



Review

Is sexiness cumulative? Arguments from birdsong culture

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‘Cumulative cultural evolution’ broadly describes the process by which cultural traits accumulate improvements to efficacy over generations of social learning and innovation. The term can arguably be applied without much controversy to the cultural evolution of tool use, for example. However, it has recently gained momentum in the aesthetic realm as well, where it has been used to describe changes to sexually selected cultural traits. These, the argument goes, can gain efficacy in the sense of evoking stronger emotional responses from receivers. Here, we use examples from birdsong literature to outline our objections to the application of cumulative cultural evolution to cultural traits that achieve popularity based on no standard other than social or sexual preference. Moreover, we distinguish between categories of cultural traits that are preferred for different functional reasons, presenting arguments for or against describing changes to each as improvements. We conclude by proposing that a detailed and nuanced understanding of the mechanisms and outcomes of cultural change is of more service to behavioural and cultural science than a fraught binary distinction between what we can and cannot label ‘cumulative’.

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The term ‘cumulative cultural evolution’ (CCE) has gained popularity since the 1990s as a conceptually distinct subcategory of cultural evolution, despite disagreement among cultural evolutionary theorists as to its precise definition. CCE was originally conceived by [Boyd and Richerson \(1995, 1996\)](#) as a process whereby social learning permits functional traits to accrue changes over generations, allowing cultural traditions to reach levels of complexity that no individual is likely to invent *de novo*. Today, it is generally agreed that any example of CCE should demonstrate the successive addition and retention of *improvements* to a trait, an iterative process characterized by [Tomasello \(1999\)](#) as a ‘ratchet effect’. This sequence of events was codified by [Mesoudi and Thornton \(2018\)](#) in a set of four proposed core criteria for CCE, summarized as follows.

- (1) A variant of a trait arises through innovation or trial and error.
- (2) The variant is socially transmitted throughout a population.

(3) The variant results in an increase in the cultural fitness of the trait or the inclusive genetic fitness of the learner (we will address the implications of these ideas in a later section).

- (4) The first three steps are repeated.

The stipulation by criteria (3) and (4) of sequential improvements is what distinguishes CCE from cultural evolution in the broadest sense, which requires only the accumulation of changes across generations of social transmission, regardless of functionality or complexity.

While improvement over time is the dominant theme in current concepts of CCE ([Boyd & Richerson, 2005](#); [Gruber et al., 2022](#); [Kirby et al., 2008](#); [Mesoudi & Thornton, 2018](#); [Rawlings et al., 2021](#); [Sinclair et al., 2021](#); [Williams & Lachlan, 2022](#)), the role of complexity and the requirement that a trait surpass an individual's inventive capacity are still debated. For instance, echoing [Tomasello \(1999\)](#), [Williams and Lachlan \(2022\)](#) argue that evidence of either improvement or ‘increased behavioural complexity/elaboration’ should meet [Mesoudi and Thornton's \(2018\)](#) third core criterion for CCE. However, complexity (admittedly another ill-defined term) and functional efficacy are distinct properties and do not always evolve in tandem. As [Gruber et al. \(2022\)](#) point out, an increase in efficacy may signal a reduction in complexity, such that improved

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traits become more easily transmissible than their precursors, mitigating the cost of acquisition to a learner. Thus, Gruber et al. (2022) favour limiting CCE to behavioural traits that demonstrably gain efficiency, whether by increases in complexity, as in tool use practices in New Caledonian crows, *Corvus moneduloides* (Logan et al., 2016), and chimpanzees, *Pan troglodytes* (Boesch et al., 2017), or by decreases, as in shortened navigational routes in homing pigeons, *Columba livia* (Sasaki & Biro, 2017), and migratory bighorn sheep, *Ovis canadensis* (Jesmer et al., 2018), assuming these traits are socially learned.

The relevance of an individual's ability to conceive of a given cultural trait independently is also a point of contention. Sasaki and Biro (2017) and Rawlings et al. (2021) follow Boyd and Richerson (1996) in considering a case to qualify as CCE only if the trait in question has been elaborated beyond what can be achieved in a single lifetime, arguing that empirical methods be developed to test this criterion. However, the process of building improvements upon previous generations of knowledge takes place irrespective of an individual's ability to recapitulate that process (Sinclair et al., 2021). And it is undoubtedly less costly to learn a complex behaviour from a social model than it is to invent one by trial and error. Juvenile New Caledonian crows are capable of modifying and using tools in the absence of adult models (Kenward et al., 2005), but in the wild they readily use tools discarded by their parents to refine their foraging skills, and this early socially facilitated experience appears to inform their tool-manufacturing techniques later in development (Holzhaider et al., 2010). Thus, the interaction of innate tendencies and social influence makes it difficult to demonstrate an individual's full innovative capabilities in a natural social setting. More generally, characterizing one mechanism in terms of the impossibility of an alternative mechanism is not typical or easily tractable in biology, nor arguably elsewhere in science.

