#### Animal cultures matter for conservation

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Understanding the rich social lives of animals benefits international conservation efforts

Animal culture, defined as "information or behavior—shared within a community—which is acquired from conspecifics through some form of social learning" (1), can have important consequences for the survival and reproduction of individu-als, social groups, and potentially, entire populations (1, 2). Yet, until recently, conservation strategies and policies have focused primarily on broad demographic responses and the preservation of genetically defined, evolutionarily significant units. A burgeoning body of evidence on cultural transmis-sion and other aspects of sociality (3) is now affording critical insights into what should be conserved (going beyond the protection of genetic diversity, to consider adaptive aspects of phenotypic variation), and why specific conservation programs succeed (e.g., through facilitating the resilience of cul-tural diversity) while others fail (e.g., by neglecting key repositories of socially transmitted knowledge). Here, we highlight how international legal instruments, such as the Convention on the Conservation of Migratory Species of Wild Animals (CMS), can facilitate smart, targeted conservation of a wide range of taxa, by explicitly considering aspects of their sociality and cultures.

### CONSEQUENCES OF SOCIAL KNOWLEDGE

An important aspect of social learning is the speed with which new behaviors can potentially spread through popula-tions, with effects that may be positive (e.g., adaptive exploi-tation of a new food source) or negative (e.g., increasing conflict with humans, such as when sperm whales learn to remove fish from longlines) (2). Transmission can be medi-ated by an inherent propensity to adopt innovations [e.g., "lobtail" feeding in humpback whales (1)], or curbed by cul-tural conservatism [e.g., southern resident killer whales' per-sistent foraging specialization on Chinook salmon (2)].

Social learning can result in the emergence of subpopula-tions with distinctive behavioral profiles, erecting social bar-riers, as observed in distinct vocal clans of sperm whales (see the figure). Culturally mediated population structure has im-portant implications for conservation efforts (4), as it can influence species-wide phenotypic diversity and adaptability to changing conditions (5). In some cases, such as humpback or blue whale song, cultural variation can reflect demography and facilitate more efficient, or less invasive, assays of con-temporary genetic population structure (1, 4).

Most pro-foundly, culture can play a causal role in establishing and maintaining distinct evolutionary trajectories (6).

Another consequence of social learning can be the in-creased importance of key individuals as repositories of accu-mulated knowledge, making their targeted protection particularly important for the persistence of social units. For example, the experience of African elephant matriarchs (see the photo) has been shown to positively influence the fertility rates of younger females in their social group, through the transmission of information about the social and ecological landscape (7). Yet, traditional approaches to species conser-vation often prioritize younger individuals for their direct re-productive potential.

Positive conservation outcomes can depend on the resto-ration of cultural knowledge. For example, because whooping cranes learn migratory routes socially, human surrogates in ultralight aircraft can guide naïve, captive-bred birds along their first migration, potentially boosting the effectiveness of reintroduction programs (8, 9). Similarly, without the benefit of socially inherited knowledge, bighorn sheep and moose translocated to unfamiliar habitats can take generations to master the skill of tracking the seasonal distribution of high-quality forage (10). Social learning can also be exploited to ameliorate human-wildlife conflict, for example, by artifi-cially "seeding" desirable behavior, such as avoidance of par-ticular foods or sites (3, 11).

To improve the efficacy of conservation efforts, we there-fore argue that it is critical to consider the interplay between social structure and the transmission of social information. This may be particularly important if different categories of individuals vary in their propensity to innovate, or are more likely to be copied by naïve group members (11). In some cases, populations may be structured into distinct cultural units with differing resource requirements. For instance, cul-tural transmission of vocal patterns among sperm whales in the Eastern tropical Pacific results in distinct vocal clans (1) (see the figure). Clans vary in their feeding success during El Niño and La Niña oceanographic cycles (1), meaning that if these cycles increase, as predicted under climate change, pop-ulation-level impacts may not be uniform.

