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#### Review



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# A deepening understanding of animal culture suggests lessons for conservation

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A key goal of conservation is to protect biodiversity by supporting the longterm persistence of viable, natural populations of wild species. Conservation practice has long been guided by genetic, ecological and demographic indicators of risk. Emerging evidence of animal culture across diverse taxa and its role as a driver of evolutionary diversification, population structure and

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demographic processes may be essential for augmenting these conventional conservation approaches and decision-making. Animal culture was the focus of a ground-breaking resolution under the Convention on the Conservation of Migratory Species of Wild Animals (CMS), an international treaty operating under the UN Environment Programme. Here, we synthesize existing evidence to demonstrate how social learning and animal culture interact with processes important to conservation management. Specifically, we explore how social learning might influence population viability and be an important resource in response to anthropogenic change, and provide examples of how it can result in phenotypically distinct units with different, socially learnt behavioural strategies. While identifying culture and social learning can be challenging, indirect identification and parsimonious inferences may be informative. Finally, we identify relevant methodologies and provide a framework for viewing behavioural data through a cultural lens which might provide new insights for conservation management.

#### 1. Introduction

A key goal of conservation is to ensure the adaptive potential and long-term persistence of viable populations by maintaining genetic and phenotypic diversity [1]. To achieve this, it is necessary to identify population units in need of conservation, and identify, evaluate and mitigate threats. Standard rubrics for defining units to conserve rely on identifying groups with distinct evolutionary or demographic trajectories (figure 1). International and national conservation frameworks and laws consider the threat status of units to conserve through the assessment of population trajectories, abundance, range dynamics and extinction risk (e.g. IUCN Red List, Endangered Species Act (USA)). We argue that considering animal social learning and animal culture (hereafter 'culture') could augment these conventional conservation approaches and decision-making, by informing the identification of units to conserve and assessing their viability.

The importance of behaviour for conservation biology has been increasingly recognized [2,3]. However, a systematic review of the literature reveals learning and social behaviours were 'rarely considered' in wildlife conservation and management ([4, p. 744]). Our objective is to provide a practical framework to enable conservation managers to consider how culture may impact the viability and structure of certain animal populations and influence animals' responses to conservation strategies. We start by defining animal social learning and culture. We then explore how these processes may influence the transmission of behaviours related to survival and reproduction, and thus provide evidence that social learning might influence demographic processes in a way that impacts population persistence and viability. Next, we delve deeper into the interface of social learning and culture across several behavioural contexts (figure 2). We provide examples where the linkages between conservation and social learning have been demonstrated for endangered species. However, to further elucidate some of the underlying cultural and demographic processes, we also provide examples from species of lower conservation concern, to assist researchers and practitioners in identifying scenarios where social learning may be important for the conservation of endangered species, or for distinct population segments. Finally, we provide a framework (figure 3) to guide the integration of culture and social learning into current conservation and management efforts for social species.

Acknowledging the bias in the existing literature towards the most studied species, which are often more social and/or viewed as cognitively 'advanced', we highlight the crucial role that cultural transmission can play in guiding effective conservation responses. For example, this was recently achieved through the integration of culture and sociality into aspects of the management framework of the Convention on the Conservation of Migratory Species of Wild Animals (CMS) [5] (electronic supplementary material S1). 'Concerted Actions' approved by the Parties to the treaty, based on cultural data now inform the conservation management of eastern tropical Pacific sperm whales (Physeter macrocephalus) and 'nut-cracking' western chimpanzees (Pan troglodytes verus) (electronic supplementary material, S1, S4a, S4c) under CMS. Importantly, the aim is not to divert resources from critical conservation needs, or towards cultural species, but to apply scientific knowledge from this field to advance conservation priorities and assist conservation practice.

#### 2. Social learning and culture

Social learning has been defined as any learning process that is facilitated by the observation of, or interaction with, another animal or its products [6-8]. An individual may learn new behaviour, like how to open a nut, asocially. Social learning, in contrast, involves the transmission of information from one animal (model) to another (observer), which results in the observer learning the behaviour. Social learning can occur along differing sensory channels (e.g. visual, olfactory) and through a variety of mechanisms such as local enhancement and emulation [8] (electronic supplementary material, S2, glossary). Socially learnt behaviour can flow via: vertical transmission from parent to offspring; oblique transmission from older to younger, often unrelated, individuals; horizontal transmission between peers of the same generation [9]; and even between species [10]. All except the first of these pathways of transmission differ significantly from the dynamics of genetic transmission in the spread of behaviours. It should be noted that, like genetic variation, socially learnt behaviour can be adaptive, non-adaptive or neutral with respect to fitness [11]. However, unlike genetic inheritance, in many circumstances, social learning can facilitate the rapid transmission of behaviour across a diversity of contexts including foraging, migration routes and mate choice [12-16], with potentially significant implications for conservation management.

Social learning may also lead to the transmission of information through groups, giving rise to local behavioural (cultural) variants that persist over time and generations. Culture is defined here as information or behaviours shared within a group and acquired from conspecifics through some form of social learning [7,17]. While this is a broad definition, it allows researchers to identify and measure potential cultural behaviours of conservation value [7]. Culture and its critical foundation, social learning, are observed in a wide variety of different social systems (see [18]). While socially learnt behaviour—and in some cases culture—have increasingly been documented across a wide range of invertebrate and vertebrate species [18], many adaptive behaviours do

unit	definition	example in conservation framework	
evolutionary significant unit (ESU)	evolutionary units that show genetic or heritable phenotypic distinctiveness, and that demonstrate isolation, such that there is a restricted flow of information that determines genotype or phenotypes, from other such units [62,63]	IUCN species or sub-species; Canadian Designatable units	(b) DIP3
demographically independent population (DIP)	internal demographic processes (births, deaths) more important to population persistence than migration [60,61]	IUCN subpopulation: distinct groups between which there is little demographic or genetic exchange; US MMPA; IWC populations; Australian EPBC populations	
cultural variant (CV)	the particular form or variant of the cultural trait (behaviour) displayed by a group or population (derived from [9])	varies depending on context: can be within, among or equivalent to DIP or ESU. Shown here within DIP (see figure 2 for other examples)	OCV2 DIP1

**Figure 1.** (*a*) Description and overview of conservation units (ESUs, DIPs and CVs) and how they are used in current conservation frameworks. (*b*) Example of the potential relationship between ESUs, DIPs and CVs: one ESU comprises three DIPs of different sizes, with two CVs found at different frequency in each of the DIPs. (Online version in colour.)

not require social input to develop. Conversely, socially learnt behaviour does not necessarily generate sustained or stable cultures, if, for example, it is related to transient resources. Nevertheless, group-wide behavioural variants (or their products) can be assessed to evaluate the possibility that they are socially learnt from conspecifics.

The precautionary principle (electronic supplementary material, S2, glossary) should be applied when assessing the conservation significance of behavioural patterns against the strength of evidence for social learning. For example, in species with endangered populations, information on social learning should rapidly be incorporated into management plans if there is suggestive evidence that these processes might play a role in survival or reproductive rates, even if it is not conclusive [19]. In many species, it is difficult to determine the mechanism of social learning through observation alone. Nevertheless, in a small number of species, including bluehead wrasse (Thalassoma bifasciatum), great tits (Parus major), meerkats (Suricata suricatta), vervet monkeys (Chlorocebus aethiops) and chimpanzees, controlled studies have provided strong evidence that behaviours spread through groups and over generations via social learning [15,16,20-22]. Such work represents a 'gold standard' of evidence for social learning and culture. However, these controlled studies may have ethical implications, or may not be feasible, particularly in the wild or in endangered species, where observed patterns of behavioural expression can instead be used to infer the presence of cultural processes [23–25]. Indeed, controlled studies can be vital for informing conservation by shaping our understanding of the fundamental principles of social learning and cultural transmission, and how they interface with demographic processes (e.g. anti-predator and survival training [26]).

