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The role of great ape behavioral ecology in One Health: Implications for captive welfare and re-habilitation success

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Abstract

Behavior is the interface through which animals interact with their environments, and therefore has potentially cascading impacts on the health of individuals, populations, their habitats, and the humans that share them. Evolution has shaped the interaction between species and their environments. Thus, alterations to the species-typical “wild-type” behavioral repertoire (and the ability of the individual to adapt flexibly which elements of the repertoire it employs) may disrupt the relationship between the organism and its environment, creating cascading One Health effects. A good example is rehabilitant orangutans where, for example, seemingly minor differences from wild conspecifics in the time spent traveling on the ground rather than in the forest canopy can affect an individual's musculoskeletal and nutritional health, as well as social integration. It can also increase two-way transmission of infectious diseases and/or pathogens with local human populations, or potentially with neighboring wild populations if there are no geographical barriers and rehabilitants travel far enough to leave their release area. Primates are well known ecosystem engineers, reshaping plant communities and maintaining biodiversity through seed dispersal, consuming plants, and creating canopy gaps and trails. From the habitat perspective, a rehabilitant orangutan which does not behave like a wild orangutan is unlikely to fulfill these same ecosystem services. Despite the importance of the diversity of an ape's behavioral repertoire, how it compares to that of wild conspecifics and how it alters in response to habitat variation, behavior is an often under-appreciated aspect of One Health. In this review, focusing on orangutans as an example of the kinds of problems faced by all captive great apes, we examine the ways in which understanding and facilitating the expression of wild-type behavior can improve their health, their ability to thrive, and the robustness of local One Health systems.

KEYWORDS

behavior, captivity, great ape, One Health, orangutan, re-habilitation

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1 | INTRODUCTION

All organisms are deeply interconnected with the environments in which they live; in which their bodies, brains, behavioral ecology, and life histories have evolved and within which they must obtain all the resources they need to thrive. Great apes (hereafter: apes) are no exception to this rule: all of their systems are finely tuned to the constraints and opportunities provided by the natural environment (through processes of evolution, development, physiology, and learning), from the composition of their microbiome (Clayton et al., 2016), through their anatomy (Crompton, 2016), to their ability to plan for foraging opportunities (Ban et al., 2016; Janmaat et al., 2013, 2014), to the lengths of their inter-birth intervals (Charnov & Berrigan, 1993; van Noordwijk et al., 2018; Wich et al., 2004). In turn, this interconnection with the natural environment determines the ecosystem services (i.e., the benefits provided to humans by the natural environment) to which the apes contribute, through seed dispersal, seed, leaf and bark predation, and shaping biodiversity by consuming plants and creating canopy gaps and trails (Tarszisz et al., 2018). Finally, the quantity, quality, and interconnectedness of the natural environments available to apes, and their degree of habituation to humans influences the degree of contact between them and local human populations (Narat et al., 2017; Woodford et al., 2002). These have implications for the transmission of infectious diseases and/or pathogens in both directions, and therefore has direct implications for both human and ape health. Recognizing and addressing the negative consequences of this overlap of human, non-human animal and environmental domains is at the core of One Health, defined as “the collaborative efforts of multiple disciplines, working locally, nationally, and globally, to attain optimal health for people, animals, and our environment.” (One Health Initiative Task Force, 2008, p. 9).

Behavior is the interface through which great apes interact with the environment. Nevertheless, to date its importance has often been under-appreciated in One Health considerations. In this review, we focus on the ways in which the behavior of captive or re-introduced apes can influence their own health and in turn, that of the ecosystems in which they live and the human populations which share them. These apes pose unique challenges to One Health (compared to wild populations and deliberately habituated wild populations: Woodford et al., 2002) because they have typically been habituated to humans after their original illegal removal from their natural habitat as infants or young juveniles, and during care that follows confiscation from these situations (Russon, 2009). These two very different experiences of human contact may elicit mixed responses towards humans in these apes. Moreover, as a consequence of their capture, they have often missed out on infancy and early juvenility with their mothers and/or natural groups and have thus lost a key window of opportunity for learning the natural behavioral profiles of their species (Schuppli, Forss et al., 2016; van Noordwijk & van Schaik, 2005) or sex (Ehmann et al., 2021).

While all species of great apes face similar challenges, we focus on the example of orangutans (*Pongo abelii*, *Pongo pygmaeus*, and

Pongo tapanuliensis) since they experience a variety of captive care settings, and because they are currently the only great ape taxon for which there are active and systematic programs of re-introduction into natural habitat which follows IUCN best practice guidelines (Beck et al., 2007). Thus, in the next section, we discuss in detail the ways in which the behavior of wild orangutans contributes to their ability to find food, rest, balance risk and opportunity, interact with conspecifics and reproduce successfully, and how these behaviors are constrained by captive environments. We then consider how natural behavioral profiles can be encouraged in rescued orangutans, describing some of our recent work with the Enclosure Design Tool (EDT) (Thorpe et al., 2021) to illustrate our ideas. Finally, we discuss the possible One Health benefits of this approach. We include captive settings in which lifelong care is provided from intake until the end of an animal's life, as well as rehabilitation/re-introduction care in which apes are rehabilitated and prepared for eventual release into natural habitats or managed/protected environments in which they will live independently of human care.

1.1 | How does the behavior of wild and captive orangutans differ?

To understand how captivity impacts on the complex interactions between the behavior of orangutans, their environment, and their health, we need to understand the range of behaviors that they use in the wild to survive and thrive, and how these are shaped by the particulars of their immediate environment. Here “environment” includes their physical environment, heterospecific organisms (predators, prey, inter-specific competitors), as well as their social and cultural environment.

