reintroduction and rehabilitation, among others.

Recommendations

Recommendation 1. Enhance communication around animal culture and social complexity, especially in areas with human-wildlife conflict (HWC).

The group noted that resolving issues of human-wildlife conflict (HWC) was important because it would increase tolerance for animals and increase interest in their conservation. Ultimately, the goal was to move from "conflict" to "co-existence" scenarios with active intervention plans. The group discussed the importance of the need to distinguish between "impacts" – e.g., the economic loss due to depredating livestock – and "conflict", which was a social debate and conflict among stakeholders over ways to manage impacting species (Redpath et al. 2013). Mitigating and preventing the impact were expected to prevent and reduce conflict, for the conservation of wildlife and the well-being of people. This assumption admittedly did not account for negative attitudes some humans had toward some wildlife species independently from any impact they might generate (large carnivores are a particular example). Emphasizing the role of culture and social learning in complex social animals might enhance attitudes toward these species. The inclusion of social behaviour and social structure and complexity would enhance our appreciation of biologically-sound ways to enhance impact-mitigation, hence more properly informing the socially-based decision-making process to solve and reduce conflict.

Experience among group members highlighted the importance of a participatory approach among all stakeholders and that it was crucial that researchers shared information with stakeholders in plain, accessible language. Managing stakeholder expectations was crucial in the process, especially to improve understanding that coexistence situations rarely "resolve" but evolve and require monitoring effort and a toolbox of options for mitigation (see also Recommendation 2). Experience in East Africa (Kenya; elephants and lions) suggested that early discussions and feedback increased a sense of ownership and improved communication between stakeholders, facilitating evolving agreements, as well as containing the spread of unwanted behaviour (crop raiding, livestock depredation) by addressing vulnerability (farm defence, herding practices).

Specific recommendations:

a) Develop a suite of case studies to explain why taking account of social complexity and animal culture is important and has value for coexistence planning, including the development of site-specific examples for circumstances where HWC occurs.
b) Recognize that human traditional and local knowledge are important aspects of situation-specific human-wildlife interactions at multiple levels and should be considered in developing conservation strategies (Williams & Whiting 2016).

Recommendation 2. Utilize animal (and human) social learning to facilitate better conservation outcomes in HWC.

To address HWC, researchers might benefit by starting with an examination of the underlying causes, which might be ecological (such as a temporary food limitation or range expansion into human-dominated landscapes) or anthropogenic, e.g. a change in human activity pattern. The group also discussed the idea that HWC occurred when either the humans or the animals did not "know the rules" when sharing space and resources with other species, which might occur because of changing circumstances (e.g. elephants moving back into former range post-poaching, sharing space with inexperienced human neighbours). Experience showed that researchers needed to have a toolbox of options, rather than relying on single options for dealing with HWC because smart, social animals would continually learn and adapt to human mitigation measures.

If conservation efforts were successful enough, protected wildlife species would increasingly tend to expand into human-dominated urban, suburban and agricultural or pastoral areas. This introduced the idea of conservation planning at the landscape scale, where the likelihood of frequent and recurrent impacts would be expected and where changes in human attitudes/practices were unlikely. Creating a "landscape of coexistence" (Oriol-Cotterill et al. 2015) entailed defining zones at the landscape scale where conservation goals could favour animal species to improve their conservation status (i.e., accounting for social integrity and complexity) in certain zones, while in other areas priority was given to human activities.

The group noted that mitigation measures would work only if the interested parties (e.g. fishermen, ranchers, farmers) were willing to adopt them fully. This related to the functional distinction between impact and conflict. Main affected stakeholders should become part of the solution and their acceptance of the mitigation measures was an essential component of HWC mitigation. Even where human commercial activity was prioritized, management should integrate animal culture and social complexity into the assessment of interventions in the short, medium and long term.

Specific recommendations include:

a) View HWC as a "cultural arms race" in which both animals and humans are engaged over the long-term;
b) Develop a toolbox of mitigation measures. Mitigation measures may work only in the short-term but must run long enough to enable the spread of learning. The

success of mitigation strategies may be underestimated if efforts stop too early – e.g. migrating elephant populations take longer to learn about beehive fences, because not all population members are immediately exposed;

c) Adopt a pro-active approach. Utilize understanding and the shape of social learning curves (e.g., Roger's innovation curve; Rogers 1962) to target mitigation measures at the early stages during the "window of opportunity" in which only a few individuals are involved (Figure 1);
d) Develop ways to avoid spatio-temporal overlap. The best mitigation measures are likely to be ones that reduce the opportunity for social learning to occur in animals. For example, land-use planning in Kenya is designed to separate incompatible wildlife and agricultural zones; in fisheries, traps or aprons can prevent sperm whale depredation (Arangio 2012); and avoiding the disposal of cattle carcasses near ranches can prevent food conditioning in wolves (Western Wildlife Outreach 2014).
e) Review and assess the efficacy of lethal control measures as applied to highly social species. Culling can affect social network stability and information transfer via social learning opportunities. Destabilising results of culling include elephant behavioural responses (Slotow et al. 2000), disease transmission in badgers (bovine TB; Bielby et al. 2014) and attempts to control wolf populations to reduce livestock depredation or allow recovery of large herbivore populations for hunting purposes.

Recommendation 3. Move beyond counting numbers when assessing the conservation status of highly social species and the outcomes of conservation actions.

For highly social species, the group emphasized the need to move beyond simply counting individuals when assessing conservation status or the efficacy of management interventions meant to reduce HWC. Rather, we needed simple and practical metrics that enabled us to assess whether a population's social structure was intact and functioning, thereby ensuring social learning and endurance of cultural adaption through generations. We needed to explicitly incorporate sociality into traditional demographic approaches, such as population viability analyses and population dynamic models. We also suggested re-thinking conservation concepts, such as "recovery" when it came to highly social animals, so that conservation practitioners would ask themselves questions such as "what are we trying to recover in these populations"? (age structure? social units? cultural diversity?) and "how would we know when we have achieved these goals"?

Specific recommendations include:

a) Develop "social indices" for assessing the conservation status of highly social species, designed to measure social structure. Such indices should be situation-specific, might be based on existing metrics, and ideally based on data that are simple to collect. The approach could include representing estimates of the presence/absence of recognizable social units, (such as the presence of matriarchs or dominant males); the age of adult females/males; social group size (e.g., pack size, social stability and site fidelity in social, territorial carnivores such as wolves); or some aspect of foraging or mating system (such as the degree of sexual dimorphism or number of reproductive males [see explanation in Group D]). The group agreed that developing such as measure was beyond the scope of the current workshop but should be considered for future workshops.
b) Investigate new and existing analytical methods for assessing the influence of sub-lethal impacts on animal sociality and culture, on vital rates and population-level demographics (done in parallel with point (a). See also Group D).
c) Investigate "lag to recovery" across multiple taxa and assess whether attributes such as "highly social" correlate with differences in time to recovery (as demonstrated for cetaceans by Wade et al. 2012).

d) Examine the opportunity to borrow principles from the ecological literature that describe concepts such as potential persistence and vulnerability of highly social species.
e) Review the functional association between social learning and social complexity in highly social species and their ecological role, where social complexity affects conservation outcomes beyond the single population/species level i.e., ecosystem functioning and services (e.g., trophic cascades of apex predators; such as those described for wolves in Yellowstone, USA, (Ripple et al. 2014; Fortin et al. 2005) (but subsequently contested and counter-contested; East et al. 2017; Beschta & Ripple 2018).
f)

Table 1. Examples of collisions between human and animal interests and their potential consequences. See text for additional details.