One common tool to detect the presence of culture is the ethnographic method or the method of exclusion, where cultural processes are inferred if ecological and genetic processes can be ruled out [24]. This may reveal a regionally distributed checkerboard of behavioural variants through the examination of multiple populations or social groups spread across the landscape (e.g. [25,27]). However, the exclusion method is vulnerable to both over and under-attribution of cultural causes where researchers fail to recognize subtle environmental factors shaping individual plasticity or genetic change. For example, chimpanzees' use of long versus short stems to dip for ants was originally thought independent of habitat differences [27], but later detailed studies suggested the choice reflected local variations in the severity of ants' defensive biting [28]. Conversely, the approach may neglect cultural behaviours that are adaptations to different local environments [24], such as tool use to crack shellfish in long-tailed macaques (*Macaca fascicularis*) [29].

Correlational studies can identify culturally transmitted behaviours where social learning experiments are not possible (e.g. [12]). For example, if the vertical transmission is suspected to play a role in learning foraging strategies, correlations can be assessed between neutral genetic markers, as proxies for relatedness or parental lineages, and stable isotope markers, as proxies for foraging patterns (e.g. [12]). It can be parsimonious to infer that social learning plays a role if a correlation is detected, particularly in species with multiple or generalist foraging strategies which suggest behavioural plasticity or phenotypic variation within a population, or in species where social learning has been previously observed. Vertical culture may be reasonably inferred as a determinant of foraging behaviour, if there is a strong correlation between the foraging measure and a uniparentally inherited genetic marker (e.g. mtDNA) that is unlikely to influence foraging directly [30]. Correlation between functional nuclear DNA markers and foraging behaviour could be indicative of a genetic component to the behaviour, but gene-culture coevolution can also create such patterns [31].

This approach has been questioned in the past due to the assumption that genetics plays a strong role in determining many behaviours [32]. However, the patterns of genetic diversity within populations and species are shaped by the demographic, adaptive and stochastic processes that govern genetic drift, gene flow, mutation and Darwinian selection. In this context, the genetic component of behavioural traits is considered to be shaped by many genes that often have only small effect sizes and moderate heritability [33]. Neutral genetic markers typically used to assess relatedness and parentage are, by definition, less likely to be influenced by Darwinian selection than genes underpinning behavioural variants. While it is sometimes possible to conclusively rule out genetic effects in the described scenario by cross-fostering experiments to discover if they acquire their adopted or Downloaded from https://royalsocietypublishing.org/ on 19 June 2021

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chimpa (79) meerka elepha	whales	conservative foraging strategies and vocal dialects	unlikely to switch to alternative prey source when prey preference depleted	managed as distinct cultural units	committee on the status of endangered wildlife in Canada (COSEWIC) DIP, MMPA, ESA
meerka elephar	anzees	nut-cracking foraging strategy	potential access to additional food source during dry season when fruit is scarce	investigation of potential benefits or costs of nut-cracking behaviour	CMS concerted action: collaboration across range states
elephar	ats [20]	social learning and teaching of foraging strategy to young	pups learn to locate and recognise prey, and handle difficult/potentially dangerous prey e.g., scorpions	disturbance that interrupts pathways of transmission may reduce population survival	within population cultural variant
	ants [43]	crop-raiding leads to negative human- wildlife conflict	older males protect and guide younger males; experienced fence breakers serve as repositories of knowledge	'cultural arms race' requiring ever-adapting management	
griffon [80]	n vultures	locate food in chain reaction of information transfer	visual contact with a number of conspecifics required to achieve efficient foraging	successful reintroduction: early-stage supplemental food and simultaneous release large numbers individuals in same location	IUCN designated critically endangered
bottlen dolphir	nose ins [14]	multiple socially learnt foraging strategies	higher survival rate for tool-using dolphins during heat wave	manage 'sponging', 'shelling' cultural units	within-population cultural variant
golden tamarir	n lion ins [26]	knowledge of forage and predator avoidance	reintroduction survival rates extremely low-failed to forage effectively and recognise predators	food provisioning and nest-sites: reintroduced animals survive long enough to socially learn basic life skills	reintroduce with wild elders
whoopi	ping ; [67]	socially learnt migratory routes	increased survival resulting from social learning of migration to suitable habitat	reintroduction: use social learning mechanisms to seed migratory routes; social learning important in multiple behavioural contexts	
the cod and [81]	nd herring	learning established migratory routes from adults	if ratio juveniles to adults too high oblique transmission interrupted; reduced offspring survival and reproduction	stochastic events required to reintroduce recent released fish to migratory routes	
bighon [71]	rn sheep	green wave surfing (synching movements with waves of plant growth)	translocated sheep fail to migrate when moved into unfamiliar landscapes	potential to harness emulation or local enhancement by intervening to seed knowledge in a sub-set of individuals	
right w	whales	socially learnt migratory destinations	unknown flexibility to migration route and destination— high human use areas increase ship strike, noise pollution	vessel restrictions e.g., Boston harbour, for migrating North Atlantic right whales	southern right whale wintering grounds considered DTPs (IWC, New Zealand & Australian domestic legislation), MMPA, ESA
beluga [82]	a whales	socially learnt migratory routes and destinations; socially learnt avoidance of ice entrapment	exploitation may disrupt beluga societies, impact ability for populations to recover and recolonise habitats where extirpated	maintain viable populations in all habitats, protect migration corridors, continued protection from direct exploitation	Fisheries and Oceans Canada, wildlife management boards, IWC, MMPA, ESA
sperm'	whales	acoustic codas identify populations; provide proxy for foraging strategy; cultural clans have different movement patterns	differential foraging success in different oceanographic conditions; movement patterns important for how clans mitigate effects of El Nino-like events	manage acoustic clans as units to conserve	CMS concerted action: multiple range states collecting data, MMPA, ESA
humpb	back s [25]	horizontal transmission of song variants; vocal markers for populations	male sexual display-disruption may impact reproduction but details unclear	rapid assessment tool for identifying and assessing population connectivity; identification of units to conserve	could be incorporated by IWC; MMPA, ESA
New C crows [	Caledonian [83]	vocal dialects	some aspects of tool-assisted foraging behaviour may be socially transmitted, with potential fitness consequences	vocal dialects may provide 'markers' for rapidly mapping variation in tool-related behaviour	
corn bu	untings	vocal dialects indicate breeding population; lack of clear dialects indicate recent recolonisation, relative unsuitability of habitat	both sexes breed within natal dialect, behaviourally fragmenting continuous population; low settlement density, lack clear dialects indicate habitat suitability	potentially a rapid assessment tool for habitat quality and population connectivity	could be used by national conservation bodies to assess effective population size/habitat suitability

Figure 2. Some examples linking social learning across behavioural contexts, to vital rates and conservation policy. Implications for reproduction, survival or adaptation. Mitigation strategy: mitigation strategy linked to animal culture. \*Additional references per species are provided in electronic supplementary material, table 52. Image credits—Chris Huh: humback whale, killer whale, right whale, sperm whale (https://creativecommons.org/licenses/by-sa/3.0/).

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Figure 3. A conceptual framework for incorporating evidence and inference on social learning and animal culture into conservation policy and practice (silhouettes indicate examples discussed in main text and electronic supplementary material; see text for details). Image credits—Chris Huh: humpback whale, killer whale, sperm whale; Kent Sorgon: wrasse (https://creativecommons.org/licenses/by-sa/3.0/). (Online version in colour.)

biological parents' foraging strategy [34,35], this is often not ethical or feasible for endangered species.

Culture can be one of many influences that shape behaviour and new modelling approaches now integrate ecological, social and genetic factors into analyses of behavioural variation (e.g. [36]). For example, network-based diffusion analysis (NBDA) has been used to investigate the social transmission of behaviours in chimpanzees [37], humpback whales (*Megaptera novaeangliae* [38]) and bottlenose dolphins (*Tursiops* sp. [39]) by quantifying the extent to which social network structure explains the spread of behaviour [36].