1.2 | Finding food

The Asian tropical forests inhabited by primarily frugivorous orangutans are difficult environments in which to find food. Many trees in their native forests fruit unpredictably, irregularly, and asynchronously, and individual trees may have ripe fruit for short periods of time, creating intraspecific competition for food (van Schaik & Pfannes, 2005). Natural variation in periods of food availability may exacerbate the challenge of finding food. For example, in Southeast Asian Dipterocarp forests, irregular “masting” events are common in which periods of high abundance of fruit are interspersed with long, sometimes multi-year, periods in which fruit availability is very low (Knott, 1998, 1999, 2005). Southeast Asian peat swamp forests are non-masting, but between peat swamp forests where orangutans are studied, there is substantial variation in the timing and frequency of flowering and fruiting events between sites, even where climatic conditions are very similar (Harrison et al., 2016). This means that orangutans need to store fat when food availability is high and/or be equipped to resort to “fallback foods” (i.e., the resources used by a species when preferred foods are scarce: Marshall &

Wrangham, 2007, p. 1220) when preferred food availability is reduced (Conklin-Brittain et al., 2001; Harrison et al., 2010). Wild orangutans therefore often live under high nutritional stress: they regularly experience a negative energy balance whereby they must metabolize their own fat reserves (Knott et al., 2009; Knott, 1998) to produce energy to compensate for limited food availability. Despite these strategies, a recent study has shown that the estimated lean body mass of wild Bornean orangutans of all age-sex classes is significantly lower in low fruit availability versus high fruit availability periods (O'Connell et al., 2021).

The result of living in such environments is that orangutans often need to travel substantial distances each day to find food, monitoring fruiting cycles of trees, and adapting their behavior to capitalize on fruit availability (Morrogh-Bernard et al., 2009). Traveling and navigating as efficiently as possible to find high-quality foods is critical in balancing energy expenditure and intake (Vogel et al., 2017). There are at least three important elements of efficient travel while foraging. First, orangutans need to use locomotor behaviors that minimize energy expended moving between and within feeding patches. Second, they need to plan their routes between resources efficiently, considering their current energy needs and availability of different foods. Finally, they need to know how to process and consume food safely and efficiently.

1.3 | Efficient travel and navigation

Orangutans are, by preference, ripe fruit eaters, but ripe fruits tend to be situated at the periphery of tree crowns, where the branches available to support their weight are dispersed, discontinuous, and extremely flexible. For orangutans, this favors traveling through the forest canopy because the energetic cost of crossing forest canopy gaps by descending to the ground, crossing terrestrially, and climbing back up into the forest canopy can be up to 23 times more expensive energetically than crossing arboreally (Thorpe et al., 2007). As a consequence, orangutans have one of the broadest repertoires of positional behavior of all the primates, allowing unique, physically and cognitively advanced locomotor strategies to control branch flexibility and cross gaps in the canopy (Thorpe & Crompton, 2006; Thorpe et al., 2009).

Moving and resting safely in such dynamic and complex environments also requires individuals to learn which supports will safely bear their weight, which can be bent or swayed to allow them to cross gaps in the canopy and which postures and locomotor modes should be used to minimize the chance of falls from different kinds of support. This relationship will change as the individual grows and increases in body size and strength (Chappell et al., 2015), and as dynamic processes of forest growth, decay and decomposition change the strength of supports, including known or previously used ones (Thorpe & Crompton, 2006). Thus, apes need to adapt their choice of supports frequently, and viable travel routes will consequently change. Nevertheless, there is evidence that at least flanged male Sumatran orangutans plan their travel routes: they have been

shown to communicate their direction of travel in advance, orienting the direction of their long calls in their main travel direction despite frequent pauses and detours (van Schaik et al., 2013). Furthermore, Bekko (2018), studying one community of East Bornean orangutans, found that they established and used habitual routes that accessed significantly greater numbers of feeding and nesting resource trees and large trees than comparable control locations. This suggests that orangutans' habitual routes are shaped by key resources, but also constrained by canopy connectivity which is provided by large trees.

In contrast, orangutans in captive settings are provisioned with food either fully or partially (e.g., in large prerelease islands where natural foraging is often supplemented by human-provided food). Thus, finding food in captivity rarely requires orangutans to move much, and captive enclosures (even large forested outdoor enclosures) severely limit orangutans' opportunities for arboreal travel compared to their wild counterparts. This is particularly the case for the more challenging forms of locomotion which they would usually employ while foraging in the peripheral branches of tree crowns (Thorpe & Crompton, 2005). This lack of travel between feeding patches has an impact on captive orangutans' energy balance, and musculoskeletal system (Thorpe et al., 2021). Sarmiento (1985) found significant morphological differences between the musculoskeletal systems of captive and wild orangutans, suggesting that these were a consequence of differences in locomotor behaviors. For example, in captive orangutans he found reduced attachment areas for carpal-metacarpal ligaments (related to a reduction in forelimb suspensory behavior), and higher femoral torsion, reflecting increased frequency of terrestrial quadrupedal locomotion and decreased frequency of vertical climbing (Sarmiento, 1985). It also means that their spatial abilities and episodic memories are less exercised or developed by the challenge of keeping track of the food availability within their range and planning routes (van Schaik et al., 2013). Furthermore, food is often provided at regular and predictable times of day and distributed on the ground of enclosures, so orangutans lack the ability to control when they forage or feed and are encouraged to forage on the ground. Both factors compromise the energetic demands of feeding and create competition with others for access to food.