Human-wildlife conflict	Impacts on social structure	Climate change impact on social learning, sociality	Human understanding of animal culture and sociality
Socially learned predation (“depredation”) by whales, dolphins, and pinnipeds on fisheries and by terrestrial carnivores (e.g., tigers, lions, wolves, and bears) on livestock and domestic animals (e.g., pets) Socially transmitted fence-breaking and crop raiding by elephants Socially transmitted behaviour in which large carnivores attack humans and/or damage human property e.g. beehives, crops, fruit tree raids by bears	Social disruption in dolphins during commercial tuna fishing Removal of ‘problem’ animals (e.g. baboons) by local authorities Poaching key individuals (e.g. alpha male wolves) Targeted collection of large adults (e.g. dominant male, fecund female lizards) or parental units (e.g. parrots) Road kill sleepy lizards that are part of long-term pair bonds.	Reptiles, particularly lizards: restricted daily activity for social learning	Lethal control of wolves results in pack instability, increases number of breeding pairs, increasing depredation on livestock Culling elephants disrupts age-related learning and social status, generating abnormal (aggressive) behaviour profiles

Table 2. Two dimensions of human-wildlife impacts that compromise conservation

Impact	Examples	Outcomes
Human on Animal	*Direct*: Trophy hunting, Wildlife trade, Commercial fishing, Culling *Indirect:* Climate change, Habitat modification	Removal of key individuals may have population-level consequences; Disruption of social groups may limit population recovery and disrupt community structure and ecosystem function
Animal on Human	Depredation (commercial fisheries/ livestock), Crop raiding, Foraging in urban areas (for garbage, pets)	Lack of support for species, or interest in conservation efforts; Increased support for eradication

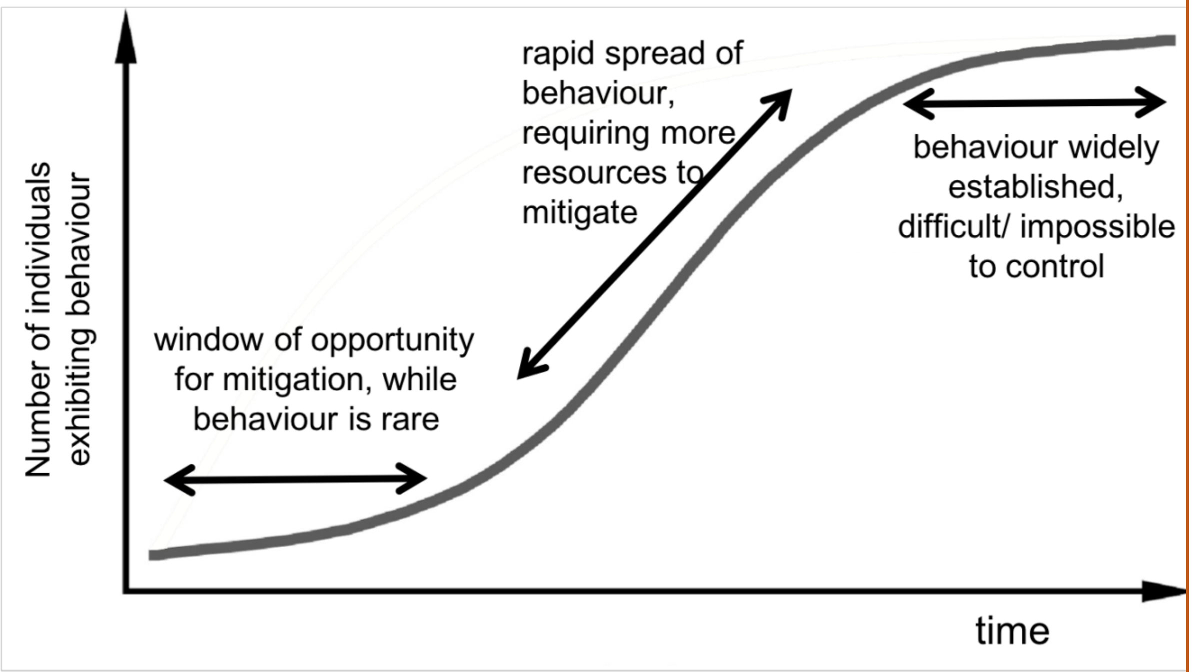


Figure 1. A schema depicting social learning and the mitigation of human-wildlife conflict based on Rogers (1995) “Diffusion of Innovations”. During the “window of opportunity” phase crucial mitigation measures include; forming multi-stakeholder groups; creating common language around how animal social complexity shapes landscape ecology and resource use (how and why humans and animals overlap); generating conservation interventions focused on identifying, separating and attempting to break association to prevent escalation of impacts and conflict.

GROUP B
'Wildlife sages': Conserving valuable cultural diversity in wildlife

Particular concentrations of important cultural information may occur at several levels within a species. Important information or behaviours may reside in, or be used by, particular individuals within a group, in classes of individuals (such as matriarchs), or in whole groups, communities or populations, and yet be absent in other individuals or regional subsets of the species' range. A distinction may be made between efforts directed at the conservation of particular cultural repositories themselves, such as a community that displays a unique behavioural profile transmitted culturally, or at the conservation of critical cultural capacities in the population of interest. Reintroduction projects that relied on humans acting as temporary repositories of cultural phenomena that had gone extinct in the wild, and were then incorporated into the reintroduction process, could be considered a further major type of conservation approach dependent on the recognition of cultural processes in the animals concerned.

1. **Conserving cultural *repositories***

Historically, the overarching goal of conservation efforts had been framed predominantly in terms of preserving 'biodiversity', conceptualized in genetic terms. The discovery of widespread animal culture – a 'second inheritance system' (Whiten 2005) that had significant survival consequences – argued to expand this core concept to include phenotypic diversity, with a potentially key component being cultural diversity. Accordingly, a case could be made for conserving a unit that was defined by its cultural identity, rather than purely by its genetic identity.

As one of two illustrative test-cases, we considered the example of nut-cracking using natural hammer materials (wood, stone) in wild Chimpanzees. This behaviour had been documented at eight different research sites that spanned over 500 km of the range of *Pan troglodytes verus* in West Africa, but was known not to occur over most of the remainder of Chimpanzees' range in Central and East Africa, including the range of *P. t. verus* to the east of the Sassandra N'Zo River (figure 2). Multiple sources of observational and experimental evidence demonstrated that nut-cracking was dependent on cultural transmission from existing experts, but only in this western Chimpanzee population (Whiten 2017a); nut-cracking was thus a particularly distinctive and well-documented case among the multiple putative traditions now reported to exist amongst great apes (39 among Chimpanzees, and over 30 and over 20 in Orangutans and Gorillas respectively; Whiten et al. 1999; van Schaik et al. 2003; Krutzen et al. 2011; Robbins et al. 2016).