In the sense of Gruber et al.'s (2022) criterion of increased transmissibility, definitions of cumulative cultural evolution have seemingly not undergone CCE themselves. The only broad consensus among theorists is that CCE involves successive improvements to cultural traits, which still leaves us with the key question: what precisely constitutes 'improvement'? Mesoudi and Thornton's (2018) third core criterion remains nebulous territory, and proposed animal examples of cultural improvement reveal a range of interpretations. To carve out a meaningful conceptual space for CCE within cultural evolutionary theory, we must either agree on the limits of the term and make a binary distinction between what does and does not qualify as improvement, or take the less hardline and perhaps more informative approach of considering the subtleties of each cultural process without attempting to hold it to a particular standard. Whiten's (2019) discussion of cumulative culture in animals, for instance, allows for the possibility of increased efficiency or complexity in traits undergoing directional change without demanding either; however, this highlights rather than resolves the question of when directional change constitutes improvement.

Birds offer ever-widening opportunities to study the spread of cultural traits in the areas of foraging, navigation and communication (Aplin, 2019). Socially learned vocalizations in oscine songbirds provide an ideal space in which to explore the conceptual nuances of cultural evolution and improvement, as they arguably evolve by the widest known variety of selective mechanisms in nonhuman animal culture (reviewed in Derryberry & Luther, 2021; Searcy et al., 2021; Williams, 2021). Here, we touch on different aspects of songbird culture and analogous human behaviours in the context of CCE, with a particular focus on whether traits evolving by sexual and other forms of social selection should be characterized as improving.

DOES VOCAL COMMUNICATION EVOLVE BY CCE?

The idea of cultural improvement intuitively calls to mind technologies like computers in humans and foraging tools in nonhuman animals, which are incontrovertibly refined by users over time. Osiurak and Reynaud (2020) refer to this class of improvement as 'cumulative technological culture', assigning it its own subcategory of CCE.

However, if we think about cultural traditions more broadly in terms of increasing efficacy and transmissibility (as in Gruber et al., 2022), certain aspects of learned communication also qualify as CCE. The evolution of human language is characterized by the emergence of hierarchical structures and generalizable vocabulary that make it easier to learn and apply. Kirby et al. (2008) demonstrated this process over 10 generations of iterated learning in a laboratory setting. In their experimental paradigm, each participant unknowingly learned an alien language describing colour, shape and movement using the previous participant's outcomes. Under two different sets of initial conditions, structure emerged over time that made the language more readily learnable by subsequent generations, with no intent on the part of the participants.

In Kirby et al.'s (2008) experiment, learning biases drove cultural evolution toward linguistic structures that encapsulated information with greater economy, a process that falls in line with many definitions of CCE. Fehér et al. (2009) recorded a similar sequence of cultural evolutionary steps governed by genetic learning biases in laboratory-reared zebra finches, *Taeniopygia guttata*. Male isolates were provided as song models for young birds, who in turn served as models for the next generation of learners. Over four generations of recursive learning, the young birds adjusted the abnormally prolonged syllables and irregular rhythms of their tutors, rendering the final products recognizable as wild-type zebra finch songs.

Although analogous processes have yet to be documented in wild bird populations, simple structures exist in some oscine birdsong that suggest the optimization of communication over time. Specifically, introductory song segments are often highly stereotyped across a population, signalling species identification, while segments that follow can vary widely in ways that facilitate individual recognition (Williams, 2021). Rattling cisticolas, *Cisticola chiniana*, in sub-Saharan Africa (Benedict & Bowie, 2012) and Nuttall's white-crowned sparrows, *Zonotrichia leucophrys nuttalli*, in California (Baker & Thompson, 1985) are two distant taxa that share this strategy. In fact, the introductory whistle of white-crowned sparrow song is so central to effective communication, that it has been genetically assimilated as a learning bias: hearing the whistle triggers juvenile birds to memorize what follows, even if what follows is heterospecific song (Soha & Marler, 2000).

If the ability to heed conspecific signals amid the cacophony of a soundscape before processing information peculiar to any individual singer is equally beneficial to all signal users, the ability to perceive a signal in the first place is still more crucial. And oscine song often culturally evolves to propagate more successfully in a given acoustical environment. There is ample evidence that songbirds adjust to the low-frequency ambient noise of urban environments both by raising the minimum frequency of song over generations of cultural evolution and by adjusting frequency plastically in response to changing noise levels (Derryberry & Luther, 2021). Similarly, silvereyes, *Zosterops lateralis*, sing syllables at lower rates in urban environments (Potvin et al., 2011), and great tits, *Parus major* (Hunter & Krebs, 1979), and rufous-collared sparrows, *Zonotrichia capensis* (Handford, 1988), culturally evolve slower trills in densely forested habitats, avoiding obstruction by the acoustic reflectivity of buildings and trees, respectively.

Informational structure and acoustic adaptation in language and learned birdsong make persuasive candidates for cultural improvements, because they can be indexed objectively to functions shared by and benefiting all users of a trait. In other words, they are adaptive traits that can spread via 'cultural selection' for reasons that transcend subjective preference alone, i.e. by virtue of being more easily adopted, emitted, perceived or understood. For the sake of completeness, we acknowledge that such traits can also arise and spread by genetic evolution, as in acoustic adaptation in subsocial passerine birds (Seddon, 2005), or by a combination of genetic biases and social input. But to the degree that they are culturally transmitted, we would argue that certain broadly shared aspects of vocal communication systems do undergo CCE by most definitions.

