

SYMPOSIA PAPER

# Animal Culture and Animal Welfare

Simon Fitzpatrick<sup>1\*</sup>  and Kristin Andrews<sup>2\*</sup> 

<sup>1</sup>Department of Philosophy, John Carroll University, University Heights, OH, USA and <sup>2</sup>Department of Philosophy, York University, Toronto, ON, Canada

\*Corresponding author. Emails: [sfitzpatrick@jcu.edu](mailto:sfitzpatrick@jcu.edu); [andrewsk@yorku.ca](mailto:andrewsk@yorku.ca)

(Received 14 October 2021; revised 08 March 2022; accepted 21 April 2022; first published online 30 May 2022)

## Abstract

Following recent arguments that cultural practices in wild animal populations have important conservation implications, we argue that recognizing captive animals as cultural has important welfare implications. Having a culture is of deep importance for cultural animals, wherever they live. Without understanding the cultural capacities of captive animals, we will be left with a deeply impoverished view of what they need to flourish. Best practices for welfare should therefore require concern for animals' cultural needs, but the relationship between culture and welfare is also extremely complex, requiring us to rethink standard assumptions about what constitutes and contributes to welfare.

## 1. Introduction

There is now abundant evidence of *culture*—socially inherited patterns of behavior and information, including group-specific traditions—in a wide variety of nonhuman animals, including apes, monkeys, various terrestrial mammals, cetaceans, birds, fish, and even insects, such as bumblebees and fruit flies (Whiten 2021). Given that these cultural practices are part of the behavioral repertoires that influence how animal populations adapt to their respective environments, prominent researchers have argued that the cultures of wild animals have important implications for conservation efforts (Brakes et al. 2021). In this paper, we explore another important implication of the recognition that many species are cultural species: the bearing of animal cultures on questions of animal welfare and the ethical treatment of animals in agriculture, zoos, sanctuaries, research facilities, and various human-managed environments.

We argue that many captive animals, like their wild counterparts, are cultural beings, that best practices for welfare should require concern for animals' cultural needs, and these needs are distinguishable from their physiological and social ones. For instance, animals can be harmed when cultural capacities and practices important to them are impeded or disrupted intentionally or unintentionally by management practices, even when they are not physically harmed and their social relations remain intact.

The relationship between culture and welfare is complex, presenting significant challenges for human caretakers, and requires us to move beyond some standard

assumptions about what constitutes and determines welfare for such species. Introducing culture as a welfare concern transcends typical concerns about “natural” behavior and the affective states of animals that are central to standard conceptions of animal welfare. Cultural well-being may also come into conflict with common conceptions of harm reduction. Just as some important human cultural practices involve tissue damage, such as piercing and tattooing, animals may engage in important cultural practices that appear harmful. The recognition that behaviors may be cultural can also cast new light onto their welfare implications—for instance, helping us to understand whether behaviors classified as “abnormal” and reflective of negative welfare should really be understood as such.

We will argue that the ability to have a culture is an essential need for cultural beings. Thus, just as conservation efforts should include preserving not just a species’ biological material and environments, but also their cultural diversity, we will argue that welfare efforts should include supporting the development of culture and preserving cultural diversity in captive contexts.

The paper will proceed as follows: section 2 will provide some background on the evidence for culture in nonhuman animals and recent work on the conservation implications of this research. Section 3 will explore various ways in which the welfare of animals may be shaped and impacted by their cultural environment (or lack thereof). Section 4 will discuss how these welfare implications transcend typical concepts of what constitutes and determines welfare in the literature. Section 5 will suggest two arguments for why we should regard captive animal cultures as having more than just instrumental value. Thinking about animal welfare in terms of culture has a number of rich implications that we can only touch on in this paper, and we will conclude with some remarks on the broader question of the ethics of captivity for cultural species.

## 2. Background: animal culture and conservation

“Culture,” in the most inclusive sense used in the animal literature, refers to *socially inherited patterns of behavior and information* (Heyes 2020). Central to this broad understanding of culture is *social learning*: the acquisition of behavioral dispositions and information from other agents and/or their products. Some of the earliest work on social learning and culture in animals came from observations of the transmission of novel behavior from one animal to others, such as potato washing in Japanese macaques spreading from one juvenile to others in the troop, and milk-bottle-opening behaviors spreading through populations of birds in the United Kingdom (Whiten 2021).