There is no one-size-fits-all method to identify social learning or culture. Feasibility, financial or ethical constraints make it unlikely that some behaviours would ever be definitively shown to be socially learnt. While the inference approaches listed above do not directly test social learning through experiments, they can provide robust, parsimonious inference for the presence of cultural processes underpinned by social learning based on patterns of behavioural expression. Identifying social learning per se is important whether or not this social learning gives rise to local cultural variation. Social learning can be a cause, a consequence or a marker of phenotypic diversity, of demography and vital rates, of population genetic structure, and of ecological niche separation (e.g. [40,41]). Conservation outcomes depend on demographic processes. If social learning can influence demography, then it follows that conservation practitioners may benefit from considering cultural processes.

## 3. Conservation through the lens of social learning and culture

Given the conservation challenges associated with rapid environmental change and habitat degradation, maintaining the long-term persistence of viable natural populations requires conservationists to focus on maximizing survival prospects and reproductive outputs of individuals, social groups and populations. To illustrate the links between these demographic parameters and social learning, we draw on examples from a wide variety of species, of the varying threat level. The processes elucidated in these examples have relevance for the management of many species, regardless of their conservation status. Indeed, while some examples in this section may not be of immediate conservation concern, many countries actively manage species and populations to avoid them slipping into such categories; therefore, understanding the influence of culture on demographic processes is highly relevant. Multiple sources of social information can generate the diversity of responses to resource availability and predation pressures [42,43]. What conservation relevant insights might be overlooked by assuming that populations-and social groupsare behaviourally homogeneous? We contend that increasing evidence on social learning and culture provides novel perspectives for addressing this question.

Social learning can create phenotypic variation among individuals and groups that can lead to differences in locating food, developing and propagating specialized foraging royalsocietypublishing.org/journal/rspb

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strategies, accessing important habitat or avoiding predators or other risks [18]. Such differences can generate variation in individual fitness within a population and-when such benefits are conferred widely across a social group-can influence vital rates and structure populations [44,45]. First, cultural knowledge may act as a buffer, providing an opportunity to flexibly exploit environments in periods of resource scarcity. Second, in spatially variable environments, social learning can act to 'fine-tune' behaviour to local conditions, a 'resident knowledge' that transient or inexperienced individuals cannot exploit, unless they are able to learn from residents [34]. Third, innovations in response to novel challenges and opportunities can spread via social learning to establish new cultural behaviours, providing a route to exploit new resources [22]. In one of the most famous examples of innovation spread, great and blue (Cyanistes caeruleus) tits learnt to break the foil tops of milk bottles delivered to doorsteps and drink the cream beneath, a behaviour that subsequently spread across Britain and Ireland [46]. However, cultural constraints can also limit the spread of adaptive behaviour, depending on the species and context (e.g. [47]).

Quantifying how social learning and culture generate behavioural variation and influence the dynamics of social groups and populations can yield important insights for conservation by examining effects on vital rates. Distilling precisely how social learning and culture can scale up to influence abundance and density, and thus population dynamics, under different scenarios, is challenging. A practical starting point is examining the influence of social learning on two key vital rates—survival and reproduction—as well as the central conservation question of what units to conserve. How population resilience may be impacted is explored in electronic supplementary material, S3.

#### (a) Influence of social learning on survival

Building on innovative research on model organisms [20,22,37], consideration and utilization of social learning has proved important for increasing survival in managed populations [2] (electronic supplementary material, S4a). In the case of golden lion tamarins (Leontopithecus rosalia), survival rates of reintroduced animals were initially extremely low (13%) [48]. An intensive post-release programme involving supplemental feeding and nest-site provisioning allowed reintroduced animals to survive for long enough to learn basic life skills, doubling survival rates. The offspring of these captive-born re-introduced animals then showed a survival rate of 70%, suggesting that social learning and scaffolding from elders can make a critical contribution to survivorship during reintroductions [26]. In another example, to maximize post-release survival of captive reared critically endangered Hawaiian crows (Corvus hawaiiensis), young birds are conditioned to recognize a potential natural predator, the Hawaiian hawk (Buteo solitarius), and to exhibit context-appropriate anti-predator behaviour (A. L. Greggor et al., unpublished data). In addition to learning to avoid danger, Hawaiian crows may socially learn key skills required to forage efficiently, communicate in a species-typical manner and breed successfully [49] (see electronic supplementary material, S4a). These examples illustrate the importance of seeking to maintain individuals as 'repositories of knowledge' that may span a number of behavioural contexts and ensuring individuals scheduled for release are behaviourally competent, thus impacting conservation success.

Social learning can also provide access to novel, highquality forage, potentially via less energy expenditure than through individual exploration. Socially learnt foraging strategies can also buffer against adverse effects of environmental variability. For example, long-term behavioural studies show bottlenose dolphins in Western Australia have multiple foraging strategies, including socially learnt use of sponges as tools to help extract prey [50]. A recent marine heatwave led to a 5.9% and 12.2% decrease in the survival rate of dolphins that did and did not use tools, respectively. These data indicate that socially transmitted tool use may have buffered a section of the population against the cascading effects of habitat loss on prey species [14]. More broadly, this example highlights how survival in bottlenose dolphins is linked to phenotypic variation. This lesson may be applicable to the conservation and management of other species that show heterogeneity in foraging strategies that could stem from social learning.

#### (b) Influence of social learning on reproduction

Variation in reproductive output among females in a population can provide a quantifiable indicator of population health [51] and can be influenced by social learning in complex ways across different scales. For example, individual female bottlenose dolphins in Brazil that specialize in socially learnt cooperative foraging with fishermen may have a fecundity advantage related to increased seasonal prey resources [52]. At a group scale, the sharing of social information by experienced older African elephant (Loxodonta africana) matriarchs increases group survival and reproductive success, by providing information on the level of threat posed by elephants from other social groups and by predators in the wider environment [53]. Management plans should incorporate the understanding that matriarchs act as 'repositories of knowledge' and that the loss of these individuals (e.g. culling or translocation) can have population-level impacts that persist for decades [54].

Considering broader population units, sperm whale social units cluster into 'clans' identified by acoustic dialects. Reproductive success varies between clans, which is thought to be associated with socially learnt foraging strategies [7,55] and perhaps alloparental care patterns [56], with potential population-level consequences. Foraging variation among clans can lead sub-populations to respond differently to environmental change, such as the El Niño oceanographic phenomenon. Noting this differential success between acoustic clans, in 2017 the Parties to CMS agreed a Concerted Action to further explore the implications of the clan structure for the conservation of sperm whales in the eastern tropical Pacific [57]. While the influence of social learning on reproductive success is apparent, it is not yet clear how environmental changes influencing feeding success impact clan survival; such information is essential for understanding population dynamics within clans and across the species.

### (c) Influence of social learning and culture on units to conserve

Social learning and culture can promote demographic isolation between groups or populations with relevance to

management and conservation (demographically independent populations (DIPs); figures 1 and 2 [3,47]). For example, killer whales (Orcinus orca) can exhibit highly conservative socially learnt prey specializations to the extent that separate, endangered fish-eating Southern Resident killer whale social units forage on fish (e.g. chinook salmon, Oncorhynchus tshawytscha) specific to individual river systems [58]. The population abundance of this social unit has declined along with its preferred prey. This reliance on a single river system and cultural reluctance to switch food sources clearly links the importance of understanding foraging culture with conservation management. This demographic isolation can also lead to genetic divergence and speciation through mechanisms such as assortative mating [59]. Figure 2 highlights examples where culture provides valuable data on the delineation of units to conserve at different scales (DIPs [60,61] and evolutionary significant units (ESUs) [59,62]). We direct readers to recent reviews [11,59] that delve into the role of culture as an evolutionary force leading population segments towards distinct evolutionary trajectories as ESUs (figure 1) [41,63] and highlight the role of gene-culture coevolution in this process.