However, when we start drilling down to components of vocal communication tied to individual identity and preference, conceptual territory becomes fuzziest. The idiosyncrasies of language found in a speaker's vocabulary, dialect and grammatical construction depend on variables such as the speaker's origin, sources of learning and aesthetic preferences, none of which can be assigned an objective value independent of speaker identity. For example, although the cultural evolution of proper naming conventions in humans is a universally adaptive innovation, because it permits quick reference to individuals in a complex society even in their absence (Conein, 2011), any specific proper name is a product of ephemeral tastes and carries no inherent benefit. In fact, baby names in modern Western culture tend to cycle on a frequency-dependent basis, rising in popularity when they are rare and declining when they are common (Newberry & Plotkin, 2022). Few people would argue that calling a baby Olivia (popular in 2022) instead of Sophia (popular in the 2010s) is suggestive of the 'improvement' of proper names, especially if Sophia will likely cycle back to popularity in a decade or two. In short, if the value of a trait can only be understood in the context of a transitory societal preference for it, that trait cannot meet any objective standard that would undergird the notion of improvement.

Nevertheless, Mesoudi and Thornton's (2018) elaboration of their third core criterion for CCE includes a trait's improved ability to evoke an emotional response in a receiver, for example the 'aesthetic attractiveness of art or dress styles'. Their goal is apparently to broaden the scope of CCE to include cultural traits that gain popularity even in the absence of direct fitness benefits to users, i.e. traits that improve their 'cultural fitness'. Williams and Lachlan (2022), in their review of birdsong literature, endorse the inclusion of aesthetic preferences in the criteria for CCE, as do Garland et al. (2022) in their paper on cumulative song culture in humpback whales, *Megaptera novaeangliae*.

Setting aside for a moment the difference between a cultural trait that is preferred for the functional benefit it confers to all users and one that is currently fashionable but reliant on ephemeral tastes, we feel that another important distinction has been glossed over here. An aesthetic trait might be preferred because it originates with an individual of high social status or taps into a sensory bias, in which case its cultural fitness increases irrespective of its potential benefit to any given user. But a cultural trait may also elicit an emotional response by functioning as an honest indicator of the quality of the user, in which case it can indirectly increase the user's reproductive fitness. Imagine a virtuoso violinist playing a Paganini Caprice: it is the player's early training, stamina and innate skill, and not the Caprice alone, that elicits the audience response. Thus, the locus of improvement has been redirected from the cultural trait to its user. Each of these manifestations of aesthetic preference presents a challenge to the concept of improvement, as we explore in the next section.

DOES SEXINESS EVOLVE BY CCE?

In permitting emotional or aesthetic response as an indicator of improvement, Mesoudi and Thornton (2018) shift the conceptual spotlight from the trait itself to the effect it produces in the receiver, which is arguably the sole measure of its value (Munro, 1955). This creates an open invitation to argue the case for CCE in sexually selected cultural traits, because they 'improve' by eliciting stronger responses from potential mates and rivals.

Williams et al. (2013, 2022) make precisely this argument. Thanks to their meticulous longitudinal data collection on Kent Island, New Brunswick, Canada over three decades, they have documented perhaps the first observation of two sequential population-wide changes in an oscine song in the wild. Savannah sparrow, *Passerculus sandwichensis*, males at the study site first replaced one song element (the 'high note cluster') with another (the 'click train') over time and then began increasing the number of clicks in their click trains. Playback experiments confirmed that males respond to longer click trains with more aggression and females with greater copulatory interest, and dynamical time modelling supported strong selection, as opposed to neutral drift, as the mechanism guiding the cultural changes.

Williams et al. (2022) argue that, because the novel song characteristics more emphatically elicit aggression from males and appeal to females, this constitutes an increase in efficacy, qualifying their results as CCE. However, although the successive additions accompanied by heightened response certainly constitute a ratchet effect of sorts, as far as we know there is no quality inherent in click trains that suggests the change is irreversible. If sexiness in birdsong is a matter of arbitrary shifts in preference tied, for example, to rare-form or sensory bias, can sexiness really improve in the same way foraging tools improve? And does characterizing novel sexy traits as improvements add dimension to an observation?

Sinclair et al. (2021) offer an excellent interdisciplinary discussion of the problematic nature of improvement in aesthetic domains. They argue that, while ratchet effects exist within human musical genres, such as increasingly sophisticated use of dissonant harmonies or notational techniques, the cultural evolutionary history of music is broadly characterized by the rise and fall in popularity of different compositional schools. There is no overarching progress toward evoking an ultimate emotional state. Furthermore, aesthetic experience in response to art is inextricable from cultural background and cannot be assigned value through any universal consensus.

If oscine birdsong behaves similarly to human music, with trends that evoke sexual response rising and falling for reasons not tied to any objective standard, then describing specific traits under sexual selection as evolving by CCE would not do justice to the bigger temporal or geographical picture. A song rising in popularity would constitute the upswing of a cycle rather than a ratchet effect, and the same song would not necessarily take hold in every population.