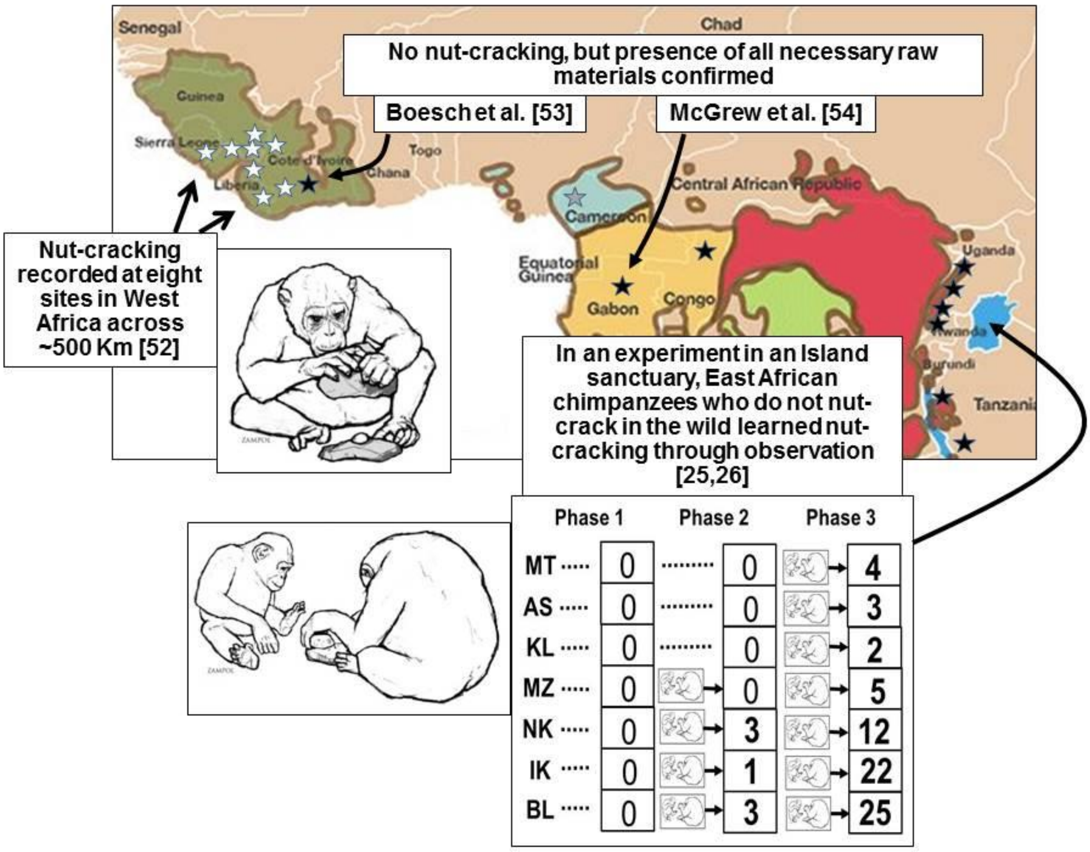


Figure 2. Nut-cracking by Chimpanzees using natural hammer stones and wood has been recorded at multiple study sites in West Africa (white stars) but is known to be absent elsewhere across the species' range, including locations where the availability of all raw materials has been confirmed. Multiple forms of evidence establish nut-cracking as culturally transmitted, including experiments with seven juvenile East African chimpanzees in the Ngamba island sanctuary in Lake Victoria, which initially showed no nut-cracking (phase 1) but when exposed to nut-cracking by an older individual, began to develop the skill (phases 2 and 3) (After Whiten 2017a, b).

Given the critically endangered status of Chimpanzees and that the nut-cracking culture spanned the borders of the four adjacent States of Guinea, Sierra Leone, Liberia and Côte d'Ivoire, the nut-cracking cultural population could be proposed to merit special conservation status on the basis of the following considerations:

(i) Fitness: There was evidence that nut-cracking, along with other forms of tool use, was essential to survival through the dry season when fruit was scarce, and hence chimpanzees' persistence in this western-most portion of their habitat (Yamakoshi 1998).
(ii) Scientific interest: These phenomena importantly extended our understanding of animal ecology and evolutionary biology underling conservation considerations (Whiten 2017b).
(iii) Public interest and investment in conservation: The existence of such cultural phenomena in other species was of great interest to the public, with well-recognized effects on the public's willingness to donate funds to related conservation efforts.
(iv) Relevance to Human Evolution: The percussive technology involved was of high scientific importance given the three-million-years-plus phase of the stone age in our own hominin evolutionary history (Whiten, Schick and Toth 2014; Whiten 2015).

An ambitious study, 'The Pan African Programme: the Cultured Chimpanzee' of the Max Planck Institute for Evolutionary Anthropology, was underway using camera traps, quantification of resource availability, and other rapid assessment techniques to survey further behavioural diversity amongst chimpanzees across 40 African study sites, and had already revealed forms of behaviour previously unknown (Vaidyanathan 2011, Kuhl et al. 2016).

A second test-case referred to Killer Whales, in which different communities had developed very different hunting specializations, with some feeding specifically on various groups of other marine mammals while others fed exclusively on fish and even penguins. Killer Whales displayed a strong matrilineal social structure with tight family groups, and these dietary preferences appeared to be culturally transmitted from older individuals within each group, as did their songs and migration dispositions. These cultural differences between populations were further illustrated by distinct differences in vocalizations among groups (Ford et al., 2000). These different cultural traits distinguished a number of isolated groups or 'ecotypes' (Ford et al., 2000; Pitman and Ensor, 2003; Riesch et al., 2012), each essentially a cultural repository for specializations in foraging and other behaviours. While currently recognized as a single species (*Orcinus orca*), there was genetic and morphological support for at least some ecotypes being different species (Morin et al., 2010). To conserve the full biodiversity of these whales it could now be seen to be necessary to recognize and preserve the diversity of these ecotypes.

As in the chimpanzees, there were multiple justifications for measures to conserve such cultural groups:

(i) Fitness: While strong specialization within ecotypes could make some groups more vulnerable to declines in relevant prey species, it could more generally support the resilience of these whales, allowing potentially rapid exploitation and expansion as the availability of suitable prey items fluctuated.
(ii) Ecology: As apex predators, Killer Whale ecotypes had important ecological roles within their specialized niches.
(iii) Public interest: Killer Whales had a high public profile and there was a great deal of public interest in preserving specific cultural groups, such as the resident groups of British Columbia/ Washington.
(iv) Relevance to human evolution: Studying the very strong cultural patterning of this species provided insights into the evolution of human culture as well as animal culture more generally, particularly the role of culture as a potential reproductive isolation mechanism.

Specific Recommendations

Cultural units should now be considered as units meriting conservation efforts, contrasting with the traditional focus on species, and on genetics. The working group offered the two cases above as 'proofs of concept' for this proposal.

These considerations began to suggest criteria that mighty be used to consider conservation strategies in further significant and culturally defined units, requiring the assembly of information including the following.

Table 3. Potential variables relevant to conservation of culturally defined units/populations

	CMS Listing	**cross-border?**	**fitness consequences**	**ecological significance**	**Public interest**	**Relevance to human evolution**
P.t.verus	Appendix I & II	4 countries	Survival through seasonal bottlenecks	high	high	percussive technology, cultural diversity
O. orca	Appendix II	multiple coastal jurisdictions	population resilience	high	high	cultural diversity
others …						

2. Conserving cultural *capacities*

Cultural knowledge can form a significant source of locally adaptive behaviour, improving the ability of individuals to survive and populations to persist in the face of human-induced and/or rapid environmental change.