## 4. Ecological studies through the lens of social learning and culture

Evidence for social learning can be identified across several behavioural contexts, perhaps most commonly across the contexts of foraging, migration and communication. These contexts are often the focus of conservation actions. Therefore, our aim is to provide a roadmap to understand the contexts under which social learning may be relevant and to consider ways the field can contribute to promoting conservation outcomes. We hope the examples (electronic supplementary material, S4a–c; figure 2) will encourage readers to re-examine their data using a cultural lens to investigate whether social learning is important for managing and conserving their species.

#### (a) Foraging

Social learning plays a vital role in the development of foraging behaviour in many species. Where foraging strategies are socially learnt, innovations can spread rapidly through a social group, facilitating the exploitation of new resources in the environment. For example, young male elephants learn crop-raiding techniques from experienced older males [43] leading to negative conservation outcomes (figure 2). Alternatively, cultural conservatism may lead to an inability to switch prey species despite dwindling resources, as changing foraging techniques to exploit alternative prey may be costly. Failure to recognize that species with multiple foraging cultures may have multiple resource requirements (e.g. killer whales [47]) could undermine conservation efforts.

Direct assessment of diet can be achieved through observations of feeding or using morphological or DNA-based assessments of prey remains found in scat, stomach contents or lavages (e.g. [64]). Stable isotope or fatty acid analyses of tissue or scat can be used to infer foraging location and trophic level [65], where opportunities for direct observations are limited. In one recent example, stable isotope analysis of whisker samples provided strong evidence that young banded mongooses (Mungos mungo) inherit their foraging niche from specific (non-parent) adult cultural role models [35]. Importantly, intraspecific foraging specialization may have real-world consequences for survival and reproduction for endangered species (see electronic supplementary material, S4a). For example, multiple lines of evidence have now established nut-cracking, a foraging specialization limited to sub-populations of critically endangered Western chimpanzees, as a socially learnt and culturally transmitted behaviour that may be essential to survival through the dry season when the fruit is scarce. Noting this specialization and the critically endangered status of these sub-populations, in 2020, the Parties to CMS agreed a Concerted Action to further explore the implications of nut-cracking culture for the conservation of this species (electronic supplementary material, S1 and S4a).

#### (b) Migration

In some group-living species or those with extended periods of parental care, the first migration of an individual's life is often with conspecifics. The migration route and/or site learnt can therefore be horizontally transferred from conspecifics [66] or vertically transmitted from parent to offspring (e.g. in whooping cranes, *Grus americana* [67] and southern right whales, *Eubalaena australis* [12]: figure 2), helping ensure that offspring are able to find ephemeral resources in highly patchy environments [68]. Individuals can maintain these socially learnt migratory behaviours across time, leading to a form of cultural conservatism, which can be of relevance to conservation. For example, migratory route fidelity influences management unit designation and the spatially patchy recovery from the hunting of some baleen whale species [40].

Migration movements have been studied directly using field observations and marking methods (e.g. genotypes and photo-identification), and indirectly using stable isotopes and DNA from tissue [12,69]. Genetic pedigrees have been combined with long-term field data, for example, to demonstrate fine-scale extended kin structure at migratory destinations in light-bellied Brent geese (Branta bernicla hrota), supporting the hypothesis that site choice has a cultural component [66]. Increasingly, migration movements are studied directly using animal-attached bio-loggers, which provide high-quality fine-scale movement data [70], used to infer links between breeding, stopover and feeding grounds. For example, translocation experiments exploring the cultural basis of migratory behaviour, such as those conducted on big horn sheep (Ovis canadensis) and moose (Alces alces), provide strong evidence for the importance of cultural behaviour for conservation reintroductions [71] (electronic supplementary material, S4b). Similar patterns are found comparing genetic relatedness and proxies for foraging grounds, such as stable isotopes, in cetacean species (e.g. [12]; figure 2; electronic supplementary material, S4b). Adults with migratory experience and knowledge of suitable habitats may be particularly important as 'knowledgeable individuals' for reintroduction efforts or for preserving existing populations.

#### (c) Communication

Vocal communication—the transfer of information or influence between individuals using sound signals—is routinely

studied within the context of social learning and culture using acoustic recordings often supplemented with genetic, identification marks and bio-logging information to provide context (e.g. [72]). Comparisons of vocal differences among groups or populations can require large geographic ranges to be covered, and long-term monitoring for those species that change their vocalizations over time (e.g. via cultural evolution; see electronic supplementary material, S4c). Group-specific or geographic dialect differences become apparent when examining displays across a region and can be used as a cost-effective measure in rapid assessment of population structure [44]. In many cases, cultural conformity to a vocal display within a group appears a key factor in the formation and maintenance of dialects [73]. Acoustic clans in sperm and killer whales offer clear examples of vocal dialects defining groups to conserve, with linkages to vital rates and a CMS Concerted Action in the former, and COSEWIC DIP, USA MMPA and ESA management protection in the latter (figures 2 and 3; electronic supplementary material, S4c). Such vocal differences can be very long lasting and/or lead to reproductive isolation between populations, correlating with genetic differences (e.g. [72,74]). Finally, severe population declines can result in loss of song culture, as shown in critically endangered regent honeyeaters (Anthochaera phrygia) [75]; cultural decline may be a precursor to extinction thus providing an important conservation indicator [75].

#### 5. Conceptual framework and future directions

Maintaining the adaptive potential and ensuring the longterm persistence of viable natural populations requires conservation managers to focus on maximizing the survival prospects and reproductive outputs of individuals, social groups and populations. An understanding of animal social learning and culture has significant potential to help maximize the impact and efficiency of conservation efforts (electronic supplementary material, table S1). Specifically, understanding linkages between culture and vital rates, cultural evolution, and adaption to rapid global change, will be critical for incorporating culture into management plans. Central to the approach we advocate here is a need to understand the circumstances under which social learning and culture are likely to impact population viability through phenotypic variation (figures 1-3, §3). Additionally, we argue that social learning and culture can be important indicator (§3c) and a resource for resilience in the face of anthropogenic change (figure 2). Social learning and thus cultural evolution may provide opportunities for adaptive behaviours to spread in response to environmental change [76]. Conversely, social learning may prevent the spread of adaptive behaviour, potentially hindering recovery, if conformity is high or some other mechanism promotes cultural 'conservatism' (e.g. killer whale [47]). It may also have a subtle and complex role in resistance to disturbance as the result of knowledgeable elders acting as repositories of social knowledge, as for example in African elephants and killer whales [53,77]. The examples given here are relevant to endangered species, but may also provide insights for those species not currently of conservation concern; managers work to ensure that populations do not decline into threatened status, after all.

Identifying culture and social learning is challenging. While there are a growing number of relatively well-studied species, in the majority of cases, detailed behavioural data are sparse. Indirect identification and parsimonious inferences (e.g. correlation) may therefore be informative. With this perspective in mind, figure 3 provides a framework to guide the integration of data on culture and socially learnt behaviour into current conservation management, and electronic supplementary material, table S1 provides specific recommendations. Within this framework, the first step is to review the evidence, or opportunity, for culture or social learning. Second, how social learning/culture may interact with demographic processes and impact conservation efforts is evaluated and suitable assessment tools are proposed. Third, we suggest how culture could be brought into current conservation frameworks and assessments. For example, if data show that culture or social learning is influencing vital rates of discrete social groups, it could be integrated into population viability analyses. Thus, where salient, phenotypic variation arising from cultural, as well as ecological and genetic processes, could be informative for assessing demographic separation between potential units to manage and conserve [3], and incorporated into national and international conservation frameworks (e.g. IUCN), following published examples (figure 2).