1.4 | Processing foods effectively

Orangutans consume an enormous variety of foods, including both preferred foods and fallback foods, many of which need to be identified as edible, accessed at the right stage of the plant's development, and processed to access edible parts or remove inedible/toxic parts. There is large variation between sites, but at 14 of the 15 sites surveyed, orangutans consumed on average more than one vegetation item from each species, so they need to recognize the species as edible (Russon, 2002) and understand how to process each part of the species appropriately. For example, at Ketambe, a mean of 1.35 vegetation items per species were consumed from 379 plant species, while at Tanjung Putting 1.38 vegetation items per species were consumed from 203 plant species (Russon et al., 2009). Accessing a

large proportion of their typical food items (30%–50%) relies on complex processing skills such as extractive foraging of embedded foods (those requiring extraction from an inedible matrix, such as insects embedded in wood: Schuppli, Forss et al., 2016). Processing may also involve performing different manipulations in different situations. For example, one fruit might have edible pulp which must be scraped from the skin (with the skin and seeds discarded), whereas another has inedible pulp, but edible seeds (Schuppli, Forss et al., 2016). Orangutans must be able to find, access and process fallback foods when they are hungry and low on energy (Harrison & Marshall, 2011), despite many of these fallback foods having physical or chemical defenses against predation (Coley & Barone, 1996; Marshall & Wrangham, 2007; Russon, 2002). For each of the techniques described above, orangutans need to somehow acquire the requisite information and skills, most likely from the mother and peers (Schuppli, Forss et al., 2016), and also through individual exploration and trial and error learning (see, e.g., Russon, 2006).

In contrast, food provided in captivity is usually simple to consume, requiring minimal processing compared to wild foods, as constraints on budget and food availability mean that orangutans are provided with foods normally intended for and sold in human markets. This reduces the amount of time that orangutans spend occupied with food processing and reduces the cognitive challenges presented (Russon, 2002). These same constraints also reduce the diversity of foods available compared to the number of food types consumed by wild orangutans. Russon (2002) found that rehabilitant orangutans re-introduced to the forest initially showed a reduced dietary breadth compared to wild orangutans and ignored several permanently available fallback foods that are important to wild orangutans, but which they had not encountered in captivity. Orangutans gradually increased their dietary breadth, added more fallback foods to their diet, and improved their processing techniques, but this change occurred over several years post-release. Similarly, Basalamah et al. (2018) found that re-introduced orangutans in Kehje Sewen spent more time foraging on fruit and less time on flowers and invertebrates than wild orangutans, which they suggested might reflect the greater processing expertise required for these items, and also spent more time feeding on terrestrial herbaceous vegetation than wild orangutans. It is also possible that these orangutans did not recognize many of the flowers and invertebrates found there as food as they would not have encountered them during their rehabilitation or pre-capture lives.

Human crops (particularly fruits) also typically contain a much higher sugar content compared to wild foods, and a lower fiber content (Cabana et al., 2018; Plowman, 2013; Schwitzer et al., 2009). This can have broad implications for captive orangutan health, since aspects of orangutan morphology and physiology (such as the enamel thickness of orangutan molars: Vogel et al., 2008) suggests that they have evolved to consume physically tough foods which tend to be high in fiber and low in sugars (Yamagiwa, 2004). Excess sugar in the diet can increase levels of obesity (which is linked to cardiac disease), since reduced activity levels in captivity mean that energy intake may exceed expenditure (Cabana et al., 2018), and compromise dental

health (Plowman, 2013). Increased sugar content in captive diets also seems to increase the occurrence of aggression and regurgitation and re-ingestion. Several studies have shown that reducing sugar intake, by decreasing the proportion of ripe fruit in the diet, decreases aggression (see, e.g., Britt et al., 2015) and regurgitation and reingestion in captive primates, including orangutans (Cabana et al., 2018). Furthermore, there is evidence from two species of folivorous non-human primates that captive diets result in a shift away from their natural gut microbiota towards a microbial community which is characteristic of humans with a typical Western diet (Clayton et al., 2016), possibly because of a lack of natural dietary fiber in the diet (O'Keefe et al., 2015; Sonnenburg et al., 2016). This has currently unknown consequences for the health of captive primates, but the gut microbiome has a critical role in primate nutrition, metabolic and immune system health (Clayton, Al-Ghalith, et al., 2018). Research on the orangutan microbiome is at an early stage (S. Unwin, personal communication), but the implication is that formerly captive orangutans may have difficulty digesting and extracting nutrients from naturally occurring foods that their wild counterparts routinely consume.

1.5 | Rest and safety

1.5.1 | Balancing risk and opportunity

Orangutans face a variety of dangers from their physical environment and the other organisms within it, and must therefore be cautious, ignoring novel items at most life stages (Forss et al., 2015). However, there is an important balance to be struck: if individuals never approach unfamiliar objects, their behavior will be constrained, and they will miss out on opportunities which might be important for their survival (Hills et al., 2015). Orangutans in the wild explore and learn what is safe to approach through social learning as infants, “peering” closely when their mother is engaged in activities like feeding or nest building (Schuppli, Meulman et al., 2016; van Schaik et al., 2016).

Whatever mechanisms orangutans use to acquire information about what is safe and what should be avoided, the information is important in several contexts. Orangutans need to avoid predators such as large felids (e.g., clouded leopards *Neofelis diardi*), or other dangerous animals such as venomous snakes. In most cases, young orangutans probably learn this information by observing fear or avoidance reactions shown by their mother. Individuals also need to learn how to respond appropriately to such threats, such as whether to attack or avoid the predator. Humans are also an important category of threat for orangutans (indeed, for all wild ape species), with serious One Health implications for both humans and orangutans. Humans frequently persecute orangutans, for example, killing or capturing them for the illegal bushmeat or pet trades, or injuring them in human-wildlife conflict incidents on agricultural land or illegal logging sites. In addition to the direct risk of death or injury to the orangutan in such encounters, these human interactions also increase the probability of bidirectional pathogen or disease transfer between

orangutans and humans through consumption of bushmeat or through the fecal-oral route (Narat et al., 2017).