This could potentially be through three main mechanisms. First, cultural knowledge could act as an 'ecological buffer', allowing animals to creatively exploit environments in periods of scarcity. Evidence included comparative analyses in birds, for example, suggesting that a propensity for cognition and social learning could act to expand the range of environments that species could successfully inhabit (Sol et al. 1995). Second, in spatially variable environments, culture could play an important role, acting to 'fine-tune' behaviour to local conditions, and even potentially provide 'resident knowledge' that more transient individuals/species could exploit (Slagsvold & Wiebe 2007; Seppanen 2007). Third, innovations in response to novel challenges and opportunities could spread via social learning through social networks to establish new cultural behaviours, providing a mechanism by which some species could exploit new beneficial resources (Aplin et al. 2015). In one of the most famous early examples of the spread of innovations, tits (*Parus major*, *Cyanistes caeruleus*) learnt to open milk-bottles to eat cream in urban areas, a behaviour that subsequently spread across Britain and Ireland (Fisher & Hinde 1949).

Many environments were now changing under anthropogenic influences too rapidly for genetic evolutionary processes to keep track, and these cultural processes could be an important way in which species could show resilience. However, to facilitate these processes, it could be important to 'future-proof' populations to conserve the *capacity* for innovation and social learning, to give rise to new adaptive cultures. This relied on preserving three *building blocks of cultural capacity* – demography and phenotypic variation, social network structure, and population connectivity.

1) *Demography*

Preserving the phenotypic variation in the population was vital both in preserving existing cultural knowledge and for providing the capacity for new cultural behaviours to arise in future. In practice, this would often consist of preserving the social structure of groups (i.e. not disrupting dominance hierarchies), and maintaining age structure in populations. Older and more dominant individuals might be repositories of knowledge (Greggor et al. 2016).

For example, in Whooping Cranes, the migration routes of juveniles were more efficient when they migrated with older individuals, and the benefits to juveniles improved with increasing age of the adults they flocked with (Mueller et al. 2013). This need to preserve the older individuals in the population might represent a need for a shift in our thinking on hunting and fishing, e.g. trophy-hunting practices, as taking large/older individuals might result in a disproportionate loss of cultural knowledge in the population. Evidence for this effect came from studies in ocean fisheries, where over-harvesting of large/old individuals could lead to loss or changes in migration routes (Brown & Laland 2005; Petitgas et al. 2010).

A further case study for the importance of preserving age structure came from Killer Whales, well known for their strong matrilineal social structure (Ford et al. 2000). Unusually for mammals, females lived well beyond reproductive senescence. This might have value to group survival through the older females acting as repositories of knowledge about foraging areas and strategies that might be important during times of environmental perturbation. The preservation of older females in Killer Whale family groups might therefore be important to preserve cultural capacities within the group and enhance group fitness.

However, in addition to these considerations, in many species the evidence suggested that juvenile and low-ranking individuals might be the most innovative and exploratory (Perry et al., 2017). Accordingly, they might represent an important source of new adaptive information in populations. This contrast in the different potential roles played by juveniles and adults highlighted the need to maintain the entire age structure of populations, rather than focusing on harvesting or conserving one particular age class.

2) *Social network structure*

Information was transmitted through animals' social network ties (Aplin et al. 2015; Hobaiter et al. 2014). Therefore, to maximize cultural capacity in populations, social structure and social connectivity needed to be maintained. The assessment of these social network structures needed to be species-specific. In some species, a proxy of *group size* might be sufficient; while in other species social network structure might be better assessed monitoring *variation in social associations* or *social connections between groups*.

In general, innovative behaviours would be more likely to spread in species with highly fission-fusion based social systems, and possibly in more "egalitarian" societies, where dominance hierarchies were not steep. More specifically, in many species, some classes of individuals connected otherwise disparate groups (e.g. dispersing juveniles, transient individuals). In these cases, preserving such "social brokers" (Lusseau & Newman 2004) might be particularly important to prevent the social fragmentation of populations.

3) *Population connectivity*

Maintaining healthy populations across the entire range of the species might be vital in preserving locally adaptive cultures. For example, individuals in one local area might have a 'resident expertise' or display 'local traditions' not possessed by the entire population, and if this sub-population was lost, then the rest of the population mighty be slow to recolonize this part of the historical range. For example, heavily depleted fish stocks often established different migration routes after recovery (Petitgas et al. 2010), and Right Whales had been slow to re-establish migration paths following whaling, for example in New Zealand (Carroll et al. 2014).

Resident knowledge could also be transmitted between species, with some species acting as "information sources" for a variety of other species or communities. If these "information source" species could be identified, they might be a particularly important focus for conservation efforts. For example, Marsh Tits and Willow Tits *(Poecile spp.*) could give recruitment calls when they found new food patches, attracting other species to patchy ephemeral food sources. They thus acted as 'keystone species' in mixed species foraging flocks (Farine et al. 2015). In another example, experiments using migratory Pied Flycatchers (*Ficedula hypoleuca*) demonstrated that they used information from resident Great Tits (*Parus major*) when choosing nest sites (Seppanen 2007).

Specific Recommendations:

- Consider the overall age and social structure of populations to maintain cultural capacity.
- If particularly important classes of individuals can be identified (e.g. social brokers, matriarchs, individuals with resident knowledge), focus on protecting these individuals and their social connections.
- Where possible maintain population connections across the species' range.
- Identify any important keystone "information source" species within wider species communities, and consider their impact on the conservation of target species.

3. Reintroducing cultural knowledge

Reintroductions, in which captive animals were released into the wild in order to re-establish or boost populations, had been widely used as a conservation tool for a range of taxa including fish, amphibians, birds and mammals. However, these schemes had too often had low success rates, largely because they ignored the role of cultural processes in the development of fundamental life skills such as foraging, predator avoidance, social behaviour and nest-site selection (Sarrazin & Barbault 1996). Re-establishing cultural knowledge had therefore to be a core aim of reintroduction programmes for social animals.

In some cases, where precipitous population declines had caused cultural knowledge to be entirely lost from populations, it might be necessary to use human tutors to promote learning. For example, conservationists had successfully reintroduced migration routes for critically endangered Whooping Cranes by training individuals to follow human microlight pilots (Urbanek et al. 2010; Mueller et al. 2013: Figure 3). In subsequent migrations, these initial trained cranes could then act as effective models for other conspecifics to learn from (Mueller et al. 2013). However, the birds' success in producing surviving offspring had to date been low (Urbanek et al. 2000), probably because the reintroduced birds were hand-reared and lacked opportunities to learn parental skills from conspecifics. This example illustrated the critical importance of seeking to maintain individuals as repositories of knowledge that might span a number of domains of behaviour, from which others could learn.

Figure 3. A micro-lite aircraft on which young Whooping Cranes have imprinted is here used to guide the laying down of a migration path these naïve youngsters will learn and follow in future. Here, the micro-lite acts as a surrogate for parents which would normally be the repositories of cultural migratory knowledge passed down through generations (Mueller et al. 2013).

Another relevant example was the case of Golden Lion Tamarins (*Leontopithecus rosalia*), also critically endangered at the time reintroduction efforts were begun (Beck et al. 2002) Here the survival rates of reintroduced animals were initially extremely low (13%), as captive-born individuals failed to forage effectively and recognize predators (Stoinski et al. 2003). Later, an intensive post-release programme involving provisioning of supplemental food and nest-sites allowed reintroduced animals to survive for long enough to learn basic life skills, doubling survival rates. The offspring of these captive-born animals then showed a much improved survival rate of 70%, suggesting that social learning from parents made a critical contribution to the acquisition of fitness-related behaviour (Kierulff et al. 2012).