This framework is intended to help guide practitioners towards 'future-proofing' populations by conserving both cultural variation and the capacity for innovation and social learning to maximize the resilience of vulnerable populations. Human activities can both threaten existing cultures and provide a catalyst for new cultural behaviour [13]. The COVID-19 anthropause may provide an opportunity to examine-with an unusual degree of control-the role of social learning in species' responses to significant environmental perturbation [78]. We argue resilience relies on preserving three building blocks of cultural capacity: demography and phenotypic variation; social network structure and population connectivity. Given that such an approach is common to preserving other aspects of biological diversity, and that culture and social learning can interface in multiple ways with conservation efforts, we recommend that the IUCN establish a cross-taxa specialist group to incorporate such information into IUCN assessments. It is only through enhanced collaboration between scientists, conservation practitioners and policy makers that animal culture and social learning can be embedded into conservation practice and policy.

#### Data accessibility. This article has no additional data.

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Competing interests. We declare we have no competing interests.

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### SUPPLEMENTARY MATERIAL

2 Philippa Brakes, Emma L. Carroll, Sasha R. X. Dall, Sally A. Keith, Peter K. 3 McGregor, Sarah L. Mesnick, Michael J. Noad, Luke Rendell, Martha M. 4 Robbins, Christian Rutz, Alex Thornton, Andrew Whiten, Martin J. Whiting, 5 Lucy M. Aplin, Stuart Bearhop, Paolo Ciucci, Vicki Fishlock, John K. B. Ford, 6 7 Giuseppe Notarbartolo di Sciara, Mark P. Simmonds, Fernando Spina, Paul R. Wade, Hal Whitehead, James Williams and Ellen C. Garland (2021) 8 9 10 A deepening understanding of animal culture suggests lessons for conservation. Proc. R. Soc. B Biol. Sci. 11 DOI: 10.1098/rspb.2020.2718 12 \*Corresponding authors: P.Brakes@exeter.ac.uk, e.carroll@auckland.ac.nz and ecq5@st-13 14 andrews.ac.uk 15 S1. Links to CMS documents of interest regarding social learning and 16 17 18 S3. Resilience, density dependence and other demographic processes 3 19 20 21 22 23 Meerkats......5 24 25 26 27 Griffon vultures ......6 Hawaiian crows ......7 28 29 (b) Migration ......7 30 Bighorn sheep ......7 31 32 (c) Communication ......9 33 Sperm whales ......9 Song culture in birds and whales.....9 34 35 Elephants ......10 36 S5. Recommendations - conservation science, policy and practice ...... 10 37 Table S1 ......11 S6. Companion to figure 2 ..... 12 38 39 40 41

#### 42 S1. Links to CMS documents of interest regarding social

#### 43 learning and animal culture

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44 Report of the 2014 Convention on the Conservation of Migratory Species of

45 Wild Animals (CMS) Scientific Council Workshop on the Conservation

46 Implications of Cetacean Culture:

47	https://www.cms.int/sites/default/files/document/Inf 10 14 ScC WG Rpt on
48	Cetacean Culture Eonly.pdf
49	
50	Resolution 11.23(Rev.COP12) Conservation Implications of Animal Culture
51	and Social Complexity: <u>https://www.cms.int/en/document/conservation-</u>
52	implications-animal-culture-and-social-complexity-0
53	
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55	Wild Animals (CMS) Workshop on Conservation Implications of Animal
56	Culture and Social Complexity: <u>https://www.cms.int/en/document/report-cms-</u>
57	workshop-conservation-implications-animal-culture-and-social-complexity
58	
59	Concerted Action for the Sperm Whales ( <i>Physeter macrocephalus</i> ) of the
60	Eastern Tropical Pacific: https://www.cms.int/en/document/concerted-action-
61	sperm-whales-physeter-macrocephalus-eastern-tropical-pacific
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64	(Physeter macrocephalus), proposed Activities for 2020-2023:
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66	tropical-pacific-physeter-macrocephalus-proposed
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69	Africa (Pan troglodytes verus): https://www.cms.int/en/document/proposal-
70	concerted-action-nut-cracking-chimpanzees-west-africa-pan-troglodytes-verus
71	

### 72 S2. Glossary

73	Allee effect: a positive relationship between any component of individual
74	fitness and either numbers or density of conspecifics' [1].
75	Animal culture: information or behaviours shared within a group, and acquired
76	from conspecifics through some form of social learning [2,3].
77	Asocial (individual) learning: change in the response to a stimulus that is
78	caused by a specific experience at a certain time, and that is detectable
79	later in the organism's behaviour [4].
80	Behavioural plasticity: the extent to which individuals adjust their behaviour as
81	a function of changing conditions [5].
82	Cultural transmission: diffusion of behaviour patterns or knowledge via social
83	learning from others' actions or their consequences [6].
84	Effective population size: the number of breeding individuals in an idealised
85	population that would show the same amount of dispersion of allele
86	frequencies under random genetic drift or the same amount of
87	inbreeding as the population under consideration [7].
88	Emulation: occurs when, after observing a demonstrator interacting with
89	objects in its environment, an observer becomes more likely to perform
90	any actions that bring about a similar effect on those objects [8].
91	Horizontal transmission: cultural transmission of behaviour between members
92	of the same generation [9].

92 of the same generation [9].
 93 Local enhancement: the demonstrator attracts the observer's attention to a

94	particular location, which leads to the observer learning about the
95	location and its attributes [2,8].
96	Oblique transmission: cultural transmission of behaviour from older, non-
97	parent models to a younger generation.
98	<i>Phenotypic plasticity:</i> the ability of a genotype to produce different phenotypes
99	in response to different environmental influences [6].
100	Precautionary principle: At its most basic, the precautionary principle is a
101	principle of public decision making that requires decision makers in
102	cases where there are 'threats' of environmental or health harm not to
103	use 'lack of full scientific certainty' as a reason for not taking measures
104	to prevent such harm [10].
105	Production imitation: after observing a demonstrator performing a novel
106	action, or novel sequence, that it has never performed before, an
107	observer then becomes more likely to perform that same action or
108	sequence of actions [8].
109	Social enhancement of food preferences: occurs when after being exposed to
110	a demonstrator carrying cues associated with a particular diet, the
111	observer becomes more likely to consume that diet [8].
112	Social facilitation: occurs when the mere presence of a demonstrator affects
113	the observer's behaviour [8].
114	Social information: any informative input that is generated by the behaviour of
115	another organism [11].
116	Social learning: any learning process that is influenced by the observation of,
117	or interaction with, another animal or its products [2,4,8].
118	Stimulus enhancement: the demonstrator's behaviour draws attention to a
119	particular stimulus [2,8].
120	Vertical transmission: cultural transmission of behaviour from parent to
121	offspring [9].
177	

#### 123 S3. Resilience, density dependence and other demographic

#### 124 processes

125 Various factors can affect the spread of socially learnt behaviours through a population. These include the type of social structure [12], the degree of 126 127 conformity within the population [13], which type of individuals are exhibiting the behaviour (model-based bias) [14] and other forms of learning bias [2,15]. 128 Population stability and density-dependent processes may also influence the 129 130 propagation of socially learnt and other sources of social information [16]. Considering the manner in which social learning can influence resilience in 131 132 populations may also provide valuable insights for conservation. It has been 133 proposed that resilience in biological systems should be considered as having 134 two key features: resistance and recovery [17]. Resistance describes the instantaneous sensitivity to external disturbance, whereas recovery involves 135 136 the internal processes which return a system back toward equilibrium [17]. 137 Applying this approach, social learning has a role in the recovery aspect of 138 resilience, by providing opportunities for adaptive behaviours to spread in response to environmental change [18]. Conversely, social learning could 139 140 prevent the spread of adaptive behaviour if conformity is high, potentially 141 hindering recovery [19]. It may also have a subtle and complex role in

142 resistance to disturbance as the result of knowledgeable elders acting as 143 repositories of social knowledge, e.g., in African elephants, *Loxodonta* spp. and killer whales, Orcinus orca [20,21]. The interplay between these two 144 145 components of resilience and features such as precariousness [22] provide 146 fertile ground for exploring the multifaceted influence of social learning on 147 group and population dynamics. 148 149 The Allee effect ([1], Glossary S2) can arise as the result of reduced 150 effectiveness of information transfer when population densities decline. For 151 example, dispersing oceanic fish such as herring (*Clupea*) and cod (*Gadus*)

152 recruit into populations and learn established migratory routes from

153 experienced adults through the social transmission of knowledge [23].