Overall, the evidence suggests that captivity is likely to increase captive orangutans' familiarity with humans, their crops and their artefacts, and therefore decrease the levels of caution with which orangutans approach humans. It may also decrease their caution towards natural hazards. The low diversity and safe nature of food and other objects encountered in captivity, and the provision of safe, stable, and highly predictable supports mean that captive orangutans (particularly those entering captivity at a young age) have little exposure to natural dangers. IUCN best practice guidelines recommend "protected exposure to some predators" during the rehabilitation process (Beck et al., 2007 p. 12), but in practice this can be difficult to achieve. Captive orangutans which have access to natural forest areas (either through outdoor enclosures, forest schools, or pre-release islands) do have the potential to experience a variety of natural supports including compliant supports. However, if natural forest enclosures are not large enough for the number of orangutans they house, the trees and other vegetation will not be able to recover from damage and will degrade in quality, providing fewer useful learning experiences. This can perhaps be avoided in well-designed and managed forest schools by caregivers rotating the areas used to allow time for recovery.

A lack of caution is of no great consequence for individuals which will be cared for and protected in sanctuaries for their whole lives but has major implications for the health of those that will be re-introduced to the wild, where an inappropriate lack of caution and neophobia might result in injury or death. For example, a re-introduced female orangutan in Bukit Tiga Puluh died after being bitten by a snake while in a nest (Y. Jaya, personal communication). Orangutans being rehabilitated for re-introduction also need to distinguish between familiar humans who provide care for them, and unfamiliar humans who may cause them harm. Even if they make this distinction, dependence on humans causes more general problems for the adaptation of orangutans post-release: for example, rehabilitant orangutans that are more strongly human bonded have been shown to spend more time on the ground and use less effective foraging strategies post-release than those that avoided human contact (Riedler et al., 2010).

1.6 | Resting safely

Orangutans, like all apes, usually make a fresh nest each night in which to sleep (Prasetyo et al., 2009; van Casteren et al., 2012), as well as "day nests" in which to rest during the day. Unlike some other ape species, orangutans' nests are almost always constructed arboreally (Prasetyo et al., 2009; van Casteren et al., 2012). There is still considerable debate about whether apes' arboreal nests primarily function as antipredator measures, for thermoregulation, to avoid vectors of disease like malarial mosquitos (Koops et al., 2012), or to facilitate high-quality sleep (which can also be achieved by nests on the ground: Samson & Shumaker, 2015). These explanations are not

mutually exclusive and may differ between ape species and between sites within species. Whatever the functional explanation, nest-building is undoubtedly a highly complex skill to learn. Orangutans need to know which tree to select (Carvalho et al., 2014; Hernandez-Aguilar et al., 2013; Samson & Hunt, 2014; van Casteren et al., 2012), and how to choose, bend and weave branches. Greenstick fractures (whereby one side of each branch is broken but the other remains intact to keep the nest attached to the tree), are critical in building a safe and structurally sound nest which will both support the weight of the animal and withstand wind-induced tree movements (van Casteren et al., 2012).

In contrast, captive environments often lack appropriate nest-building opportunities. In some cases, there are no suitable base structures on which apes can make nests as they would in the wild. Solid arboreal platforms or metal "baskets" may be provided, but platforms may be sufficiently comfortable for the apes to use as they are, and baskets may be too deep or lack the firm support apes prefer (Anderson et al., 2019). In addition, practical constraints in centers make it difficult to provide sufficient material of a suitable type from which to construct a nest with a sturdy rim and softer center (van Casteren et al., 2012). Where captive apes have access to naturally forested outdoor enclosures, it is possible for them to build natural nests, though if the density of individuals in the enclosure is too great, trees will not have sufficient time to recover from the damage induced by the nest-building activity. Simpler forms of nest building are possible by weaving together detached vegetation and/or piling up material on a solid horizontal surface (Anderson et al., 2019). Cut browse can serve this purpose, but if it is not provided in sufficient quantity, apes will often consume the leaves and stems instead of using them to build nests. Combined, this lack of opportunity tends to mean that most captive apes never acquire the skills needed make sufficiently complex, comfortable nests, or they make them at ground level rather than arboreally. Sleeping at ground level (rather than arboreally at a height above 10 m; Carvalho et al., 2014) may expose individuals to disease vectors such as malarial mosquitoes (Koops et al., 2012), predators, or pathogen contaminated feces, which can cause upper respiratory tract infections (Markham, 1990; Zimmermann et al., 2011). Samson and Shumaker (2013) showed that captive orangutans which made and slept in more complex beds experienced better sleep quality. Thus complex, arboreal nests are important in a One Health context to prevent disease, predation and to facilitate proper rest.

1.7 | Living together and reproducing

Relationships with conspecific individuals are critically important for all ape species, even for orangutans which live in dispersed societies, unlike chimpanzees, bonobos, and gorillas (Malone et al., 2012). Social behavior has several important purposes, for example, enabling orangutans to manage intraspecific competition for resources, disperse and establish a home range, find a mate, reproduce, and rear young successfully, and to transmit the information and skills necessary for survival to their offspring.