#### CETACEANS, AND BEYOND

Despite mounting evidence that aspects of sociality can have far-reaching implications for wildlife conservation, interna-tional policy forums—where most large-scale conservation strategies are conceived—have so far not engaged substan-tially with the challenges and opportunities presented by this new scientific perspective. A notable exception is the CMS Scientific Council, which has conducted work at the interface of cutting-edge science and international policy-making.

The CMS signatories work to develop collaboration be-tween range states for the conservation of species that move across jurisdictional boundaries. They agree to support re-search, to endeavor to provide immediate protection for mi-gratory species listed in CMS Appendix I, and to work toward developing agreements for the conservation and manage-ment of migratory species in CMS Appendix II. Although, like many other international agreements, CMS does not have a compliance mechanism, its standing committee is in the pro-cess of critically reviewing the impacts of its decisions, to im-prove effectiveness (background CMS documents are available in the supplementary materials).

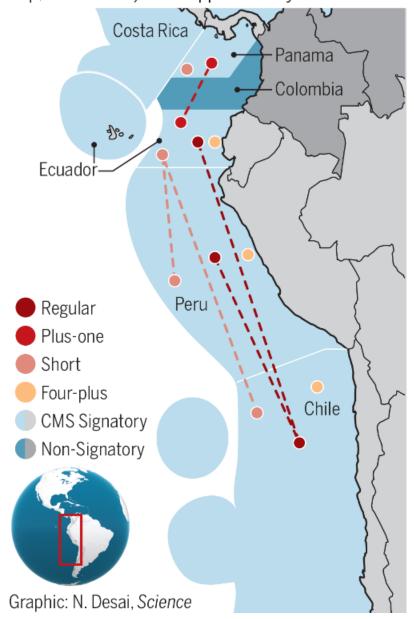
Impetus for an animal culture initiative was provided by a growing body of evidence for social learning and culture in cetaceans that raised important questions about how best to conserve these animals (12). The CMS Scientific Council's preexisting expertise in evaluating threats to aquatic mammals made CMS a natural avenue for examining these issues further. In 2014, a formal consultation revealed an extensive range of circumstances in which social structure, social learn-ing, and cultural variation in whales and dolphins can affect the planning or outcomes of conservation efforts. This culmi-nated in the adoption of a ground-breaking resolution, through which the CMS signatories formally acknowledged the importance of social learning and culture for the conser-vation of some highly social species.

Following the 2014 resolution, the CMS Scientific Council established an expert group to broaden the scope of this ini-tiative beyond cetaceans. The group determined that social learning has conservation relevance across a wide range of vertebrate taxa, including birds, fishes, and many marine and terrestrial mammals (1, 3). At a 2018 cross-taxa CMS culture workshop in Parma, Italy, the authors of the present article reviewed relevant evidence, with a particular focus on species in which social learning has the potential to strongly influence migratory behavior, habitat use, foraging, or inter-action with human activities. On the basis of this work, we recommend, among other things (for details, see table S1): augmenting the designation of evolutionarily significant units; conserving individuals that are critical repositories of social knowledge; refining the criteria used for identifying and prioritizing species and populations for assessment; im-proving reintroduction schemes through strategic manage-ment of social knowledge; planning effective mitigation strategies for anthropogenic impacts using aspects of social-ity; systematically cataloging the dimensions of cultural di-versity; and raising awareness about the value of conserving animal cultures.

The overall aim of this initia-tive is to maximize the efficacy of con-servation efforts through enhanced consideration of sociality in gen-eral, and social learning and (both adaptive, and seemingly arbi-trary) cultural pro-cesses in particular. Under-standing the im-portance of behavioral diver-sity will benefit conservation poli-cies both when as-sessing the status of potentially vulnerable popula-tions (e.g., when delineating units to conserve, by ac-counting for cul-tural segregation) and when devising effective conservation strategies (e.g., by identifying key repositories of social knowledge). Achieving these ambitious goals will require a con-siderable amount of work. For example, although there is broad agreement that successful reintroduction programs require in-dividuals to be behaviorally competent (8), for many species it will still be necessary to establish the degree to which key be-haviors are socially learned [e.g., migratory routes in birds (9, 13)]. To facilitate progress, we highlight a few additional oppor-tunities, both in terms of particular species that may merit fur-ther consideration and promising research approaches.