However, if a stock collapses and the ratio of juvenile to experienced individuals becomes too high, this obligue social transmission chain can be

156 interrupted. Simulations show how overexploitation can push populations

towards tipping points, precipitating collapse. Subsequent recovery is

158 dependent on stochastic events that reintroduce groups of adults, likely

- 159 contributing to the slow recovery of cod and herring populations despite years 160 of protection [24].
- 161

#### 162 **S4. Species examples by behavioural context**

163 (a) Foraging

#### 164 Chimpanzees

Below, we provide a tractable example using chimpanzees as a key case 165 study to show how differences in foraging strategies between social units may 166 167 have implications for conservation (see also figure 2). Human impacts such as logging have reduced chimpanzee behavioural diversity, some of which is 168 169 now known to be culturally based [25] and may have conservation 170 consequences [26]. For example, multiple lines of evidence have now 171 established nut-cracking, a foraging specialisation that appears limited to sub-172 populations of critically endangered Western chimpanzees (Pan troglodytes 173 verus), as a socially learnt and culturally transmitted behaviour. An early 174 report of nut-cracking in central African chimpanzees (Pan troglodytes elliotti) 175 in Cameroon [27] remains to be confirmed by systematic surveys: it was not 176 found in recent surveys by the PanAf research programme [25] but remains a 177 tantalising indication of a second cultural island for this behaviour. Experimental evidence shows that juvenile Eastern African chimpanzees 178 179 exposed to nut-cracking by an older individual began to develop the skill 180 [28,29]. This confirms the behaviour is not explained by genetic differences between eastern and western populations. Other studies have confirmed all 181 182 necessary materials are present at locations where the behaviour is absent, 183 ruling out environmental explanations for the distribution of the behaviour 184 [28,29]. Along with other forms of tool use, nut-cracking may be essential to survival through the dry season when fruit is scarce, and hence may be an 185 186 important skill for chimpanzees' persistence, potentially providing a link to vital 187 rates from a conservation management perspective in the western-most

portion of their range [30]. Noting this socially learnt foraging specialisation in
Western chimpanzees and the critically endangered status of these subpopulations, in 2020 the parties to CMS agreed a Concerted Action to further
explore the implications of nut-cracking culture (see S1).

192

#### 193 Meerkats

194 In meerkats (Suricata suricatta), a cooperatively breeding mongoose species, every aspect of the foraging niche is shaped by vertical and oblique social 195 196 learning. By following experienced adults, exploring areas that adults have 197 explored and sampling food that adults provide, young meerkat pups learn 198 about productive microhabitats within which to search for food [31], and what 199 types of food are safe to eat [32]. Meerkats are also one of only a handful of 200 species for which there is strong experimental evidence for teaching, whereby 201 adults play an active role in helping pups to learn how to handle difficult and 202 potentially dangerous prey such as scorpions (genera Parabuthus and Opistophthalamus) [33]. Experiments also suggest that novel foraging 203 information can spread within as well as between generations, generating 204 205 cultural differences between groups [34,35]. Insights such as these into the 206 processes and patterns through which naive individuals acquire skills and 207 knowledge play an important role in informing conservation efforts, as any 208 disturbance that interrupts pathways of transmission may reduce the viability 209 in terms of survival of the population.

210

#### 211 Great tits

212 Not all socially learnt foraging specialisations are inflexible and lead to vulnerability. For example, an experiment on great tits (Parus major) 213 demonstrated how an introduced foraging technique can spread rapidly 214 through social networks to become established as a very stable local culture 215 216 [13]. In a further experiment which altered the foraging resources, the tradition 217 was not constrained but rather shifted rapidly to a more optimal technique [36]. These results were considered to be facilitated by the fission-fusion 218 219 social system and rapid horizontal learning observed in this species. Thus the 220 manner in which cultural information is transmitted and the nature of the social 221 dynamics may determine how flexible a social unit is to change. For instance, 222 vertically transmitted foraging techniques may impose less flexibility and 223 greater vulnerability to ecological change in comparison to horizontally 224 transmitted (within generation) foraging choices that can be refined by 225 individual experience [37].

226

#### 227 Elephants

228 Socially learnt foraging preferences may also lead to negative human-wildlife

229 interactions. African elephants commonly forage on crops wherever they co-

230 occur with farmers. Elephants usually prefer cultivated food sources, even

when wild food sources are plentiful, due to the higher calorific payoffs.

Electric fences may help deter crop raiding, but they are extremely expensive

to deploy and elephants quickly learn techniques to break them, increasing

- maintenance costs. Elephants learn raiding techniques from each other;
- 235 young males in particular learn from experienced older males, and often raid

236 crops in the company of close associates [38]. While raiding defended farms,

- 237 male elephants have been observed to guide and protect younger males from
- 238 farm defenders. Experienced fence breakers serve as a 'repository of
- 239 knowledge' and help spread this behaviour among a population, exacerbating
- human-wildlife conflict. Beehive fences may provide a more cost-effective 240
- alternative than electric fences [39]. This human-wildlife conflict represents a 241
- 242 'cultural arms race' in which both animals and humans are engaged over the 243
- long-term, resulting in the need for long-term and ever adapting management.
- 244

#### 245 **Killer whales**

246 Killer whales, well known for their strong matrilineal social structure [40], have been grouped into ecotypes based on socially learnt prey specialisation that is 247 248 also associated with variations in their acoustic dialects [41]. Killer whales 249 exhibit highly conservative prev specialisation and are reluctant to consume 250 other forms of prey available to them, which may constrain population 251 resilience [19]. For example, separate social units within fish-eating killer whales forage on fish (e.g., chinook salmon, Oncorhynchus tshawytscha) 252 253 specific to individual river systems [42], and different social units within 254 mammal-eating killer whales can specialise in hunting different species such 255 as gray whales (Eschrichtius robustus) or harbour seals (Phoca vitulina) [43]. 256 Clearly, these conservative foraging specialisations are cause for concern 257 regarding long-term survival and reproduction of the social unit as 258 anthropogenic pressures increase. These behavioural specialisations may 259 have rapidly led to the reproductive isolation, and genetic divergence in 260 response to persistent dietary specialisations, observed between the ecotypes 261 [44]. This appears to be the best example of culture-genome co-evolution outside humans studied to date, but evidence is accumulating for others [6]. 262

263

264 The value of age and experience for reproduction is demonstrated in species such as killer whales (Orcinus orca) and short-finned pilot whales 265 266 (Globicephala macrorhynchus), where females exhibit post-reproductive 267 lifespan (PRLS) - a rare life-history stage in vertebrates. An adult stage which 268 involves complete reproductive cessation seems counter-intuitive to individual 269 fitness maximisation, and although multiple interacting mechanisms may 270 result in PRLS [45], it is thought to have evolved in these species primarily as the result of benefits conferred from grandmothers transmitting social 271 272 information to their descendants [20,46]. For example, in resident-type killer 273 whales, higher survival rates have been recorded in offspring with post-274 reproductive mothers still alive [47] and with grandmothers still alive [48]. 275 Older females act as 'repositories of knowledge' about foraging areas and 276 strategies that may be important during times of environmental perturbation. 277 The preservation of older females in killer whale family groups may therefore 278 be important for the purposes of preserving cultural capacities within the 279 group and enhancing survival and reproduction. 280

- 281 **Griffon vultures**
- 282 Effective transfer of information through a network - for example, finding food -
- 283 can become compromised at low population densities (e.g., the Allee effect).
- Some critically endangered populations of griffon vultures (genus Gyps) find 284