1.8 | Social interactions and reproductive behavior

Wild orangutans have dispersed societies (Malone et al., 2012), in which individuals mostly range alone or in mother-offspring groups, temporary peer friend groups, or temporary male-female consortships, but need to interact with neighboring and transitory individuals that are attracted to preferred feeding patches and mating opportunities (Singleton et al., 2009; Spillmann et al., 2017). However, the demands of social interactions differ between the sexes and between flanged and unflanged males and between kin and non-kin females. Adult females tend to be philopatric (Arora et al., 2012; van Noordwijk et al., 2012). They associate with maternal female relatives, and will allow their offspring to play together, while usually avoiding unrelated or unfamiliar females and actively preventing their offspring from engaging in social play (van Noordwijk et al., 2012). Adult males and females may form temporary consortships in which they range and feed together for a period of time, but flanged males never affiliate with each other and, particularly in Sumatra, are intolerant of unflanged males (Utami Atmoko et al., 2009). Adult males disperse away from their natal area and have home ranges that are much larger than those of females (Arora et al., 2012). Flanged males use “long calls” to communicate their presence to females and deter lower-ranking rival males while attracting higher-ranking males (Spillmann et al., 2017). Sumatran orangutan females with dependent offspring use these calls to remain within “earshot” of a flanged male, possibly to gain protection from harassment and possible danger to her offspring by other males (Mitra Setia & Van Schaik, 2007; van Schaik et al., 2013), since unflanged males may try to obtain a mating by force (Utami Atmoko et al., 2009). In contrast (as discussed above), receptive females will use flanged male's calls to approach dominant flanged males. Thus, keeping track of multiple third-party relationships and monitoring the location and status of other individuals is likely to be a cognitively demanding task for both sexes (Byrne & Bates, 2010). Furthermore, orangutans of either sex may learn about appropriate social and sexual behavior towards others through observing their mother's interactions (Utami Atmoko et al., 2009), thereby reducing the risk of injury in social encounters.

For captive orangutans, the physical constraints of enclosure size and the inability of individuals to choose who to associate with have important impacts on their behavior and health. Fission–fusion is impossible in many captive settings: individuals are unable to separate from others so that they are inaccessible or even just out of sight. Group size in zoo-housed orangutans has been shown to be associated with higher endocrine and behavioral markers of stress in permanent groups, but not when individuals had some freedom to choose their associations (Amrein et al., 2014). This effect of group size on social stress was stronger for Bornean orangutans (which lead more solitary lives in the wild) than for Sumatran orangutans (Weingrill et al., 2011). Captive environments with very large, naturally vegetated enclosures or islands may provide enough space and visual cover to enable a degree of fission–fusion. However, avoiding the associated problems is generally difficult for rescue and

rehabilitation centers. Staff have little or no control over the number or demographic composition of individuals entering their care because they have an obligation to take in any individual in need. Males growing into adulthood will need a substantially larger space than females, so fewer males than females can be accommodated in a single enclosure (e.g., cage, small forested island) at any one time. As a consequence, males towards the end of adolescence that are no longer suitable for forest school settings often have to be moved to cages until a place becomes available for them on a prerelease island, on which the final rehabilitation processes and assessments are made before release (F. Sulisty, pers. comm.). This, therefore, slows their progress towards re-introduction relative to females and contributes to centers having a “surplus male” problem, even though the sex ratio at intake is close to 1:1 (F. Sulisty, personal communication). Housing multiple adult males is a problem commonly faced by rescue and rehabilitation centers. Even where they are housed in single-occupancy cages, they can routinely hear, see or even touch each other through the bars, which contrasts strongly with the wild-type behavioral profile of limiting aggression by avoidance. This makes it more difficult to house individuals of either sex without causing social stress or excessive aggression, and exacerbates problems caused by unbalanced sex ratios and/or age profiles.

Since IUCN best practice guidelines (Beck et al., 2007) state that potential sites for re-introduction should not contain an existing wild population, female orangutans in rescue or rehabilitation centers or re-introduced to the wild will lack maternal kin networks. As far as we know there is currently no evidence about whether social bonds between non-kin females that develop during the rehabilitation process can replace the benefits provided by maternal kin networks. Re-introduced orangutans of both sexes must also familiarize themselves with the unfamiliar forest site when released. This puts females at a greater disadvantage than males compared to their wild counterparts because females are usually philopatric, that is, establish home ranges adjacent to their mothers, so they would already have some familiarity with the area and its residents when they assume independence (Ashbury et al., 2020). However, independent males have few or no opportunities to roam large distances in rescue or rehabilitation centers as adult males would in the wild, and so would have limited experience of how to navigate an area calling or searching for females and managing aggression with other males. In summary, captive orangutans will acquire limited and distorted social knowledge during development which may impair their ability to employ species-typical social behaviors or make the correct decisions to manage aggression. While release sites are now carefully chosen to minimize the possibility of contact between wild and re-introduced orangutans (Beck et al., 2007), males can travel long distances, so a lack of species-typical social behaviors will cause problems if geographical factors enable their leaving the release area and contacting wild populations. These problems are exacerbated if individuals have been removed from their mothers very early and/or kept illegally by humans as pets for a long period before being taken into a center.

1.9 | Social learning and enculturation

Social learning plays a very important role in the way that apes interact with their environments. Orangutans have relatively long inter-birth intervals in the wild (mean of 7.5–8.5 years where the previous infant was alive and there was no evidence of miscarriage: van Noordwijk et al., 2018), during which infant and juvenile offspring remain closely associated with their mother. While young orangutans may get some opportunities to learn from other adults when their mothers encounter them (e.g., while foraging or consorting with a male), the majority of what a young orangutan learns is acquired through his or her mother.

In captive environments, orangutans very likely lack the appropriate role models (i.e., knowledgeable individuals of the appropriate age and/or sex) from which to learn. Moreover, if all individuals in the group have been raised in a captive environment, the developmental and cultural processes that enable orangutans to adapt to their local habitat will not be available (Krützen et al., 2011), and social learning could generate maladaptive behavior (Franz & Matthews, 2010). These issues have implications for how well re-introduced orangutans survive and interact with each other in their release area. More generally, close association between humans and all non-human apes in captivity risks fundamentally changing apes' behavior through processes of enculturation or "self-domestication" (a suite of changes to traits hypothesized to be caused by selection against aggression: see Damerius, Graber, et al., 2017; Hare et al., 2012).