A narrower conception of “culture” refers to group-specific *traditions*: socially transmitted patterns of behavior and information that are common to members of a group, but differ between subpopulations of the same species, and persist over time. In the case of chimpanzees—the first nonhuman species identified as having such traditions—there is clear evidence of stable group differences across various domains, including tool use and foraging behaviors, grooming, courtship, and communication (Whiten 2021), that persist through generational turnover and immigration of females from neighbouring groups (van Leeuwen 2021). These include arbitrary customs and “ways of doing things around here,” such as hand-clasp

grooming style and the practice of wearing grass in ears observed in one group (van Leeuwen et al. 2014). Researchers working with whales and birds have documented similar stable group differences in song dialects, migratory routes, and so forth (Whitehead and Rendell 2015; Aplin 2019), and there is an increasing range of taxa being studied for their cultural behavior, including insects (Danchin et al. 2018).

Now that the existence of animal culture has become widely accepted, prominent animal culture researchers have started to explore the broader implications of these discoveries. Notably, Brakes et al. (2021) have suggested numerous direct implications for conservation efforts aimed at protecting populations vulnerable to extinction, including “linkages between culture and vital rates, cultural evolution, and adaptation to rapid global change” (2021, 8).

These stem from the idea that culture provides a second inheritance system, alongside genetic inheritance (Richerson and Boyd 2005). Like genetic variants, cultural variants may be passed down from one generation to the next and may increase, decrease, or be neutral with respect to an organism’s reproductive fitness. Consequently, understanding the role of socially learned practices in the lifeways of subpopulations of endangered species, how they shape their interactions with their environment (and with us), and how those practices are transmitted and maintained is vital for conservationists seeking to identify subpopulations at greatest risk and assess the efficacy of mitigation strategies. For instance, culturally variable foraging or migratory strategies may mean that subpopulations of the same species have different abilities to weather environmental changes caused by climate change or habitat destruction, requiring us to think differently about the threats they face. Similarly, understanding the role of social learning in, for instance, crop-raiding behaviors in elephants, may help us to mitigate such human-wildlife conflicts. And the effectiveness of reintroduction programs may stand or fall on details about the role that cultural knowledge played in the adaptive success of original populations and our ability to ensure that reintroduced animals have the requisite knowledge. Efforts to restock northern cod, for instance, seem to have been undermined by the lack of knowledge of migration routes in the young fish, which would have been passed down to naive juveniles from older fish (Whitehead 2021).

Next to the implications of wild animal culture, the implications of captive animal culture remain underexplored, though we will build on some important previous discussions (Savage-Rumbaugh et al. 2007; Hopper et al. 2016; Benz-Schwarzburg 2019; Hopper 2021; Whitehead 2021).

### 3. Culture and welfare

While much of the pioneering work on animal social learning and culture has been conducted with wild or free-ranging populations, many of the most important studies have been conducted with captive populations (Whiten 2021). There is evidence of social learning in farmed animals, such as cattle, pigs, sheep, and chickens (Nawroth et al. 2019), as well as species commonly used in biomedical research, such as rats, mice (Galef 1996; Valsecchi and Galef 1989), and fruit flies (Danchin et al. 2018). Indeed, if the recent history of animal culture research is any guide, it seems likely that we are underestimating the extent of cultural complexity beyond high-profile examples in primates and cetaceans (Schuppli and van Schaik 2019). We will therefore

proceed on the assumption that, while there is going to be significant variation in the nature and extent of cultural capacities across taxa, many species of captive animals, from those used in agriculture and biomedical research to those in zoos, are cultural species.

The existence of culture immediately raises three issues relevant to welfare.