It was concluded that wherever possible, reintroduction schemes should seek to promote the cultural transmission of fitness-related knowledge and skills, by exposing captive-born individuals to experienced conspecifics, both during rearing/rehabilitation and when being released back into the wild. For instance, for flocking birds such as psittacines, soft-release protocols sought to promote social integration post-release by setting up perches and feeding stations to promote aggregation of individuals, both amongst these individuals and then with wild, experienced conspecifics (White et al. 2012), an approach for which there was some evidence of success also from the Golden Lion Tamarin project.

Finally, to evaluate and improve success rates for reintroductions, we recommended that all schemes kept systematic, detailed records of data on individuals' social interactions and exposure to relevant stimuli (e.g. different food types; predators) both pre- and post-release, as well as their subsequent survival and reproductive success. Attention should also be given to the possibility that behaviour patterns resulting from a phase of captivity, such as loss of fear of humans, did not have negative consequences after release into the wild.

Collaborators from the scientific research community might also be invited to become involved, to benefit from the unique opportunities to learn the impacts of social learning during re-introduction programmes.

Recommendations:

- Wherever possible, individuals scheduled for re-introduction should be exposed to experienced conspecifics interacting with a range of stimuli they are likely to encounter in the wild (e.g. conspecifics; foods; predators)
- Where cultural knowledge has been entirely lost in the wild, in some circumstances human tutors should be used to re-establish desired behaviour, especially in the first release generation.
- In species that show parental care, intensive support should be provided to support breeding, when future generations are predicted to learn from the most competent surviving conspecific parental models.
- Likely social learning biases should be taken into account; for example, individuals may be more likely to learn from adults, or from resident individuals.
- Staff should monitor and maintain data as detailed as is practicable encompassing individuals' social interactions (e.g. social affiliations; exposure to human or conspecific models) and exposure to stimuli pre- and post-release

GROUP C
Socio-geography: Social learning, range recovery and migration, island populations

The group members saw socio-geography as the integration of culture and social learning into the broader field of conservation biology, linking the importance of culture and social learning to existing spatial understanding of range dynamics and migration in macroecology and biogeography (e.g., Keith and Bull, 2017). Our taxonomic expertise centred on cetaceans and birds and our discussions covered aspects of behavioural ecology, acoustics, genetics, biologging and biochemical markers. We considered that the three main ways that culture and social learning shape phenotypic diversity, demography and population structure are (1) learning and transmission of behaviours; (2) effective transmission of information through social networks and (3) the promotion of isolation among animal sub-groups. These processes could act as modes of transmission of information that can be long-term (e.g. migratory routes), ephemeral (e.g. foraging patches, song variation), or both. We highlighted that a practical element of this section of the report had been to identify behaviours, environments and systems where social learning (as a potential precursor to more permanent culture) might play an important role including: social foraging; complex foraging tasks; migratory tradition conservatism; vocal learning; fission-fusion or matrilineal-unit-based social systems, long-term parental care; and, in turn, how these might influence/impact conservation status and initiatives.

1. **Goal of conservation**. The goal of conservation is to maintain the evolutionary potential and long-term persistence of viable populations of wild species: this can include maintaining cultural as well as genetic diversity.

Evolutionary potential includes the potential for changes in functional genes, as well as other processes of inheritance, including social learning. For example, in 1980 a Humpback Whale in the Gulf of Maine invented a new feeding technique. This spread through the social network of the population through horizontal social learning, and was used presumably to enhance foraging efficiency (Allen *et al.*, 2013). Other examples of rare, but possibly functional, behaviour spreading through a population included moss sponging in

Chimpanzees (Hobaiter *et al.*, 2014); and rapidly growing subpopulation of Barnacle Geese that started breeding in Iceland in the late 1980s, shortening the ancestral migration route by over one thousand kilometres: this new breeding area could act as a buffer for the whole population, the bulk of which bred in Northern Greenland, in the face of changing arctic environments (Stefánsson et al. 2015).

2. **Evolutionary potential and long-term persistence**. To maintain evolutionary potential and long-term persistence, we need to preserve
   a. Phenotypic diversity
   b. The demography and population structure of populations that will often contain a spatial component.

3. **Culture**. Animal culture is a cause (driver), consequence and marker of
   a. phenotypic diversity
   b. demography
   c. population structure

4. **Effects of culture**. Culture acts through the following processes which can be generally differentiated based on whether the information being transmitted is long-term or ephemeral, or both
   a. learning and transmission of migratory routes (long-term)
      - The social systems and site fidelity of subpopulations of light-bellied Brent Geese and White-fronted Geese were more similar to one another across a shared migration route, than they were to conspecifics using different migratory flyways (Fox *et al.*, 2002; Ackerman *et al.*, 2006; Harrison *et al.*, 2010).
   b. effective transmission of information through animal networks and an understanding of the critical densities at which these networks broke down (ephemeral)
      - A modelling study of the effects of social facilitation on vulture foraging success demonstrated that there were critical densities at which information flow broke down and sent a population into rapid decline (Jackson *et al.*, 2008)
   c. promotion of isolation of units (both ephemeral and long-term)
      - Matrilineal culture and gene-culture coevolution could drive demographic and genetic isolation in some Killer Whale populations and ecotypes, probably facilitating speciation (Riesch *et al.*, 2012; Morin *et al.*, 2015; Foote *et al.*, 2016).

5. **Extrinsic factors**. Extrinsic factors (anthropogenic or natural) could influence these processes, which in turn could affect both evolutionary potential and long-term population viability:
   a. Destroying, degrading or disrupting migratory corridors or destinations;
      - There was genetic and stable isotope evidence that Southern Right Whales have maternally-directed learning of breeding and feeding migration habitat. Whaling had extirpated whales from parts of the migration network, with a corresponding loss of cultural memory of migration destinations leading to spatially variable recovery and concerns about population viability (Carroll *et al.*, 2015). This seemed to be a more general effect with other heavily hunted species with presumed culturally-determined migration routes (Clapham *et al.*, 2008), such as Beluga Whales (O'Corry-Crowe *et al.*, 2018).
   b. Perturbing the animal network to reduce functional effectiveness of information transfer, including density dependence effects at low densities, resulting from a positive relationship between any component of individual fitness and either

numbers or density of conspecifics (e.g., the Allee effect; Allee, 1931; Courchamp *et al.*, 1999; Stephens et al. 1999).

- See 4bi (vultures).

c. Removing or reducing viability/integrity of units

- Southern resident Killer Whales were a small (<100 animals), distinct community with a highly specialized, and conservative, cultural behavioural repertoire. Both their habitat and their overwhelmingly-preferred food source (chinook salmon) were being heavily impacted by human activities, leading to substantial risk of extirpation (Lacy *et al.*, 2017).