If, on the other hand, a receiver perceives a song as sexy because of the way the singer performs it, then we need to ask whether it is sufficient to treat the song variant itself as eliciting a sexual response, or whether we need also to consider the information it conveys about the performer, for example the absence of developmental stress (Nowicki et al., 2002). If preference ultimately comes down to differences between singers of the same song type, then the locus of improvement has shifted from the cultural trait to its user. Thus, the root or source of the aesthetic variation is not socially inherited and cannot evolve by CCE.

The Savannah sparrow case appears to involve elements of both scenarios described above: (1) click trains fully overtook high-note clusters in the population for reasons that have yet to be attributed to anything other than aesthetic preference; and (2) males that sing click trains produce varying numbers of clicks, with individuals possessing longer click trains eliciting significantly stronger responses from potential mates and rivals (Williams et al., 2022). Moreover, we have reason to believe that click train length is not entirely culturally learned. There is evidence that a genetic learning bias is responsible for increasing both the mean number of clicks per train over time in the population (Williams et al., 2013) and the variation in click train length among males. If juvenile males tend to 'improve' songs by adding clicks to socially learned song models, and if their differential ability or genetically inherited tendency to do so has resulted in the extant variation in click train length, then the degree to which the most reproductively salient feature of click trains is culturally inherited is unclear.

We dig more deeply into the implications of characterizing each of these two categories of change, namely the replacement, with no objective benefit, of one song type by another in a population and the appearance of song variation that is indicative of a noncultural bias or measure of quality, as CCE in the following sections, using examples from the birdsong literature.

Rising and Falling of Trends

While it is rare to record successive shifts in song popularity in the wild, longitudinal field studies suggest that these cycles are not uncommon. In a population of indigo buntings, *Passerina cyanea*, Payne et al. (1988) found that the only reliable predictor of female preference for a song type was its current prevalence, and not any qualitative distinction. Thus, it is not difficult to imagine a demographic catalyst, such as a temporary bottleneck or a large influx of immigrants, turning the tide of favour in a new direction. Such an accident of fate might account for the novel variant of a white-throated sparrow, *Z. leucophrys*, song ending that spread from the western United States across the continent, replacing the previous variant over the course of only two decades (Logue & Leca, 2020). Similar phenomena have been documented in humpback whales. A humpback song tends to increase in complexity over generations of transmission, until a novel and much simpler song replaces it in what has been termed a 'song revolution' (Allen et al., 2018). Schulze et al. (2022) recently tracked the spread of a novel song type from a breeding population in eastern Australia to one in Ecuador over a 2-year period. The reasons behind these rises and falls may not always be clear, but their existence calls into question the long-term relevance of CCE as an explanatory process, as changes are not accumulating in the direction of a single optimum state. It is difficult to characterize one trait with transitory popularity as an improvement on the last.

There are also scenarios where a novel song elicits the strongest response from conspecifics solely by virtue of being unfamiliar, and here it is nearly impossible to argue the case for CCE. A medium ground finch, *Geospiza fortis*, male learns his single song type from his social father, and an experienced female prefers a male whose song differs significantly from her own father's, perhaps as a means of inbreeding avoidance (Grant & Grant, 1996). If a bias toward unfamiliarity were to help a novel song type take root in a population, that novel song type would not constitute an improvement on a familiar one any more than a familiar song would constitute an improvement when favoured by a nonlocal female. Each song elicits a stronger sexual response than the other in the right context, but neither does so by building on a previous version or by meeting a different objective standard. The appearance and retention of novel song types in a population might be cultural evolution in the same

way that allele frequency change due to immigration is genetic evolution (Slater & Lachlan, 2003), but it can never be cumulative in the sense of evolving by successive improvements to precursors.

Cultural Indicator Traits

In many well-studied oscine species, particular song types are preferred because they can convey a singer's prowess in navigating social interactions. For instance, song sparrow males, *Melospiza melodia*, in the western United States preferentially learn common local songs and engage in territorial song-matching contests (Akçay et al., 2013). Conformity allows birds of both sexes to assess male quality by direct comparison, and Nowicki et al. (2002) found that female song sparrows strongly prefer males who copy song tutors with high fidelity in both fine structural properties and syllable sequence. The song itself, which is the only component of singing behaviour inherited culturally, is therefore not the locus of improvement but the means of signalling a singer's developmental capacity to learn precisely.

Swamp sparrows, *Melospiza georgiana*, also conform to common local song types and engage in matching competitions, but the relevant performance measure appears to be the combination of trill rate and frequency bandwidth (Liu et al., 2018), which are constrained by beak movement. Performers that maximize both song properties elicit more aggression from males and longer copulatory displays from females (Ballentine et al., 2004; Moseley et al., 2013). The tendency of swamp sparrows to maximize the sexiness of learned songs appears to result from a genetically inherited learning bias rather than cultural evolution (Lahti et al., 2011); thus, changes over time in condition-dependent song features are unlikely to arise from the ratcheting of successive individual improvements that undergo cultural transmission.