First is the need for certain kinds of sociality for captive cultural animals (Whitehead 2021). While Harlow's isolation experiments with macaques made the need for social contact in social animals abundantly clear, the importance of types of social relationships has been comparatively neglected in the animal welfare literature. For animals who adapt to their environments in large part by learning from others, there is a psychological need for contact with a range of conspecifics occupying different roles (e.g., stage of life, status, expertise), reflective of their learning strategies. Mothers often serve as the first point of cultural contact, but in many species same age peers are also important sources of cultural knowledge, as in the case of predator recognition in minnows (Chivers and Smith 1995). In other cases, juveniles may acquire cultural knowledge from same sex adults other than a parent, as do male chimpanzees learning to hunt monkeys (Boesch 2002) and female African elephants learning how to signal sexual receptivity in their first oestrus (Bates et al. 2010). It is also likely that cultural species have a psychological need to pass on cultural information to their offspring or peers. This needn't be conscious or explicit, but may be felt nonetheless. Thus, the cultural nature of animals requires consideration of the type and quality of social partners—not just sociality, but sociality of the right types. Common management practices, such as housing animals in same-sex and same-age groups, or sex-biased groups that don't reflect typical group composition and familial and other social relationships in the wild, will, therefore, be of ethical significance.

Second is the need for the opportunity to construct cultures when none are in place. Hence, when it comes to questions about environmental enrichment, richness of the socio-cultural environment should be regarded as a factor in determining animal welfare, alongside richness of the physical environment. This has broad implications that extend into what kinds of enrichment activities and materials are provided for animals, how they are housed, and how much time they are allowed to spend with others in their social groups. We know artificial challenges like as puzzle boxes reduce stress and elicit signs of positive affect, including in livestock (Nawroth et al. 2019), and may foster better social dynamics (Hopper 2021). Social challenges could offer additional benefits. For instance, by introducing a juice fountain that requires one individual to operate while another enjoys the result, chimpanzees were provided with opportunities for cooperation and developing social conventions (van Leeuwen et al. 2021). Further research should illuminate how cultural enrichment may positively affect welfare.

Third is the need to recognize the epistemic losses and welfare effects of changing community compositions. Communities change all the time in wild populations, due to immigration, dispersal, etc., but management practices such as re-grouping, re-housing, and moving individuals from one facility to another for breeding may still be extremely disruptive to the overall functioning and welfare of the group. For instance, removing older individuals who have knowledge about rare or less frequent events, such as death, seasonality, caregiver turnover, etc., may leave naive individuals to start over in an epistemic culture-building project. Captive environments may

be more predictable than wild ones, but just as the lack of cultural knowledge on the part of reintroduced animals seems to have undermined efforts to restock endangered wild populations, it seems important that newcomers to captive environments are provided with opportunities to learn from knowledgeable individuals. For instance, Nawroth et al. (2019) cite evidence that housing dairy calves in social groups increases weaning weights compared with individual housing by facilitating their learning of grazing behavior. Goldsborough et al. (2021) describe two separate integration events in a group of captive chimpanzees, suggesting that immigrants who quickly adopt the cultural practices of the group integrate more successfully than those more reluctant to acquire the local cultural repertoire. Hence, it may be desirable for caretakers to find ways to scaffold social learning to facilitate better integration. Hopper (2021) notes the special importance of this in the case of integrating hand-reared animals.

Establishing a cultural lens on captive animal communities also enjoins us to interpret behavioral patterns in new ways. If animals have “ways of doing things around here” that they are invested in, then ethical and welfare considerations entreat us to not disrupt them unnecessarily. As when dealing with human beings from other cultures, we need to be careful not to overlook and unintentionally interfere with cultural traditions that have arisen in captive animal populations, since it may be easy to miss a cultural behavior when one is outside the group.

However, directly parallel to human cultures, the practices of particular groups may not support the flourishing of individuals. There is some evidence that rates of aggression and fighting in primates have a cultural component (Sapolsky and Share 2004). Several “abnormal” practices in captive populations appear to spread via social learning. Hook et al. (2002) provide evidence that behaviors like coprophagy (eating feces), feces smearing, pacing, hair pulling, and rocking are socially transmitted and vary between different groups of captive chimpanzees and rhesus macaques. Cannibalism in chickens, which has direct negative effects on victims, also appears to be socially learned (Hopper 2021). This creates difficult challenges for caretakers in balancing minimizing harm to individuals and avoiding disruption to group practices.