6. **Culture and conservation**. Recognizing that culture is another aspect of biology that should be considered within existing conservation initiatives we recommend that culture should be considered in the following contexts:

a. assessing populations and designating units to conserve (e.g. evolutionary significant units)

- Beluga populations in Canada were separated into eight Designatable Units (by the Committee on the Status of Endangered Wildlife in Canada) which had a range of conservation status' from "Endangered" to "Not at Risk" (COSEWIC 2004). COSEWIC assessment and update status report on the Beluga Whale *Delphinapterus leucas* in Canada. Committee on the Status of Endangered Wildlife in Canada. Ottawa. ix + 70 pp. [Online: www.sararegistry.gc.ca/status/status_e.cfm].). Some of these Designatable Units mixed during winter and spring when they mated, but the migrations to discrete summer habitats and behaviour in these habitats seemed to be culturally learned, and these were considered sufficiently distinctive to separate the designatable units.

b. introgression and hybridization

- hybridization and introgression were major threats to the species' persistence and population structure of multiple species including wolves (Adams *et al.*, 2003; Benson *et al.*, 2012; Caniglia *et al.*, 2014) and wild cats (Anile *et al.*, 2014; Steyer *et al.*, 2016). It was possible that socially learned behaviours could be eroded, modified or replaced during such events, or behaviours with a genetic or partially genetic basis could be impacted (Allendorf *et al.*, 2001). Unfortunately, evidence for this was not currently available and as such this should be a target for future research.

c. managing endangered populations: retraining, local enhancement

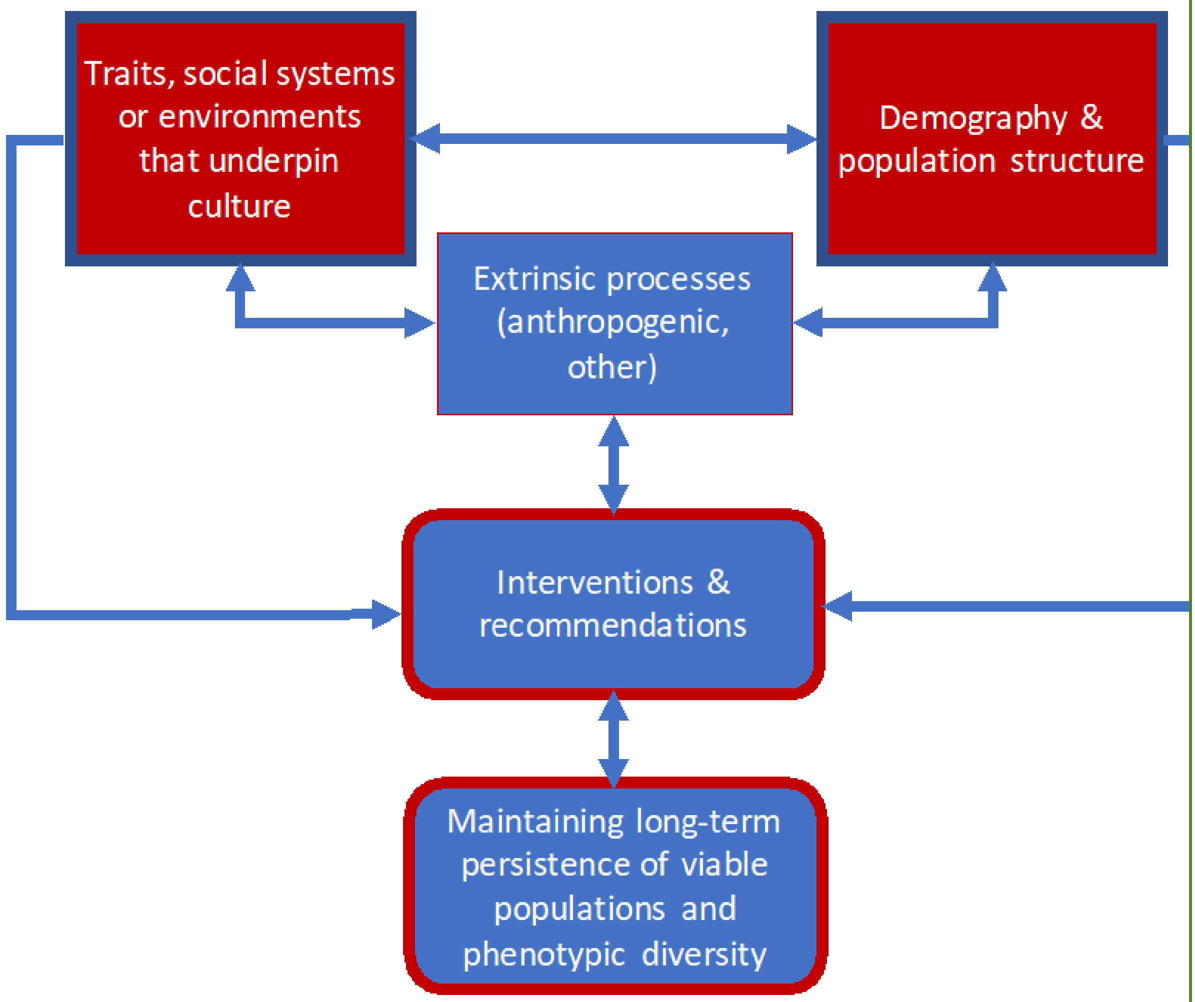
- Work was underway to preserve a suite of potentially socially-transmitted behaviours in a captive population of the critically endangered Hawaiian Crows which was used to breed birds for an ongoing reintroduction programme (Hoppitt et al. in prep.) (see also sub-group B section 3. Reintroducing cultural knowledge).
- A combination of reintroductions and vulture feeding stations was being implemented to facilitate the reestablishment of the information networks required for social facilitation of foraging (Houston and Piper, 2006). In India this had the added benefit of high-jacking social facilitation to lure vultures away from poisoned carcasses (Gilbert *et al.*, 2007).
- Northern Quolls showed taste aversion to toxic cane toads after training in captivity with a toad sausage (Indigo *et al.*, 2018). A similar approach in situ with varanid lizards using small toads resulted in conditioned taste aversion in advance of the arrival of larger, potentially-lethal introduced toads (Ward-Fear *et al.*, 2016). If such aversions could be transmitted through social learning, as had been shown for some predator avoidance behaviour (Griffin, 2004), these approaches might be especially effective. This was a potential approach for hatchery-reared fish (Brown and Laland, 2001).

d. mitigation planning for environmental change and development
   - Where there was a high level of migratory connectivity and site fidelity, which are often culturally transmitted, it had been argued that individual sites may require particular levels of protection. For example, the high migratory connectivity and extreme site loyalty shown by some geese had led researchers to argue for individual refuge designation (Fox *et al.*, 2002). North Atlantic Right Whales had a migration route, presumably culturally learned, that passed through some highly-used and increasingly-used coastal environments on the east coast of North America. A number of protection measures, such as vessel restrictions, had been introduced at various points in this route (Kraus and Rolland, 2007). However, further research was required to determine whether these sites would become suboptimal under environmental change ('ecological trap'), and the extent to which behavioural flexibility could mitigate this issue.