It could be argued that a novel song type constitutes a cultural improvement if it more efficiently communicates individual quality by allowing meaningful variation among singers, making it easier for receivers to assess potential mates and rivals. However, such an increase in efficacy would be difficult to quantify, as there are always multiple means to the same end. Chipping sparrows, *Spizella passerina*, appear to assess the same performance measures as swamp sparrows, namely trill rate and frequency bandwidth. But Searfoss et al. (2020) found that chipping sparrow populations in the western United States tend to sing faster trills with lower frequency modulation, while eastern birds favour the opposite end of the trade-off. In fact, it is the norm in many species for a population to sing multiple song types that maximize performance in different ways, allowing individuals to assess male quality through side-by-side comparison, either of two variants of the same song type or of two different song types (e.g. red-winged blackbirds, *Agelaius phoeniceus*; Cramer & Price, 2007). No particular vehicle for conveying male quality is an obvious improvement on another.

Superficially, the 'cultural fitness' of a shared song type in these examples improves as it spreads throughout a population. However, the song type per se does not directly confer fitness benefits to the singer. Rather, the singer's ability to outcompete neighbours and attract mates through high-quality performance increases his inclusive fitness, and it does so as a function of individual condition, not by populationwide cultural evolution of sexier song types.

In other species, females assess a male's quality based not on his performance of a particular song type, but on the number of song types in his repertoire (e.g. sedge warblers, *Acrocephalus schoenobaenus*; Buchanan & Catchpole, 1997). Nightingales, *Luscinia megarhynchos*, are known to invent unique songs in addition to learning the common local song types used in male–male competition, building out their repertoires through both imitation and innovation (Sprau & Mundry, 2010). Repertoire size correlates with body size,

making it a reliable proxy for condition (Kipper et al., 2006), and in that sense, a larger repertoire might be called an improvement on a smaller one. However, the improvement is a benefit reserved for individuals with fewer physiological constraints and not one that can be inherited socially. Similarly, Kroodsma et al. (1997) found that laboratory-reared grey catbirds, *Dumetella carolinensis*, exposed to varying numbers of tutor songs developed repertoires that bore no positive relationship to the degree of tutor input, suggesting that repertoire size is a function of something other than cultural transmission. Like the ability to reproduce a common neighbourhood song with the highest fidelity or fastest trill rate, the capacity to build the largest repertoire does not constitute a cultural improvement, as it apparently does not spread by social learning.

In each of the above cases, the locus of improvement is not the cultural trait itself, but the physiological condition of the individual using it. Thus, in our view, the cultural evolution of vocal communication that conveys information through condition dependence cannot be characterized as CCE.

To add yet another layer to the conversation, there are some species where song elicits response from males and females by two opposite mechanisms. Chestnut-sided warblers, *Dendroica pensylvanica*, possess one temporally stable category of song (the 'accented-ending' song) used in broadcast and mate attraction and another highly variable category (the 'unaccented-ending' song) used in male–male competition (Byers et al., 2010). Byers et al. propose that the accented-ending song permits females to assess male quality through conformity and direct comparison, while the unaccented-ending song evolves rapidly as males reshuffle local and immigrant song syllables to add nuance to repertoire-matching competitions. In fact, within 12 years of observations, unaccented-ending song types in a Massachusetts, U.S.A. population had achieved complete turnover. In the first case, it is again male quality and not song type that females assess, and in the second case, rapid cultural evolution itself (i.e. novelty generation) appears to confer the advantage in male–male competition, such that no particular song can be described as an improvement upon its precursor.

We have illustrated that strengthened sexual response in male and female songbirds can be evoked by conformity, novelty, and both properties simultaneously, as well as performance measures linked to bodily condition, such as repertoire size, trill rate and copy fidelity. Many of these rely not on shared song traits per se to confer fitness benefits, but on the quality of a given performer. So, while these traits are socially learned, they cannot progress toward any sort of evocative optimization through cultural transmission alone. Other traits cannot be characterized as evolving by the accumulation of improvements, because they rely on the perpetual generation of novelty. Yet all of these cultural evolutionary mechanisms achieve the same receiver outcomes. Does it add depth to our understanding of sexual selection in oscine song to label one ratchet-like subset of a cyclical process CCE, when so much of oscine singing behaviour achieves sexiness without successive additions to song types, or by means that are not strictly cultural?

DISCUSSION

We propose that a distinction be preserved between improvements to the efficacy of a tool or cultural behaviour in its environment, and changes that vary among individuals and benefit users differently in a way that represents improvement only by receiver-dependent standards. Both types of change may arise through the same processes, including trial and error, but the former produces a benefit indexed to a function shared by all users of a trait, whereas the latter depends entirely on the vagaries of individual preference. Both types of change can also result in differential reproductive fitness, but the causation between improvement and preference is

opposite in the two cases: a better tool is adaptive in and of itself and preferred for its utility, whereas a socially fashionable trait, which spreads irrespective of its transmissibility or ease of production, is adaptive only insofar as it evokes an emotional response. In a nutshell, the one is preferred because it is improved, and the other is improved because it is preferred.

In addition, we propose that socially fashionable traits preferred for user-independent reasons be distinguished from cultural traits that act as indicators of noncultural user characteristics. If a cultural trait serves as a proxy for body condition, developmental health or cultivated skill, then it is not preferred per se for its aesthetic value, but rather elicits an emotional response as a function of the quality of the individual reproducing it. Crucially, unlike a socially fashionable trend, the aspect of a cultural indicator trait that evokes the preference of one instance over another cannot be socially learned. Thus, it can only be described as 'improved' by noncultural standards.