- food by following other vultures in a chain reaction of information transfer (i.e.,
- local enhancement, or social facilitation; see Glossary, S2). Individual-based
- spatially explicit simulation models showed that individuals in the network
- needed to be within visual contact of other individuals to achieve efficient
- foraging [49]. Below a critical threshold density, an extinction spiral began, as the information chain became increasingly disrupted, resulting in decreased
- individual foraging success. Simultaneous release of a large number of
- individuals at the same location was recommended, allowing increased social
- facilitation, with supplemented feeding during early stages.
- 294

#### 295 Hawaiian crows

296 Managers should ensure that individuals scheduled for release are 297 behaviourally competent and that behavioural repertoires are maintained in 298 captive breeding populations. For example, to maximise post-release survival 299 of captive reared critically endangered Hawaiian crows (Corvus hawaiiensis), 300 young birds are conditioned to recognise a potential natural predator, the Hawaiian hawk (Buteo solitarius), and to exhibit context-appropriate anti-301 302 predator behaviour<sup>1</sup>. Furthermore, managers overseeing captive breeding 303 efforts are exploring ways of creating social learning opportunities: the 304 programme is transitioning to parental rearing [50]; immature birds are held in 305 large groups to enable social facilitation; and in the future, it may even be 306 possible to strategically allocate crows (of any age) to aviaries where they can 307 observe competent models in neighbouring chambers [51]. In addition to 308 learning to avoid danger, Hawaiian crows may socially learn key skills 309 required to forage efficiently [52], communicate in a species-typical manner 310 [53], and breed successfully.

311

#### 312 (b) Migration

#### 313 Bighorn sheep

314 Sometimes the key role of social learning in the development of migration 315 remains cryptic until perturbation occurs. Evidence from reintroduction 316 suggests ungulate migration may have evolved and be maintained by social 317 learning of the patterns of seasonal distribution of forage [54]. Ungulates, like 318 other herbivores, synchronise their movements with phenological waves of nutritious green plants ("green-wave surfing" [55]), resulting in migratory 319 320 movements. In the USA, groups of bighorn sheep (Ovis canadensis) were 321 earlier translocated from extant populations into vacant landscapes where 322 extirpated populations once existed [54]. After initially failing to migrate in this 323 new landscape, the population's migratory propensities increased through time as the bighorn sheep (and moose, Alces alces, in an extension of this 324 325 research) increased their knowledge of spatial and temporal patterns of 326 resource availability. The sheep appeared to learn how to exploit the 327 landscape and subsequently vertically transmitted this knowledge across 328 generations. Interestingly, seven bighorn sheep that were also translocated 329 and moved into previously re-established populations, migrated with their 330 adopted herd, which provides further evidence of cultural transmission of

<sup>1</sup> Greggor et al., unpubl. data

- 331 migratory behaviour among conspecifics [54]. This has real-world
- 332 consequences when considering reintroductions and range expansions into
- novel landscapes: knowledgeable individuals are likely key to initial foraging
- 334 success and therefore potentially survival and population growth, prior to
- achieving population-wide knowledge about the environment.
- 336

#### 337 Migratory whales

338 Populations of baleen whales (e.g., right whales, Eubalaena australis and 339 humpback whales, Megaptera novaeangliae) congregate in a single location 340 to calve in the winter, yet from that location, individuals migrate to a range of 341 locations to feed. Individual whales tend to return predominantly to the same 342 feeding area for their entire lives, which is usually the first feeding area they 343 experienced as a calf (e.g., [56,57]). Similarly, evidence for natal philopatry to migratory destinations, is also seen in beluga (Delphinapterus leucas). a 344 345 toothed whale species [58], and probably maintained across an animal's 346 lifespan.

347

348 Significant pressure on populations can arise when migratory corridors or 349 destinations are disrupted or degraded. For example, there is genetic and 350 stable isotope evidence that southern right whales have maternally-directed 351 learning of breeding and feeding migration habitat [56,59]. Whaling activities 352 have extirpated these whales from parts of the migration network, with a 353 corresponding loss of cultural memory of migration destinations leading to 354 spatially variable recovery and concerns about population viability [56]. 355 Furthermore, the culturally learnt feeding grounds could also turn into an 356 ecological trap if climate change drives shifts in productivity away from areas traditionally used by whales [37]. It remains to be seen if southern right 357 358 whales have the behavioural plasticity to exploit new prey resources in a 359 changing ocean, or if, as has been observed, their reproduction and recovery are shaped by environmental conditions and prey availability at their high 360 361 latitude foraging grounds [60,61].

362

This appears to be a more general effect in other heavily hunted species with presumed culturally-determined migration routes [62], such as beluga whales [58]. The level of sub-structuring created by culturally-driven migratory destinations needs (and has been, e.g., belugas) incorporated into conservation management. The combination of migratory culture with hunting has been hypothesised to lead to Allee effects, leading to the observed slow recovery of many baleen whale populations after whaling [62].

370

371 Finally, as a result of high levels of migratory connectivity and site fidelity, it 372 can be argued that some individual sites may themselves require specific 373 protection, as a result of the unique resources they provide. For example, the 374 high migratory connectivity and extreme site loyalty shown by some geese led 375 researchers to argue for individual refuge designation [63]. North Atlantic right 376 whales have a migration route, presumably culturally learnt, that passes through some highly and increasingly used coastal environments on the east 377 378 coast of North America. A number of protection measures, such as vessel 379 restrictions, have been introduced at various points in this route [64].

#### 381 (c) Communication

#### 382 Sperm whales

383 Sperm whales forage principally in the mesopelagic ocean and females have a multilevel social structure [65] with their social units forming larger scale 384 385 dialect groups distinguished by unique clicking patterns or codas, termed 386 vocal clans [66]. Codas are socially learnt and transmitted along maternal lines, together with other aspects of behaviour, such as movement, with 387 388 apparent consequences for foraging success [67–69]. These dialects 389 therefore provide a cultural marker for each clan. Foraging variation amongst clans can lead these sub-populations to respond differently to environmental 390 391 change. Members of two sperm whale clans studied off the Galapagos 392 Islands showed differential responses to the El Niño oceanographic 393 phenomenon. During the more frequent cool years, the "Regular" clan 394 showed higher feeding success than the "Plus-one" clan. In contrast, during 395 years with warmer El Niño conditions, the "Plus-one" clan were more 396 successful [70]. There is also evidence for differences in reproductive success 397 between clans, which is thought to be associated with these socially learnt 398 foraging strategies [2,71]. Difference in surface-time coordination and the 399 quality of social relationships, likely resulting from clan segregation, may 400 influence alloparental care giving, potentially scaling up to different calf survival rates between clans [72]. Noting this differential success between 401 402 acoustic clans, in 2017 the parties to CMS agreed a Concerted Action to 403 further explore the implications of the clan structure for the conservation of 404 sperm whales in this region [73]. While the influence of social learning on 405 reproductive success is apparent, it is not yet clear how environmental 406 changes influencing feeding success impact clan survival; such information is 407 essential for understanding population dynamics within clans and across the 408 species.

409

#### 410 Song culture in birds and whales

411 Some of the best-studied examples of cultural evolution concern bird song [74]. Many species of passerine birds socially learn details of the songs that 412 underpin successful resource defence and breeding [74], while a few whale 413 414 species show signs of song learning [75,76] which may impact reproduction. 415 In songbirds a general pattern of song learning is likely a genetic basic 416 template of own species song and a predisposition to add details learnt from 417 singing adults, often mediated by social interaction with such tutors (e.g., 418 [77]). A local dialect pattern of song variation has been shown in a number of 419 species (e.g., white-crowned sparrow) with some species showing cultural 420 evolution of local dialects (e.g., village indigo birds Vidua chalybeata [78]; corn buntings (Emberiza (Miliaria) calandra [79]). The songs of some baleen whale 421 422 species can also form dialects. Humpback whale songs are culturally 423 transmitted within a population as they show rapid, concerted change in details of population dialects from year to year [80,81]. Humpback songs can 424 425 also be culturally transmitted between populations [76.82]; a checkerboard of song variants was discovered across the South Pacific populations where 426

song types were transmitted from one population to the next, providing a clearexample of horizontal cultural transmission at a vast scale [76].