7. General recommendations

a. Collect empirical evidence of social learning network and migratory behaviour and connections
b. Develop theoretical models to inform mitigation and investigate future scenarios, e.g. as done to investigate the link between social transmission of information and viability in vultures (Jackson et al. 2008).
c. Develop rapid assessment tools and emerging technologies to provide direct and indirect evidence of social transmission, migration routes, social networks, as well as anthropogenic effects on behaviour, informing conservation and management
   - Acoustics: passive acoustic monitoring; acoustic identification of population units; autonomous recording with identification software (Zimmer, 2011)
   - Biologging: movement and activity tracking; direct and indirect encounter mapping for social network building (Krause *et al.*, 2013; Hussey *et al.*, 2015; Kays *et al.*, 2015).
   - Genetic and genomic techniques including eDNA and minimally-invasive sampling to identify kin groups, population structure and migratory connections (Arandjelovic and Vigilant, 2018; Carroll *et al.*, 2018)
   - Stable isotopes, fatty acids and other biochemical markers to delineate population segments with distinct habitat use, as well as transmission patterns of foraging behaviour
   - Proxies of culture that can be assessed more easily. For example, in tool-using New Caledonian Crows, the idea had been explored to rapidly map possible regional variation in foraging behaviour, using vocal dialects as 'markers' (Bluff *et al.*, 2010)
d. As noted in CMS Resolution 11.23: management decisions should be precautionary and assume that populations may contain discrete social elements which have conservation significance warranting further investigation.
   - Emerging indications that culture might have a conservation consequence could include: social foraging; complex foraging tasks; migratory tradition conservatism; vocal learning; fission-fusion or matrilineal-unit-based social systems, and long-term parental care

Figure 4: Schematic depicting how the desired outcome of conservation, the maintenance of long-term viable populations and phenotypic diversity, can be achieved by interventions and recommendations that consider the interrelationship between demography, population structure, extrinsic processes and culture.



GROUP D
Socio-vulnerability: Specialization versus ecological resilience

Cultural specialization of foraging

Aspects of social complexity and culture in animal populations can increase the vulnerability of species to anthropogenic and other environmental threats. Below, we describe some of the ways in which social factors can affect conservation risk. We also briefly considered whether it is possible to create a scheme to categorize species vulnerability based on their social complexity or other identifiable aspects of their social systems. However, we concluded that was a task beyond the scope of this workshop and should be explored further at subsequent workshops.

Socially complex species can contain different foraging cultures that require extensive learning of specialised foraging techniques. For example, different social units within fish-eating Killer Whales (*Orcinus orca*) may forage on anadromous fish (e.g. chinook salmon) specific to individual river systems (Ford et al. 2000, Ford and Ellis 2006), and different social units within mammal-eating Killer Whales specialize in hunting either Gray Whales or Harbour Seals (Ford and Ellis 1999).

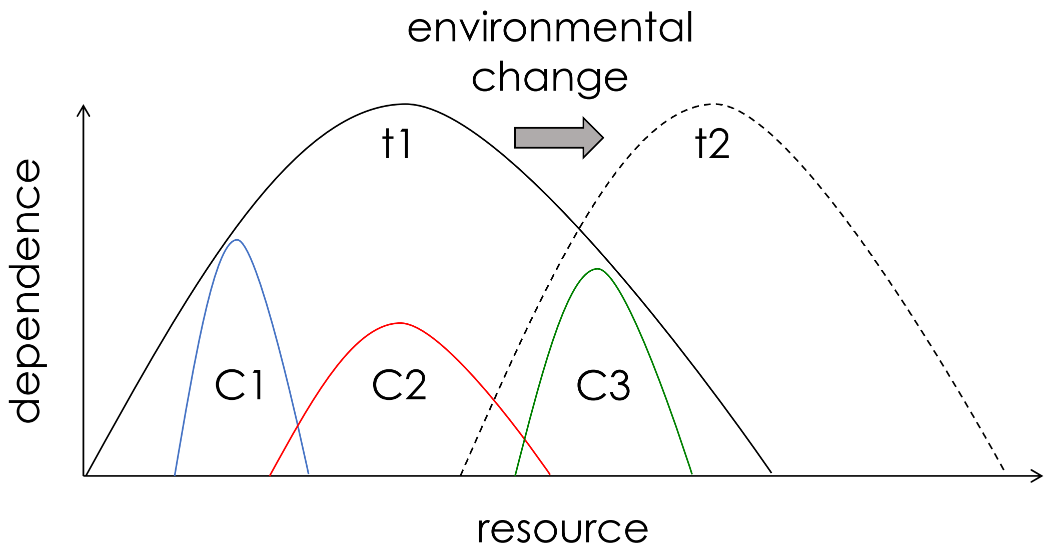
Foraging specialization amongst whale clans can lead sub-populations to respond differently to environmental change. Members of two Sperm Whale clans studied off the Galapagos showed differential responses to the El Niño phenomenon. During normal cool years, the "Regular" clan had higher feeding success than the "Plus-one" clan. Whereas, in years with warmer El Niño conditions "Plus-one" clan groups were more successful (Whitehead and Rendell, 2004). More recent investigations have shown both of those clans have been replaced in the Galapagos by two different clans (the “Short” and the “Four-plus” clans), with the authors’ interpretation being that clans with different foraging strategies relocated when those strategies were no longer efficient, rather than changing their foraging strategy (Cantor et al. 2016). The implication is that some cultural groups may relocate rather than adapt to environmental change.

Prey use also varies in terrestrial mammals. Foraging specialization between social units is also known from species such as wolves and African Wild Dogs, which could feasibly affect their response to environmental change. In Africa, some Chimpanzee communities display learnt tool use, using rocks or sticks to crack open nuts, yet this behaviour is not evident in neighbouring communities that exist within comparable habitat (Whiten, 2015). Bornean Orangutans also display evidence of learning in a cultural context, where social groups separated only by a river barrier have different diets that persist through time, which do not appear to be a direct result of resource availability (Bastian et al., 2010).

Populations of baleen whales (Right Whales, Humpback Whales) congregate in a single location to calve in the winter, yet from that location, individuals migrate to a range of locations to feed and mate. Individual whales tend to return predominantly to the same feeding area for their entire lives, which was the first area experienced for this purpose as a calf (e.g., Carroll et al. 2015; Baker et al. 2013). Similarly, evidence for natal philopatry to migration destinations, apparently parentally directed, is also seen in Belugas, a toothed whale (O’Corry-Crowe et al. 2018). Therefore, feeding areas represent cultural traditions that are vertically transmitted from parent to offspring.

Strong vertical transmission of cultural knowledge is common in socially complex species, potentially rendering individuals of those species incapable of rapidly changing behaviours under novel conditions. Therefore, this highlights a new aspect of vulnerability for these species as persistence in the face of environmental or human-induced change is compromised (Keith & Bull, 2017). For example, if a social unit has invested in learning a specific hunting technique and the target prey species decreases in abundance, it may be extremely costly, both for individuals and for the species as a whole, to change their technique to take advantage of alternative prey. Figure 5 provides a schematic representation of the vulnerability of social groups with different cultural foraging traditions in the face of environmental change, as groups are either stable, adapt or die.

Figure 5.



Cultural groups (C1, C2, C3) consume distinct resources due to socially learnt specialization of foraging strategies. Under a scenario of environmental change (e.g., increased temperatures), the resource base can shift over time (from t1 to t2) and create vulnerability dependent on the potential for cultural groups to track exploit new resources. In the example here, environmental change will result in loss of C1 and persistence of C3, whilst the persistence of C2 will depend on its capacity to forage for resources that are currently consumed with low probability.

RECOMMENDATION: Recognize that species with multiple foraging cultures have multiple resource requirements that are not clear from observations of a single cultural group. Failure to recognize and protect these multiple resource requirements could exacerbate existing conservation issues.

Vulnerability resulting from other aspects of sociality

Mating systems are another aspect of sociality that could alter vulnerability of some species. Removal of key individuals in systems that depend on a strict hierarchy for mating "rights" could be detrimental to an entire group or population. For example, in species with strong sexual dimorphism, which implies strong sexual selection, removal of key breeding males can substantially reduce fecundity even though many males remain in the population. Conversely, reductions in nomadic male lions can increase local populations due to reduced infanticide (Borrego et al 2018). Therefore, individuals are not equal. Rather, removal of individuals can scale up to impact the population through a variety of mechanisms, which could have consequences beyond predictions that assume individuals are equivalent, as many conservation targets are based upon (see Table 4 for examples from odontocete cetaceans).