Recognizing an “abnormal” behavior as cultural may also change our understanding of its relevance to welfare. In the case of coprophagy in chimpanzees, Hopper et al. (2016) argue that this behavior needn’t necessarily reflect any deficits in health and well-being of the individuals who do it, but could just be the way this particular group does things. Even if the behavior is cultural, it may still have been originally “invented” out of frustration or boredom and indicative of poor welfare, but the point remains that the “abnormality” of a cultural behavior doesn’t, by itself, indicate negative welfare. Potential cultural behaviors that involve health risks are seen in wild populations, such as chimpanzee mothers carrying their infant’s corpse (Biro et al. 2010), or capuchin hair pulling and finger-in-eye-socket games (Perry 2011). For captive populations, similarly risky activities may have to be reviewed in the context of their potential cultural importance.

Some of the ways captive animals do things “around here” include human cultural behaviors. Captive animals learn much from their interactions with humans—e.g., about feeding times, when to move to different enclosures, and how they are handled by caregivers. In many instances, they may also copy human behaviors. Hopper (2021) describes ways that this might be leveraged by caretakers to improve conditions for

captive animals, such as via “do-as-I-do” training. But we should be mindful of how human interactions with animals may shape their cultures. We can inadvertently create new cultural behaviors, such those seen in the orphaned orangutans at Camp Leaky, who acquired human behaviors such as washing fabric with soap, paddling boats, sleeping in hammocks, and siphoning gasoline (Russon and Galdikas 1993). Indeed, animals who spend a lot of time interacting with humans may even belong to *multiple* overlapping cultures—one culture amongst themselves, and another that includes the relevant humans. This is most obvious in the case of “enculturated” apes, like those involved in ape language studies, raised in multispecies groups (Fouts 1998). But multispecies cultures may exist in more subtle ways, across all sorts of captive settings from sanctuaries to psychological research labs (see, e.g., Funkhouser et al. 2021).

This brings us to our key point: We take for granted in the case of human beings that without seeking to understand the cultural practices of a particular group of individuals, we will have no idea who they are and what they need to flourish. Given the evidence of animal culture and the reach of culture into the lives of cultural animals, we should adopt a similar perspective: Without seeking to understand their cultural capacities and practices we will be left with a deeply impoverished view of who they are, what they need to flourish, and what does and does not contribute to that flourishing.

#### 4. Culture and the concept of welfare

We now wish to argue that recognizing the link between culture and welfare also requires us to rethink some standard assumptions about the concept and determinants of animal welfare.

While there are a multitude of different approaches to welfare in the animal welfare literature, in practice, most common approaches put forward by animal welfare advocates and organizations tend to emphasize the basic physical health and functioning (absence of disease, hunger, thirst), the affective state of the animal, and many add some reference to “natural” or “normal” behavior. For instance, the UK Farm Animal Welfare Council’s still widely cited Five Freedoms lists the following criteria as determinants of welfare for farmed animals:

**Freedom from hunger and thirst**, by ready access to water and a diet to maintain health and vigour.

**Freedom from discomfort**, by providing an appropriate environment.

**Freedom from pain, injury and disease**, by prevention or rapid diagnosis and treatment.

**Freedom to express normal behavior**, by providing sufficient space, proper facilities and appropriate company of the animal’s own kind.

**Freedom from fear and distress**, by ensuring conditions and treatment, which avoid mental suffering. (Farm Animal Welfare Council 2009, 2)

The last decade or so has seen greater emphasis on not just mitigating welfare compromise, as in the Five Freedoms, but also promoting “positive animal welfare” (Lawrence et al. 2019). For instance, welfare assessment frameworks like the Five

Domains have been modified to include concepts such as “positive affective engagement” and “agency” (Mellor and Beausoleil 2015). However, animal welfare remains widely understood as some combination of basic health and functioning, affective states (broadened to include more positive affective states), and for many, the ability to engage in “normal” or “species-typical” behavior.

We’ve already seen how basing an assessment of the welfare of cultural animals on conceptions of “normal” and “species-typical” behavior may be misleading. The behavior of a population of a cultural species may be quite atypical, but nonetheless important for the welfare of that population, and the “abnormality” of coprophagy may tell us nothing about the welfare of chimpanzees.