429

430 Culture is more directly linked to reproduction in passerine birds that learn 431 their song from their fathers. In many species, females both choose males based on characteristics of their song (e.g., complexity), and it has been 432 433 suggested that females will also choose males whose song resembles that of 434 their fathers, leading to mate assortment by similarity in a cultural trait. While 435 this has been suggested as a mechanism for speciation in some bird species 436 [83], in a conservation context, it has the potential to divide populations into 437 smaller effective units with reduced gene flow, with implications for population 438 viability. Declining and fragmented populations often show matched declines 439 in song diversity, and this could potentially further accelerate these affects 440 [84]. Moreover, in re-established and translocated populations, divergence in 441 local song types might make the movement and integration of individuals 442 across populations more difficult as "outsiders" face discriminatory 443 behavioural response, with possible negative implications for gene-flow and conservation management [85]. However, the social learning and vertical 444 transmission of song also means that song diversity may be used as a guick 445 446 and non-invasive indicator of population size and viability in many threatened 447 and declining species of bird [86]. 448

#### 449 Elephants

450 Predator playback studies for African elephants suggest that matriarchs act as 'repositories of social knowledge', providing information to their social unit on 451 452 the level of threat posed by other elephants and predators in their wider 453 environment. The age of the matriarch is the key factor in determining the 454 sensitivity to genuine threats and determining the nature of the response (for 455 example, mobbing behaviour directed towards playback of lions (Panthera leo) roaring, versus rapid defence and retreat in response to playback of 456 457 human voices); with older matriarchs having superior discriminatory abilities. 458 This information is accrued over a lifetime of extended learning and results in older matriarchs conferring fitness benefit on younger females in the social 459 group through increased fertility rates, as a result of the transmission of 460 461 accumulated knowledge [21,87,88]. Additional research teasing out the 462 linkages between social learning and how fertility and other vital rates are 463 impacted would be extremely beneficial. Finally, severe disruptive events, 464 such as culling and translocation, can cause disruptions to persist for decades 465 in these populations [89]. The role of older matriarchs in providing social and 466 ecological information for their social group is likely key to both survival and 467 reproduction and therefore population resilience.

- 468
- 469

#### 470 S5. Recommendations - conservation science, policy and

471 practice

#### **Table S1.** Recommendations for including social learning and animal culture into conservation science, policy and practice<sup>1</sup>

Conservation Science	Conservation Policy	Conservation Practice	
Demographic insightsLong-term demographic studies, particularly those that incorporate an ethnographicapproach and thus enable fine-scale monitoring for trends and tipping points.Targeted monitoring of populations to detect variation in vital rates between culturalvariants.	Population assessment & management Cultural variation to be applied to 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.	Raising awareness         Education and raising awareness about         the value of conserving cultural variation         within and between populations.         Addressing human-wildlife conflict         Targeted enhanced communication	
Further development of population models that capture social learning and resultant effects on survivorship and reproduction, which may also provide insights into time-lagged responses and critical points.           Cataloguing culture           Cataloguing the dimensions of cultural diversity across populations to assist in:           - Identifying and conserving cultural capacities and repositories; and	If particularly important classes of individuals can be identified (e.g., social brokers, matriarchs, individuals with resident knowledge), consider protecting these individuals and connections. Where field data are sparse, but the influence of social	about animal culture in areas with human-wildlife conflict (HWC). Utilise animal – and human – social learning to facilitate better conservation outcomes in HWC and other	
<ul> <li>Informing conservation action and strategies</li> <li>Key dimensions of cultural variation include (but are not limited to):</li> <li>a) Behavioural context</li> <li>b) Who performs the behaviour (e.g., demographic cohort, social unit, connectedness)</li> <li>c) Spatial occurrence</li> </ul>	learning on vital rates may be strongly suspected, we urge that wildlife managers and ecologists apply the precautionary principle. Social learning and culture to be included in recommendation(s) on national assessments (see Figure 2 for examples).	Conservation management strategies.     Reintroductions     For reintroduction programmes:     Individual to be exposed to     experienced conspecific models     (preferably across a range of     behavioural contexts)	
<ul> <li>d) Temporal nature</li> <li>e) Functional characteristics of trait</li> <li>f) Pathway of transmission</li> <li>Assessment tools</li> <li>Develop rapid assessment tools and emerging technologies to provide direct and</li> </ul>	Ecological significance Identify important keystone 'information source' species within wider species communities, and consider their impact on the conservation of target species. International Union for the Conservation of Nature (IUCN)	<ul> <li>Human tutors may be required to first re-establish wild behaviour.</li> <li>Account for learning biases.</li> <li>Detailed data collection on social activity pre- and post- release.</li> </ul>	
<ul> <li>indirect evidence of social transmission, migration routes, social networks, as well as anthropogenic effects on behaviour:</li> <li>a) Acoustics: passive acoustic monitoring; acoustic identification of population units; autonomous recording with identification software.</li> <li>b) Biologging: movement and activity tracking; direct and indirect encounter mapping for social network building.</li> <li>c) Genetic and genomic techniques: eDNA and minimally-invasive sampling to identify kin groups, population structure and migratory connections.</li> <li>d) Stable isotopes, fatty acids and other biochemical makers: delineate population segments with distinct habitat use, as well as transmission patterns of foraging</li> </ul>	Recommend the IUCN establish a cross-taxa issue specialist group to examine the conservation implications of social learning and animal culture. For example, the IUCN Red List categories and criteria (2000) for 'vulnerable' populations states that if the population size of mature individuals is less than 1000, or has restricted occupancy (typically <20 km <sup>2</sup> ) or locations (typically five or fewer)they should be considered for listing as vulnerable. Arguably, some cultural units may meet the IUCN criteria for vulnerable, where there is demonstrable evidence of demographic separation between	<sup>1</sup> Adapted from 'Report of the 2018 CMS Workshop on Conservation Implications of Animal Culture and Social Complexity' (supplementary material, S1)	
<ul> <li>behaviour.</li> <li>e) Proxies of culture that can be assessed more easily. For example:</li> <li>Tool-use in New Caledonian crows: rapidly map possible regional variation in foraging behaviour using vocal dialects as 'markers'.</li> <li>Chimpanzees: quantification of resource availability using camera traps, and other rapid assessment techniques to survey diversity of behaviour amongst chimpanzees across 40 African study sites.</li> </ul>	social units, resulting from 'stable' socially transmitted behaviour, which has specific implications for survivorship or reproduction. <u>Living Planet Index</u> . The Living Planet Index, (adopted by CBD), established a series of 'Essential Biodiversity Variables' (EBVs) – social learning and animal culture to be considered as an EBV.		

#### **S6. Companion to figure 2**

Behavioural context	Species	References
Foraging	Killer whales	[19,20,48,90,40–47]
	Chimpanzees	[25,26,28–30,91], also ESM S1: CMS Proposal for Concerted
		Action
	Meerkats	[31–35]
	Elephants	[21,38,39,87–89]
	Griffon vultures	[49]
	Bottlenose dolphins	[92–95]
	Golden lion tamarins	[96,97]
Migration/Movement	Whooping cranes	[98]
	Cod and herring	[23,24,99,100]
	Bighorn sheep	[54]
	Right whales	[56,59,62,101]
	Beluga whales	[58,102]
Communication	Sperm whales	[2,65–72,103], also ESM S1: CMS Concerted Action
	Humpback whales	[76,82,104–107]
	New Caledonian crows	[108–110]
	Corn buntings	[79,111]

**Table S2.** Additional references by species for figure 2

#### 478 **S7. References**

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