1.10 | Small changes can lead to cascading failures

In the previous sections, we have shown how the individual components of wild orangutan behavior contribute to their own health, that of the ecosystem in which they live and the human populations sharing their ecosystem. There is a strong network of interactions between these different components, so that small alterations in the orangutan's behavior, its environment or in the behavior of local people may lead to cascading changes throughout the system which impact different elements of One Health. Figure 1 (see Supporting Information for a description of the logic underpinning the figure) shows a conceptual sketch of the cascading changes which might result from a re-introduced female Sumatran orangutan spending less time arboreally than her wild counterparts. Studies on both wild and re-introduced apes understandably tend to focus on specific aspects of behavioral ecology and their implications at a population level (with some laudable exceptions, e.g., Wich et al., 2009), making it difficult to trace the full implications for One Health. The situation depicted in Figure 1 is therefore necessarily hypothetical, though grounded in the concrete, evidence-based problems identified in previous sections, as well as issues communicated to us by rehabilitation practitioners.

Furthermore, many aspects of poor behavioral adaptation and the cascading effects on One Health that we have outlined above for orangutans also apply to other species of great ape that differ in their

social organization. We touch on possible solutions to these problems in the following section, in addition to the problems faced by orangutans.

1.11 | How can we counter negative consequences of ape rehabilitation and re-introduction for One Health?

Forest schools make important contributions towards the rehabilitation of ex-captive orangutans for reintroduction. However practical issues (availability of sufficient staff, security of the forest school area, etc.) mean that orangutans rarely spend 24 h a day in forest environments. The remainder of their time is spent in human-constructed environments like nurseries, baby houses, and cages. Given the constraints of these captive environments, how can we modify how we house, care for, and rehabilitate captive apes to encourage wild-type behaviors and break the cycle of poor fit of behavior to environment, which results in negative consequences for One Health (see Figure 1)? Encouraging wild-type behaviors alters the behavioral profiles of captive apes to resemble more closely those of wild apes; where such changes can impact their welfare state and/or release success positively, they contribute to improving apes' ability to solve the physical and cognitive problems that are intrinsic to natural environments. Over the last 5 years, we have worked with the great ape rescue and rehabilitation community (via the Orangutan Veterinary Advisory Group and Pan African Sanctuary Alliance) to modify enclosures to encourage expression of wild-type behavioral profiles by implementing measures to overcome the captive constraints on their acquisition and expression. We have called this the EDT (Thorpe et al., 2021). The EDT consists of a framework of data collection protocols which staff at centers can use to collect data on core aspects of the current behavioral ecology of their apes, and a linked web application. Once the data has been collected, users upload their data to the web application, which automatically analyses it and compares the behavior of the captive apes to their wild counterparts, presenting the results in an accessible format to users. It then presents tailored suggestions about how centers can modify their enclosures or management practices to encourage the apes to show currently absent or underrepresented behaviors which are particularly important in the wild and/or central to improving captive ape welfare. Once users have made these enclosure modifications, they can use the same protocol to collect a post-modification data set and use the web application to determine whether the modifications have increased activity levels and the expression of wild-type behaviors in their apes.

A key concept underpinning the EDT process is that the modifications emulate the mechanics and affordances of natural habitats, to create enclosures that behave like (rather than look like) the natural habitat (Pruetz & McGrew, 2001). Thus, they present the apes with the kinds of mental and physical challenges that their wild conspecifics experience on a daily basis (Russon, 2002; Thorpe et al., 2021). This is particularly important for apes in rehabilitation centers because