Similarly, the relevance of culture to welfare transcends the affective states of animals. Here, we wish to build on a point made by Monsó et al. (2018) that conceptions of welfare that focus on positive and negative affect miss an extra set of harms that relate to the thwarting of animal capacities. They discuss the case of social animals who have capacities for empathy and sympathy and are inclined by those capacities to aid groupmates in distress—for example, a sow may feel sympathy for a piglet being castrated without anesthetic, yet be prevented from comforting them. Monsó et al. argue that this sow is “doubly harmed”: first, by the negative feelings that go along with her sensing the distress of the piglet; second, by the thwarting of her caring capacities. We wish to argue that, similarly, the thwarting of cultural capacities constitutes a kind of harm that transcends any affective states that may go along with that thwarting. If cultural animals are deprived of opportunities to engage in social learning, to take part in cultural practices, and play a role in developing and shaping such practices, something of value important for their welfare has been lost, even if this loss is not something that is felt by the animal. This harm might be characterized in a variety of different ways, including in terms of some loss of meaning to the lives of animals (Purves and Delon 2018), or via some loss to their autonomy.

Broadening the concept of welfare beyond basic physical health and functioning, affective state, and so-called “natural” or “normal” behaviors to include something like cultural autonomy, has significant ramifications. Even the most seemingly benign captive environments, such as sanctuaries, are run in paternalistic ways that focus on minimising a narrow conception of harm to animals at the expense of autonomy for the animals themselves (Donaldson and Kymlicka 2015). This can include limiting social contact, according to schedules dictated by human caretakers, removing “unruly” individuals from the social group, and carefully managing the environment to remove potential sources of danger. Here, however, there is some tension between safety and the social dynamics of the group. Cultural animals learn how to manage their environments from others, so removing all sources of danger also removes opportunities for learning that may be highly beneficial.

## 5. Conserving animal cultural diversity

Do animal cultures matter only for instrumental reasons related to conservation and welfare, or might they have value in their own right? We wish to canvass two arguments for assigning them more than just instrumental value.

The first argument (Whitehead 2021) is a simple extension of a view common among conservationists: Biodiversity is worth preserving for its own sake. One of the key claims of the animal culture and cultural evolution literature is that culture is as much part of how cultural animals adapt to their environments as genetic endowment (Richerson and Boyd 2005). This breaks down the common dichotomy between culture and biology. Hence, if biodiversity is valuable in its own right, so goes the thought, then animal cultural diversity should also be valuable, given the premise that biology and culture are inexorably tangled.

The second argument relies on the common idea that human cultures have normative status. Many think it important that endangered languages be preserved, and that diversity in ways of living is a good. For instance, the UNESCO Universal Declaration on Cultural Diversity (2001), states that “cultural diversity is as necessary for humankind as biodiversity is for nature.” The idea here is that culture is intrinsically valuable. If this is so for human cultures, why not for animal cultures?

Of course, as debates over multiculturalism demonstrate, the idea that culture has normative status is not unproblematic. Forced female genital mutilation and racial segregation don’t become ethically acceptable just because they are part of some group’s culture. The claim that culture has normative status thus cannot be about cultural practices themselves, but about the inherent value of cultural *diversity* and cultural *autonomy*. To imagine human beings without any culture or without cultural differences is not to imagine human beings. Likewise, having a culture is part of being a member of many species, from bees to chimpanzees. By valuing animals’ capacity to have and shape their cultural practices for themselves, we are not approving or seeking preservation of particular cultural contents. Rather, we are making a deeper claim: Cultural beings require culture and the ability to shape their culture to be themselves, and that they are something less if they are merely the living biological material devoid of cultural context.

## 6. Concluding remarks

In closing, we should emphasize that we have not in this paper taken any stance on the more general ethical issue of animal captivity. While space prevents us from exploring these implications fully, our discussion does clearly have bearing on this question of the ethics of captivity. Here, again, matters are complex. On the one hand, our discussion does raise significant questions about whether captive cultural animals can live well and whether even the most responsibly managed captive environments can support the welfare needs of these animals. There is growing recognition that large aquatic mammals, such as whales and dolphins, do not do well in captivity because of the complexity of their social structures in the wild and the importance of those structures for the flourishing of individual animals. Culture is central to this. Similar arguments may be made for elephants and primates.

On the other hand, cultures in a captive context can be valuable and meaningful for animals and shouldn’t necessarily be dismissed offhand as inferior to wild cultures. Captivity can change a group of animals culturally so significantly that they *cannot* be reintegrated into wild populations. Extinguishing captive cultures is also ethically significant. Moreover, as we have argued, culture can provide opportunities for improving conditions for at least some “captive natives,” to the extent that



caretakers have a responsibility to provide resources to facilitate and sustain cultural development, and an appropriate notion of cultural well-being should become part of welfare assessment frameworks for cultural species.