The thread emerging from our and Sinclair et al.'s (2021) analyses is that, if we are to draw a hard line between what should and should not qualify as cultural improvement, then CCE in the aesthetic realm applies only to the technological and structural frameworks within which individual expressivity and virtuosity may flourish. Tinits and Sobchuk (2020) offer the proliferation and diversification of roles on Hollywood film crews as an instance of CCE in the production process behind a work of art. Other examples in human culture include the manufacture of musical instruments, the development of sturdy building materials that give rise to architectural styles, and even the hierarchical structure of language, whose infinite permutational possibilities give us the beauty of poetry and fiction. With respect to learned birdsong, these frameworks would include the organization that permits rapid species recognition within a diverse soundscape and the acoustical parameters that carry signals most efficiently in a given environment. Within these confines, individual variation can arise through the virtuosic performance of popular songs, repertoire expansion and novelty generation that elicit differential sexual and aggressive response in conspecifics.

By current definitions, at least three distinct scopes for CCE exist: (1) CCE is synonymous with Osieurak and Reynaud's (2020) 'cumulative technological culture', applying exclusively to tools; (2) CCE describes any trait evolving improved universal function through increased efficacy and cultural transmissibility, including technological, communicative and navigatory advancements (Gruber et al., 2022); or (3) CCE characterizes any socially learned sequential additions that result in increased efficiency or strengthened aesthetic response (Garland et al., 2022; Mesoudi & Thornton, 2018; Williams & Lachlan, 2022). The more sweeping the definition, the more explanatory nuance is lost.

If we embrace the third option, it follows that we must either trawl the many and varied mechanisms by which sexual selection shapes cultural traits for those that resemble the telltale ratchet effect, an endeavor which strikes us as somewhat arbitrary, or else assume all instances of sexual selection driving cultural evolution to be CCE. If we choose the latter, we effectively place all cultural evolution involving any sort of social preference for one trait over another (which is arguably how all cultural traits spread) into the category of CCE, no matter how far removed the changes are from direct functional improvements. This includes artistic trends like pottery styles, which have long been reserved in the literature as exceptions to CCE, i.e. examples of cultural evolution that do not represent improvement.

Aesthetic preferences can be highly variable, frequency dependent and bound to individual social status or physiological condition, all of which make them perpetual 'moving targets' for selection. Characterizing the traits that elicit such preferences as 'improvements' stretches the term beyond conceptual utility. Since

most if not all cultural changes spread because they are preferred, we will have reasoned our way back to a nearly interchangeable use of ‘cumulative cultural evolution’ and ‘cultural evolution’. In fact, Garland et al. (2022) appear to embrace this idea, distinguishing only between cumulative cultural evolution and neutral cultural evolutionary processes like drift. In this case, the field of cultural evolution will have terminated its ability to address the important question of whether cultural changes are improvements, as all non-neutral changes would automatically qualify.

The history of ambiguity and disagreement in defining CCE has invited too broad an interpretative scope for the term. Even if we agree that evoking preference qua preference should not qualify as increased efficiency and that only objective improvement should count as CCE, we are still tasked with strictly defining ‘objective improvement’. And there is rarely a sharp line to be drawn between objective improvement and social preference within a given trait. Indeed, Williams and Lachlan (2022) artfully enumerate the many different selective forces that tend to act on birdsong simultaneously; a learned song might edge toward a higher minimum frequency and slower delivery in order to acoustically navigate an urban landscape (Derryberry & Luther, 2021), while at the same conforming to a novel social bias that favours a particular type of song content (e.g. Youngblood & Lahti, 2022). Thus it may be wrongly simplistic to divide functional cultural evolution into CCE and non-CCE categories.

The semantic identity of CCE is tenuous in the first place: all cultural evolution is cumulative in the sense that traits accumulate changes, with current forms arising from precursors. Thus, the most etymologically appropriate definition of CCE dissolves its importance as a concept. So perhaps we should abandon the binary notion of cumulative cultural evolution altogether in favour of a more nuanced consideration of cultural evolution and the various achievements, environments, inherited biases and social preferences that shape it.

Author Contributions

Franny C. Geller and David C. Lahti wrote the paper.

Data Availability

No data were used for this paper.

Declaration of Interest

None.