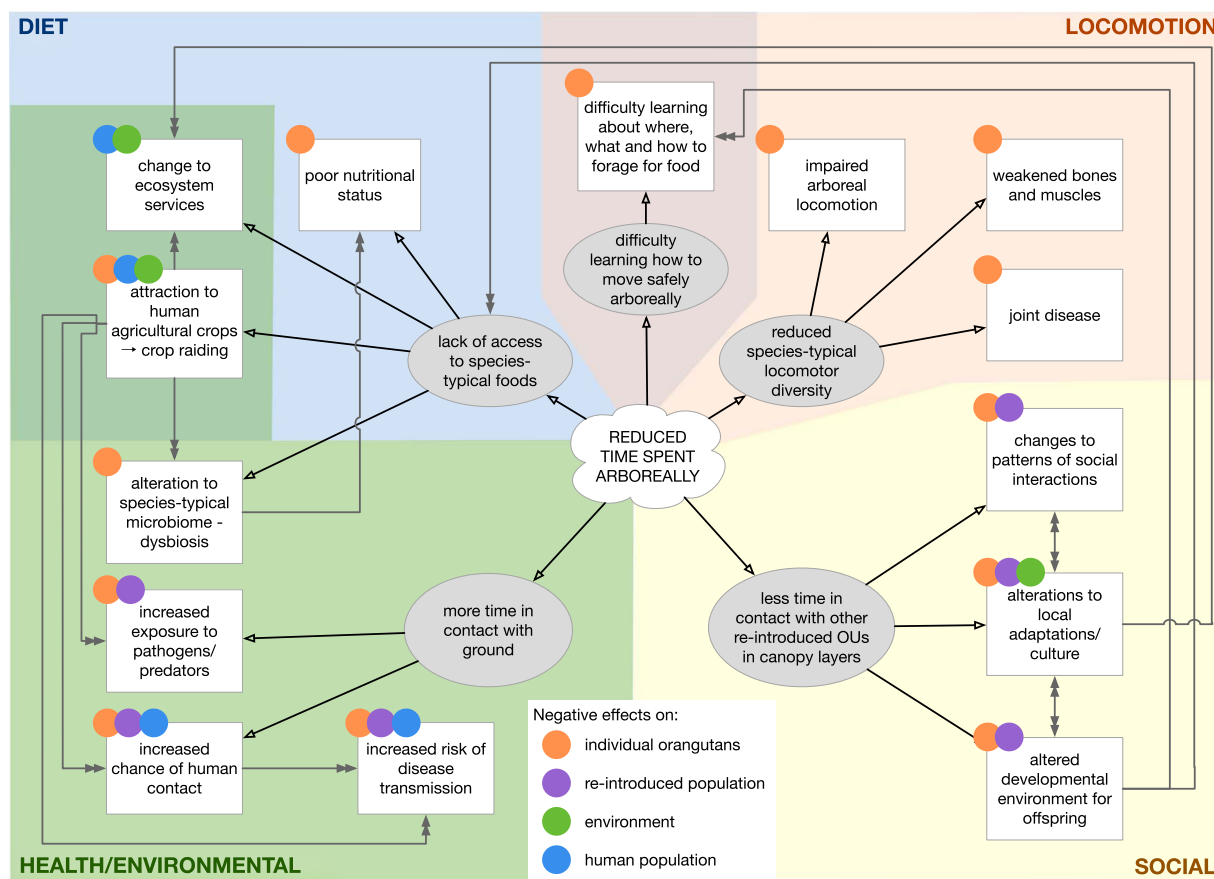


FIGURE 1 An illustration of some of the cascading One Health effects of a single behavioral difference: an adult female Sumatran orangutan (*Pongo abelii*) who spends a greater percentage of her time on the ground than her wild counterparts. The colored backgrounds represent the main domain (sphere of influence) of the effects, though cognition (not shown) influences all the domains. Gray ellipses represent behavioral consequences of reduced time spent arboreally, and white rectangles indicate One Health consequences. Open arrows indicate direct effects of behavioral changes, double-headed arrows show secondary interactions among health consequences and feedback effects on behavioral changes. Filled colored circles attached to One Health consequences indicate the target(s) of the negative effects: individual orangutans (orange); the re-introduced orangutan population (purple); the forest environment (green); or the human population (blue). S1 provides a narrative description of these effects

humans cannot adequately model many of the required behaviors (like arboreal locomotion or foraging), and they usually lack skilled conspecifics from whom to learn and/or the physical facilities to learn via their own experience. Challenging rehabilitant apes so that they use their cognitive abilities to learn general principles that they can apply to solve the range of problems they will face in the wild is a potentially powerful technique (Russon, 2002).

In the sections below, we describe how the key challenges in both lifelong care and re-habilitation/re-introduction settings for orangutans and chimpanzees can be addressed by such modifications, and the One Health benefits this can bring.

1.12 | Increasing physical and cognitive challenge in daily activities

One of the major problems is how to overcome the physical constraints on space, monotony, and predictability which limit the

physical and cognitive challenges which apes encounter in captivity. It is usually impractical or unaffordable to increase the size of existing enclosures, but key wild-type physical and mental challenges can be provided by utilizing all space available in a cage, and by modifying enclosure furniture and how food is presented (Pruetz & McGrew, 2001). Centers can encourage apes to use their available weight-bearing supports in energetically demanding ways to access resources that they value; this partially compensates for the fact that the enclosure does not permit long daily travel distances with shorter bouts of more intensive exercise. For example, the majority of solid supports in enclosures can be replaced with an interconnected grid of webbing straps made from extra-tough car seat belt material (or fire hose if this is available). These supports are compliant and so require the ape to dynamically adjust his or her locomotion and posture to adapt to the movement of the support under his or her body weight. The grid structure provides multiple routes by which individuals can travel between any two given points in their enclosure (see Figure 2a for an example). This maximizes