These are among the many implications of the link between culture and welfare that deserve further exploration.

**Acknowledgments.** Thanks to two reviewers, Jonathan Birch, Heather Browning and the LSE ASENT group, Judith Benz-Schwarzburg, Lydia Hopper, Susana Monsó, and audiences at the University of Edinburgh and PSA20/21. Funding: SSHRC Insight Grant 435-2016-1051.

## References

- Aplin, Lucy. 2019. "Culture and cultural evolution in birds: A review of the evidence." *Animal Behaviour* 147 (2019):179–87.
- Bates, Lucy, Rosie Handford, Phyllis Lee, Norah Njiraini, Joyce Poole, Katito Sayialel, Soila Sayialel, Cynthia Moss, and Richard Byrne. 2010. "Why do African elephants (*Loxodonta africana*) simulate oestrus? An analysis of longitudinal data." *PloS One* 5 (4):e10052.
- Benz-Schwarzburg, Judith. 2019. *Cognitive Kin, Moral Strangers?* Leiden: Brill.
- Biro, Dora, Tatyana Humle, Kathelijne Koops, Claudia Sousa, Misato Hayashi, and Tetsuro Matsuzawa, T. 2010. "Chimpanzee mothers at Bossou, Guinea carry the mummified remains of their dead infants." *Current Biology* 20 (8):R351–R352.
- Bosch, Christophe. 2002. "Cooperative hunting roles among Taï chimpanzees." *Human Nature* 13 (1): 27–46.
- Brakes, Philippa, Emma Carroll, Sasha Dall, Sally Keith, Peter McGregor, Sarah Mesnick, Michael Noad, et al. 2021. "A deepening understanding of animal culture suggests lessons for conservation." *Proceedings of the Royal Society B* 288 (1949): 20202718.
- Chivers, Douglas, and Jan Smith. 1995. "Chemical recognition of risky habitats is culturally transmitted among flathead minnows, *Pimephales promelas* (Osteichthyes, Cyprinidae)." *Ethology* 99 (4): 286–96.
- Danchin, Etienne, Sabine Nöbel, Arnaud Pocheville, Anne-Cecile Dagaëff, Léa Demay, Mathilde Alphan, Sarah Ranty-Roby, Lara van Renssen, Magdalena Monier, Eva Gazagne, Mélanie Allain, and Gillaume Isabel. 2018. "Cultural flies: Conformist social learning in fruitflies predicts long-lasting mate-choice traditions." *Science* 362 (6418):1025–30.
- Donaldson, Sue, and Will Kymlicka. 2015. "Farmed animal sanctuaries: The heart of the movement? A socio-political perspective." *Politics and Animals* 1 (1):50–74.
- Farm Animal Welfare Council. 2009. *Farm Animal Welfare in Great Britain: Past, Present and Future*. <https://www.gov.uk/government/publications/fawc-report-on-farm-animal-welfare-in-great-britain-past-present-and-future>.
- Fouts, Roger. 1998. *Next of Kin: My Conversations with Chimpanzees*. New York: William Morrow.
- Funkhouser, Jake, Jessica Mayhew, John Mulcahy, and Lori Sheeran. 2021. "Human caregivers are integrated social partners for captive chimpanzees." *Primates* 62 (2):297–309.
- Galef Jr., Bennett. 1996. "Social enhancement of food preferences in norway rats: a brief review." In *Social Learning and Imitation*, edited by Cecelia Heyes and Bennett Galef, 49–64. New York: Academic Press.
- Goldsborough, Zoë, Christine Webb, Frans de Waal, and Edwin van Leeuwen. 2021. "Zoo-housed female chimpanzee adopts local female-specific tradition upon immigrating into a new group." *Behaviour* 158 (2021):547–64.
- Heyes, Cecilia. 2020. "Primer on 'culture.'" *Current Biology* 30 (20):R1233–R1255.
- Hook, Michelle, Susan Lambeth, Jaine Perlman, Ronda Stavisky, Mollie Bloomsmith, and Steven Schapiro. 2002. "Inter-group variation in abnormal behavior in chimpanzees (*Pan troglodytes*) and rhesus macaques (*Macaca mulatta*)." *Applied Animal Behaviour Science* 76 (2):165–76.
- Hopper, Lydia, Hani Freeman, and Stephen Ross. 2016. "Reconsidering coprophagy as an indicator of negative welfare for captive chimpanzees." *Applied Animal Behaviour Science* 176 (2016):112–19.
- Hopper, Lydia. 2021. "Leveraging social learning to enhance captive animal care and welfare." *Journal of Zoological and Botanical Gardens* 2 (1):21–40.