# Sperm whale vocal clans

Subpopulations in the eastern tropical Pacific. Clan names are derived from their culturally transmitted vocal dialects. Colored lines indicate confirmed movements of photo-identified individuals of known clans across jurisdictional boundaries (conceptual map, not to scale). See supplementary materials.



The CMS encourages its signatories to engage in collective conservation measures through its "concerted action" mech-anism. This process is particularly relevant when considering collaboration between range states for gathering and sharing data on cultural diversity for populations that move

predict-ably across national borders. In 2017, CMS adopted a con-certed action for Eastern tropical Pacific sperm whales (see the figure). A variety of species may benefit from similar con-sideration, to evaluate the importance of aspects of their so-ciality for their conservation. This includes species as diverse as cod (not currently listed in the CMS Appendices), which appear to socially learn migratory routes, and chimpanzees (recently listed in the CMS Appendices), where a culture of nut-cracking tool use thrives in a small area of Western Africa (see fig. S1), yet spans multiple national jurisdictions and may provide access to an important food source during the dry season (3).

An important challenge is to identify those populations, or social units, that would most benefit from our proposed approach, and to predict how specific biological processes may influence conservation outcomes (11). Recent studies il-lustrate how innovative rapid-assessment techniques could aid the identification of distinct cultural units, which may be particularly vulnerable (e.g., as a result of socially learned for-aging strategies). Where socially transmitted traits—such as foraging tactics (and hence resource requirements) and vocal behavior—covary (1), it may be possible to document cultural variation with well-established, inexpensive survey protocols (4). Another approach is to harness new survey technologies, such as autonomous motion-triggered cameras, as exempli-fied by a recent attempt to chart putative cultural variation in wild chimpanzees (14) in the face of urgent threats from habitat destruction and poaching (see fig. S1). In addition, appropriately parameterized formal models may provide re-liable predictions about the impact of specific conservation interventions on sociocultural processes (5). The field of ani-mal social learning is now sufficiently mature to provide key parameters for robust modeling of some systems, where rele-vant data are available from long-term field studies and con-trolled experiments.

#### **MOVING FORWARD**

Our growing understanding of the conservation relevance of cultural variation urges that scientists and policy-makers col-laborate closely to ensure that policy is informed by the latest scientific advances. Many cultural systems are highly com-plex, and the conservation impact of cultural processes is con-text dependent, necessitating careful case-by-case consideration.

Recommendations from the Parma workshop will inform discussions at the November 2019 Meeting of the Sessional Committee of the CMS Scientific Council and the 2020 CMS Conference of the Parties in India. A key challenge will be to determine if evidence warrants explicitly recogniz-ing some distinct cultural units listed in the CMS Appendices, and how insights from this work can be used to inform con-servation efforts across the entire CMS portfolio of agree-ments.

Within the broader context of international wildlife law (15), it is important to consider the relevance of animal cul-ture for scientific assessments and policy decision-making across a range of relevant multilateral environmental agree-ments, such as the Convention on International Trade in En-dangered Species of Wild Fauna and Flora (CITES) and the Convention on Biological Diversity (CBD). We see opportuni-ties to extend our approach beyond species and issues cur-rently covered by CMS, for example, when assessing the sustainability of exports and trade through CITES processes. Such consideration is timely, because 2020 is the final year of the United Nations Decade on Biodiversity, when govern-ments will negotiate the Post-2020 Biodiversity Framework. Given the prevalence of social learning and cultures across a wide range of taxa, a comprehensive, integrated approach is essential to maintaining the natural diversity and integrity of Earth's rich ecosystems.

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#### SUPPLEMENTARY MATERIALS

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