Table 4. An example of possible mechanisms in social odontocetes where direct removals from a population can have a greater effect on population dynamics than predicted by population models with individual equivalence (adapted from Wade et al., 2012).

a. Mechanisms for which there is some evidence
Deficit of reproductive-age females (killer whales)
Deficit of adult males leading to lower pregnancy rate in females (sperm whales)
Lowered birth rate from disruption of mating systems (spinner and pantropical spotted dolphins)
Physical separation of cow/calf pairs from chase and harassment leading to death of calves (spinner and spotted dolphins)
b. Additional mechanisms suggested by the species' social systems
Loss of cultural knowledge concerning, e.g., types of alternative prey, areas where prey can be found, and ways to capture different types of prey under varying circumstances (Killer Whales, Sperm Whales, Belugas, Narwhals, Pilot Whales)
Increased risk of ice entrapment due to loss of cultural knowledge (belugas, narwhals)
Disruption of social networks by removal of key individuals leading to dispersal and potentially higher mortality rates (Bottlenose Dolphins, Killer Whales)
Loss of an important non-reproductive role by older females (Pilot Whales, Killer Whales, Sperm Whales)
Increased predation risk due to loss of social connection and "babysitting" by non-relatives (Sperm Whales)

RECOMMENDATION: Design a scheme to categorise species vulnerability based on recognizable aspects of their social structure, such as mating systems (e.g., Lang et al 2017 on social predation strategies). Such a scheme was beyond the scope of this workshop.

Another aspect of sociality and culture is recognition that a species may have habitat requirements in addition to prey resources. For example, in species that use designated aggregation areas, or "leks", for breeding (e.g., Black Grouse, fruit bats, paper wasps), the specific location can develop over time as a tradition. If the lekking area undergoes anthropogenic disruption, this could reduce the fecundity of the population until a new tradition can be developed. In some reef fishes, such as Blue-headed Wrasse, "breeding arenas" appear to be socially determined and culturally transmitted (Warner 1988). When resource bases within the arenas were altered, the fish continued to use the same area. However, when fish populations were transplanted between reefs they established new breeding arenas completely distinct from previous "native" populations. Other non-breeding locations are similarly constrained by culture. Communal use of some roosts by bats and birds (e.g. ravens) appear to be based on tradition, rather than tied to a specific resource. In other words, the locations might be somewhat arbitrary (many suitable locations may exist), but once a location is chosen the colony stays faithful to that location.

Cultural constraints can also be important for non-food resources used by some socially complex populations. For example, some Killer Whale populations use rubbing beaches, presumably to exfoliate skin, which are not shared by other sympatric populations (Ford et al. 2000). Habitat use with the presumed aim to avoid humans is seen in wolves and bears in Europe, where individuals have learned which locations in human-modified landscapes areas are safe from hunting or lethal defence of livestock (Ciucci et al. 2018).

RECOMMENDATION: Consider the location of non-food resources (e.g., breeding, health maintenance, human avoidance) for understanding and protecting habitat needs of socially complex species.

However, it should not be assumed that any culturally determined foraging specialization is inflexible and leads to vulnerability. For example, an experiment on Great Tits (*Parus major*) showed how an introduced foraging technique can spread rapidly through social networks to become established as a very stable local culture (Aplin et al. 2015). However, in a further experiment that changed the resources again, the tradition was not constrained but rather shifted rapidly to a more optimal technique (Aplin et al. 2017). Both of these outcomes were considered to be facilitated by the fission-fusion social system and rapid horizontal learning observed in this species. It is therefore possible that how cultural information is transmitted may determine how open it is to change. For instance, vertically transmitted foraging techniques may confer less flexibility and greater vulnerability to ecological change in comparison with horizontally transmitted (within generation) habitat choices that can be refined by individual experience (Keith & Bull, 2017).

RECOMMENDATION: Initiate research to determine if the mechanism of cultural transmission of information can be used as a proxy to categorize species vulnerability.

D. Identification of priority CMS-listed species or populations which may benefit from concerted action

In a discussion facilitated by Giuseppe Notarbartolo di Sciara, the CMS COP-appointed Councillor for Aquatic Mammals, it was agreed that there are a number of characteristics of the species on the CMS appendices which could be used to prioritize action within the list and also, potentially identify further species for which may also benefit from listing on the appendices.

It was noted that the taxa currently listed on the CMS appendices are likely to only represent a subset of species that exhibit social learning and cultural traditions in their migratory behaviour and movement patterns. When identifying potential candidates for listing on the appendices and also when identifying species within the list where social learning is of relevance and import to conservation initiates, it was recommended that any one or more of the following characteristics be considered:

- species with extended parental care
- species that forage in social groups
- species that exhibit complex foraging skills
- species that use social information to make foraging/movement decisions, particularly those exhibiting fission-fusion dynamics
- species that migrate in social groups

Examples might include, but not be restricted to, species that move in kin-based units (e.g. some felids, some canids, some lizards, some primates, some odontocetes, cooperative breeding species); stable non-kin based social units (e.g. some primates); colonial roosting/breeding bats and birds (e.g. seabirds); species that aggregate at food sources or at migratory stop over sites (e.g. vultures; geese).

E. Explore opportunities for synergies with other CMS agreements and initiatives

The relevance of culture and social complexity for conservation to CMS daughter agreements was discussed. Through this process, it has been recognised that social learning, culture and other aspects of sociality may be important when planning actions for the conservation of migratory species. Through this workshop and the existing expert group and via the development of collaboration between experts steered by the Parma workshop, CMS now has a new tool to support conservation activities planned by daughter agreements within the CMS family for species where there is evidence of aspects of sociality of relevance to conservation efforts.

F. Closing Remarks

There was agreement that given the fruitful discussions and importance of the subjects of animal culture, social complexity and social learning for conservation efforts, it would be worthwhile pursuing joint publications in peer reviewed journals. More details would be discussed in due course.

A process for finalizing the report of the meeting, including the sub-groups, was agreed, with the aim of having it available by the end of May for information of the 3rd Meeting of the Sessional Committee of the Scientific Council.

The Steering Group for this workshop and participants expressed their thanks to the hosts and sponsors, the Appennino Tosco-Emiliano National Park, the Fondazione Monteparma, and the Principality of Monaco, for the excellent hospitality, which had even included a delightful concert by the Corale Lirica San Rocco. Participants also thanked the Steering Group for the substantive preparations and excellent facilitation, and the Secretariat.

ANNEX 1: Agenda

A. Opening and Introductions

B. Background Presentations

1. CMS background

1.1. History, context and mandates for the workshop
1.2. CMS Scientific Council, species appendices and progress to date

2. Social learning and conservation across taxa: definitions, methods and relevance

C. Conservation Priorities for CMS-listed Species

Sub-group discussions:

- Worlds that collide: Human-wildlife conflict (HWC) and anthropo-dependence
- Wildlife sages: Conserving valuable cultural diversity in wildlife
- Socio-geography: Social learning, range recovery and migration, island populations
- Socio-vulnerability: Specialization versus ecological resilience

D. Identification of priority CMS listed species or populations which may benefit from concerted action

E. Explore opportunities for synergies with other CMS agreements and initiatives

F. Closing Remarks

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