- Lawrence, Alistair, Belinda Vigors, and Peter Sandøe. 2019. "What is so positive about positive animal welfare?—A critical review of the literature." *Animals* 9 (10):783.
- Mellor, D.J., and Ngaió Beausoleil. 2015. "Extending the 'Five Domains' model for animal welfare assessment to incorporate positive welfare states." *Animal Welfare* 24 (3):241–53.
- Monsó, Susana, Judith Benz-Schwarzburg, and Annika Bremhorst. 2018. "Animal morality: What it means and why it matters." *Journal of Ethics* 22 (3):283–310.
- Nawroth, Christian, Jan Langbein, Marjorie Coulon, Vivian Gabor, Susann Oesterwind, Judith Benz-Schwarzburg, and Eberhard von Borell. 2019. "Farm animal cognition—linking behavior, welfare and ethics." *Frontiers in Veterinary Science* 6 (2019):24.
- Perry, Susan. 2011. "Social traditions and social learning in capuchin monkeys (Cebus)". *Philosophical Transactions of the Royal Society B* 366 (1567):988–96.
- Purves, Duncan, and Nicolas Delon. 2018. "Meaning in the lives of humans and other animals." *Philosophical Studies* 175 (2):317–38.
- Richerson, Peter, and Robert Boyd. 2005. *Not by genes alone: How culture transformed human evolution*. Chicago: University of Chicago Press.
- Russon, Anne, and Birute Galdikas. 1993. "Imitation in free-ranging rehabilitant orangutans." *Journal of Comparative Psychology* 107 (2):147–61.
- Sapolsky, Robert, and Lisa Share. 2004. "A pacific culture among wild baboons: its emergence and transmission." *PLoS biology* 2 (4):E106.
- Savage-Rumbaugh, Sue, Kanzi Wamba, Panbanisha Wamba, and Nyota Wamba. 2007. "Welfare of apes in captive environments: Comments on, and by, a specific group of apes." *Journal of Applied Animal Welfare Science* 10 (1):7–19.
- Schuppli, Caroline, and Carel van Schaik. 2019. "Animal cultures: how we've only seen the tip of the iceberg." *Evolutionary Human Sciences* 1 (2019):e2.
- Valsecchi, Paola, and Bennett Galef Jr. 1989. "Social influences on the food preferences of house mice (*Mus musculus*)." *International Journal of Comparative Psychology* 2 (4):245–56.
- van Leeuwen, Edwin, Katherine Cronin, and Daniel Haun. 2014. "A group-specific arbitrary tradition in chimpanzees (*Pan troglodytes*)." *Animal Cognition* 17 (6):1421–25.
- van Leeuwen, Edwin. 2021. "Temporal stability of chimpanzee social culture." *Biology Letters* 17 (5):20210031.
- van Leeuwen, Edwin, Sarah De Troy, Stephan Kaufhold, Clara Dubois, Sebastian Schütte, Josep Call, and Daniel Haun. 2021. "Chimpanzees behave prosocially in a group-specific manner." *Science Advances* 7 (9):eabc7982.
- Whitehead, Hal, and Luke Rendell. 2015. *The Cultural Lives of Whales and Dolphins*. Chicago: University of Chicago Press.
- Whitehead, Hal. 2021. "Animal culture, conservation, and welfare." *Cultural Evolution Society Online Learning Series*. [https://learn.culturalevolutionsociety.org/animal\\_cultures\\_module/113\\_conservation](https://learn.culturalevolutionsociety.org/animal_cultures_module/113_conservation).
- Whiten, Andrew. 2021. "The psychological reach of culture in animals' lives." *Current Directions in Psychological Science* 30 (3):211–17.