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References

- Akçay, Ç. L., Tom, M. E., Campbell, S. E., & Beecher, M. D. (2013). Song type matching is an honest early threat signal in a hierarchical animal communication system. *Proceedings of the Royal Society B: Biological Sciences*, 280(1756), Article 20122517.
- Allen, J. A., Garland, E. C., Dunlop, R. A., & Noad, M. J. (2018). Cultural revolutions reduce complexity in the songs of humpback whales. *Proceedings of the Royal Society B: Biological Sciences*, 285(1891), Article 20182088.
- Aplin, L. M. (2019). Culture and cultural evolution in birds: A review of the evidence. *Animal Behaviour*, 147, 179–187.
- Baker, M. C., & Thompson, D. B. (1985). Song dialects of white-crowned sparrows: Historical processes inferred from patterns of geographic variation. *Condor*, 87(1), 127–141.
- Ballentine, B., Hyman, J., & Nowicki, S. (2004). Vocal performance influences female response to male bird song: An experimental test. *Behavioral Ecology*, 15(1), 163–168.
- Benedict, L., & Bowie, R. C. K. (2012). Rattling cisticola song features and variability across sub-Saharan Africa. *Journal of Zoology*, 287(2), 96–103.
- Boesch, C., Kalan, A. K., Agbor, A., Arandjelovic, M., Dieguez, P., Lapeyre, V., & Köhl, H. S. (2017). Chimpanzees routinely fish for algae with tools during the dry season in Bakoun, Guinea. *American Journal of Primatology*, 79(3), Article e22613.
- Boyd, R., & Richerson, P. J. (1995). Why does culture increase human adaptability? *Ethology and Sociobiology*, 16(2), 125–143.
- Boyd, R., & Richerson, P. J. (1996). Why culture is common, but cultural evolution is rare. *Proceedings of the British Academy*, 88, 77–93.
- Boyd, R., & Richerson, P. J. (2005). *The origin and evolution of cultures*. Oxford University Press.
- Buchanan, K. L., & Catchpole, C. K. (1997). Female choice in the sedge warbler *Acrocephalus schoenobaenus* multiple cues from song and territory quality. *Proceedings of the Royal Society B: Biological Sciences*, 264(1381), 521–526.
- Byers, B. E., Belinsky, K. L., & Bentley, R. A. (2010). Independent cultural evolution of two song traditions in the chestnut-sided warbler. *American Naturalist*, 176(4), 476–489.
- Conein, B. (2011). Gossip, conversation and group size: Language as a bonding mechanism. *Irish Journal of Sociology*, 19(1), 116–131.
- Cramer, E. R. A., & Price, J. J. (2007). Red-winged blackbirds *Agelaius phoeniceus* respond differently to song types with different performance levels. *Journal of Avian Biology*, 38(1), 122–127.
- Derryberry, E. P., & Luther, D. (2021). What is known – and not known – about acoustic communication in an urban soundscape. *Integrative and Comparative Biology*, 61(5), 1783–1794.
- Fehér, O., Wang, H., Saar, S., Mitra, P. P., & Tchernichovski, O. (2009). De novo establishment of wild-type song culture in the zebra finch. *Nature*, 459(7246), 564–568.
- Garland, E. C., Garrigue, C., & Noad, M. J. (2022). When does cultural evolution become cumulative culture? A case study of humpback whale song. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 377(1843), Article 20200313.
- Grant, B. R., & Grant, P. R. (1996). Cultural inheritance of song and its role in the evolution of Darwin's finches. *Evolution*, 50(6), 2471–2487.
- Gruber, T., Chimento, M., Aplin, L. M., & Biro, D. (2022). Efficiency fosters cumulative culture across species. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 377(1843), Article 20200308.
- Handford, P. (1988). Trill rate dialects in the rufous-collared sparrow, *Zonotrichia capensis*, in northwestern Argentina. *Canadian Journal of Zoology*, 66(12), 2658–2670.
- Holzhaider, J. C., Hunt, G. R., & Gray, R. D. (2010). Social learning in New Caledonian crows. *Learning & Behavior*, 38(3), 206–219.
- Hunter, M. L., & Krebs, J. R. (1979). Geographical variation in the song of the great tit (*Parus major*) in relation to ecological factors. *Journal of Animal Ecology*, 48(3), 759–785.
- Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., & Kauffman, M. J. (2018). Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science*, 361(6406), 1023–1025.
- Kenward, B., Weir, A. A., Rutz, C., & Kacelnik, A. (2005). Tool manufacture by naive juvenile crows. *Nature*, 433, 121.
- Kipper, S., Mundry, R., Sommer, C., Hultsch, H., & Todt, D. (2006). Song repertoire size is correlated with body measures and arrival date in common nightingales, *Luscinia megarhynchos*. *Animal Behaviour*, 71(1), 211–217.
- Kirby, S., Cornish, H., & Smith, K. (2008). Cumulative cultural evolution in the laboratory: An experimental approach to the origins of structure in human language. *Proceedings of the National Academy of Sciences of the United States of America*, 105(31), 10681–10686.
- Kroodsma, D. E., Houlihan, P. W., Fallon, P. A., & Wells, J. A. (1997). Song development by grey catbirds. *Animal Behaviour*, 54(2), 457–464.
- Lahti, D. C., Moseley, D. L., & Podos, J. (2011). A tradeoff between performance and accuracy in bird song learning. *Ethology*, 117(9), 802–811.
- Liu, I. A., Soha, J. A., & Nowicki, S. (2018). Song type matching and vocal performance in territorial signalling by male swamp sparrows. *Animal Behaviour*, 139, 117–125.
- Logan, C. J., Breen, A. J., Taylor, A. H., Gray, R. D., & Hoppitt, W. J. (2016). How New Caledonian crows solve novel foraging problems and what it means for cumulative culture. *Learning & Behavior*, 44(1), 18–28.
- Logue, D. M., & Leca, J.-B. (2020). Animal culture: How a new birdsong went viral. *Current Biology*, 30(16), R957–R959.
- Mesoudi, A., & Thornton, A. (2018). What is cumulative cultural evolution? *Proceedings of the Royal Society B: Biological Sciences*, 285(1880), Article 20180712.
- Moseley, D. L., Lahti, D. C., & Podos, J. (2013). Responses to song playback vary with the vocal performance of both signal senders and receivers. *Proceedings of the Royal Society B: Biological Sciences*, 280(1768), Article 20131401.
- Munro, T. (1955). Form and value in the arts: A functional approach. *Journal of Aesthetics and Art Criticism*, 13(3), 316–341.
- Newberry, M. G., & Plotkin, J. B. (2022). Measuring frequency-dependent selection in culture. *Nature Human Behaviour*, 6, 1048–1055.
- Nowicki, S., Searcy, W. A., & Peters, S. (2002). Quality of song learning affects female response to male bird song. *Proceedings of the Royal Society B: Biological Sciences*, 269(1503), 1949–1954.
- Osiurak, F., & Reynaud, E. (2020). The elephant in the room: What matters cognitively in cumulative technological culture. *Behavioral and Brain Sciences*, 43, Article E156.

- Payne, R. B., Payne, L. L., & Doehrlert, S. M. (1988). Biological and cultural success of song memes in indigo buntings. *Ecology*, *69*(1), 104–117.
- Potvin, D. A., Parris, K. M., & Mulder, R. A. (2011). Geographically pervasive effects of urban noise on frequency and syllable rate of songs and calls in silvereyes (*Zosterops lateralis*). *Proceedings of the Royal Society B: Biological Sciences*, *278*(1717), 2464–2469.
- Rawlings, B. S., Legare, C. H., Brosnan, S. F., & Vale, G. L. (2021). Leveling the playing field in studying cumulative cultural evolution: Conceptual and methodological advances in nonhuman animal research. *Journal of Experimental Psychology: Animal Learning and Cognition*, *47*(3), Article 252.
- Sasaki, T., & Biro, D. (2017). Cumulative culture can emerge from collective intelligence in animal groups. *Nature Communications*, *8*, Article 15049.
- Schulze, J. N., Denking, J., Oña, J., Poole, M. M., & Garland, E. C. (2022). Humpback whale song revolutions continue to spread from the central into the eastern South Pacific. *Royal Society Open Science*, *9*(8), Article 220158.
- Searcy, W. A., Soha, J., Peters, S., & Nowicki, S. (2021). Variation in vocal production learning across songbirds. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *376*(1836), Article 20200257.
- Searfoss, A. M., Liu, W.-c., & Creanza, N. (2020). Geographically well-distributed citizen science data reveals range-wide variation in the chipping sparrow's simple song. *Animal Behaviour*, *161*, 63–76.
- Seddon, N. (2005). Ecological adaptation and species recognition drives vocal evolution in Neotropical suboscine birds. *Evolution*, *59*(1), 200–215.
- Sinclair, N. C., Ursell, J., South, A., & Rendell, L. (2021). From Beethoven to Beyoncé: Do changing aesthetic cultures amount to cumulative cultural evolution? *Frontiers in Psychology*, *12*, Article 663397.
- Slater, P. J. B., & Lachlan, R. F. (2003). Is innovation in bird song adaptive? In S. M. Reader, & K. N. Laland (Eds.), *Animal innovation* (pp. 117–136). Oxford Academic.
- Soha, J. A., & Marler, P. (2000). A species-specific acoustic cue for selective song learning in the white-crowned sparrow. *Animal Behaviour*, *60*(3), 297–306.
- Sprau, P., & Mundry, R. (2010). Song type sharing in common nightingales, *Luscinia megarhynchos*, and its implications for cultural evolution. *Animal Behaviour*, *80*(3), 427–434.
- Tinits, P., & Sobchuk, O. (2020). Open-ended cumulative cultural evolution of Hollywood film crews. *Evolutionary Human Sciences*, *2*, Article e26.
- Tomasello, M. (1999). The human adaptation for culture. *Annual Review of Anthropology*, *28*(1), 509–529.
- Whiten, A. (2019). Cultural evolution in animals. *Annual Review of Ecology, Evolution, and Systematics*, *50*, 27–48.
- Williams, H. (2021). Mechanisms of cultural evolution in the songs of wild bird populations. *Frontiers in Psychology*, *12*, Article 643343.
- Williams, H., & Lachlan, R. F. (2022). Evidence for cumulative cultural evolution in bird song. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *377*(1843), Article 20200322.
- Williams, H., Levin, I. I., Norris, D. R., Newman, A. E., & Wheelwright, N. T. (2013). Three decades of cultural evolution in Savannah sparrow songs. *Animal Behaviour*, *85*(1), 213–223.
- Williams, H., Scharf, A., Ryba, A. R., Ryan Norris, D., Mennill, D. J., Newman, A. E., & Blackwood, J. C. (2022). Cumulative cultural evolution and mechanisms for cultural selection in wild bird songs. *Nature Communications*, *13*(1), Article 4001.
- Youngblood, M., & Lahti, D. C. (2022). Content bias in the cultural evolution of house finch song. *Animal Behaviour*, *185*, 37–48.