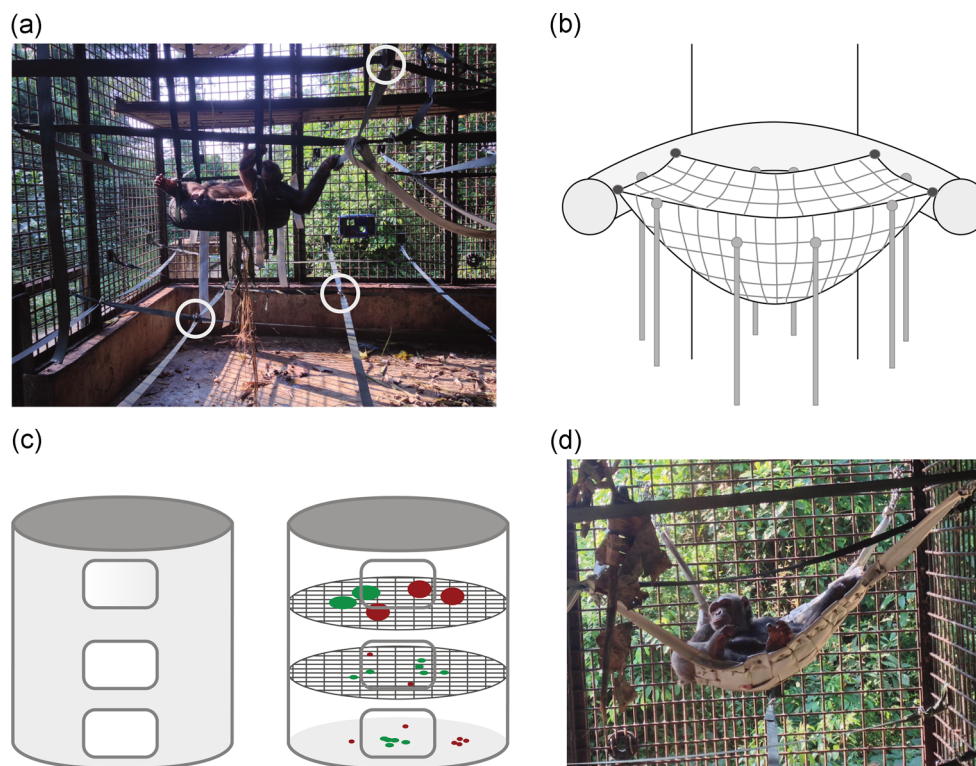


FIGURE 2 Examples of modifications to encourage wild-type behaviors in captive apes. (a) a webbing grid of supports. Circles mark crossing points where webbing straps are connected with metal D-clamps to form an inter-connected network; (b) a metal nest frame supporting a rope “nest.” Webbing straps 1 m in length are connected to the nest at one end to enable the ape to weave them into the nest structure; (c) an example of a foraging enrichment. A plastic container (such as an old water barrel) is divided internally with wire mesh “shelves” and attached to the exterior of the cage. Small corresponding apertures are cut in the barrel on the side facing the cage interior (left image), enabling the ape to reach the food placed inside (right image). Larger apertures (not shown) are made in the rear of the barrel to enable caretakers to replace food and clean the interior; (d) a hammock woven from fire hose and suspended using chains. Photos: Johanna Neufuss

space use and provides more spatial complexity, which has been shown to increase activity in zoo-housed apes (Hebert & Bard, 2000; Perkins, 1992; Pizzutto et al., 2008). It also provides an opportunity to make decisions and choices which benefit mental wellbeing (Mellor et al., 2020). In addition, the inter-connectedness of the nodes where the straps cross mimics the mechanics of the inter-connectedness of forest branches and vines and means that the compliance of the network changes constantly (and sometimes rapidly) as other individuals jump onto it or move around it (Thorpe et al., 2021). Unlike solid supports, this means that the behavior of the webbing grid changes dynamically, and individual apes need to constantly assess and adjust their postural and locomotor behavior while on it. Where apes (like adult orangutans) are typically housed individually, but in adjacent cages, the webbing grid can be extended through multiple adjacent cages to retain the unpredictability caused by the movements of other apes on the grid (Thorpe et al., 2021). The grid can be applied in any size cage and is easy to keep clean, meaning that it can be used in all enclosures from baby houses to cages. It can also provide additional supports in forest schools and prerelease islands to supplement flexible arboreal supports that have been broken or reduced in number by previous inhabitants.

There is little point in providing routes through the enclosure if the routes do not take the apes to valued resources. If enclosure modifications are to be effective, both the opportunity *and* motivation to use them need to be provided. For this reason, we consider enclosures, no matter how small, as a series of “rooms”—areas where different, preferred activities happen, and between which we can create a range of physically and cognitively challenging routes to travel from one to another (Thorpe et al., 2021). A key part of this is to combine the webbing grid with providing food on the roof of the enclosure if there is a mesh roof. This increases the time spent foraging for and processing food and makes foraging physically and mentally demanding (as it would be in the wild), as apes must both maintain their posture on dynamic, arboreal supports, and work out how to access large items of food through the mesh. For example, in the wild, orangutans use three limbs to maintain their position for more than 60% of arboreal feeding time (Cant, 1987), and also require three or more limbs to process complex food items on more than half of such bouts (Russon, 2002). Similarly, chimpanzees show anatomical specializations for torso-orthograde suspensory behaviors such as arm-hang, which are important when feeding on compliant terminal branches (Hunt, 2016). Thus, suspensory feeding provides opportunities for captive apes to develop the muscular strength and

behavioral strategies and skills needed for simultaneous postural support and food manipulation. It can also reduce direct competition over food and monopolization by dominant individuals at feeding times; smaller items of food drop through to the floor, while larger items are retained by the mesh, so individuals distribute themselves spatially, using the vertical as well as horizontal space of the enclosure (Beirise & Reinhardt, 1992; Ryan et al., 2012). This effect can be further enhanced by layering patches of wire mesh with different mesh sizes over the roof, thus selectively retaining food items on the roof in some areas while allowing it to drop through in others. If feeding from the roof is impractical or impossible, simple pulley systems outside the enclosure would allow caretakers to hoist small barrels containing food (with apertures through which the apes could reach the food) to be filled at ground level and raised level with the top of the enclosure.

Arboreal feeding can also be combined with placing some of the daily ration in various locations within large barrels attached to the outside of the enclosures. Inside each barrel, wire mesh is fixed horizontally in a series of "shelves" which can be accessed via small holes on the side of the barrel next to the enclosure, and larger holes for provisioning and cleaning on the exterior of the enclosure (see Figure 2c; Thorpe et al., 2021). Apes cannot predict at which level food items will end up (as some fall through the mesh at each level and some are retained), so must search through different holes, increasing foraging and consumption time (Rooney & Sleeman, 1998), and again providing more of a cognitive challenge.

The result of these changes is that apes spend more time in challenging postures off the ground, and more time foraging and processing food. In sanctuary chimpanzees, for example, these changes (as part of a broader suite of enclosure and husbandry modifications) increased the time the chimpanzees spent off the ground from 10% to 65% and increased the percent of time they spent foraging from 16% to 21% (Thorpe et al., 2021). In another project on rehabilitation center orangutans, the approach more than tripled the percent of time the orangutans spent in locomotion, elicited complex types of locomotion that had been absent before and increased the percentage of locomotion that consisted of key physically demanding wild-type climbing and clambering behaviors from 12% to 24% (Thorpe et al., 2021). The impact is to increase their levels of physical and cognitive activity and the proportion of their day spent actively engaged with their environment, which reduces boredom, and better prepares rehabilitants for the wild.

1.13 | Increasing dietary variety, complexity, and processing time

Overcoming the lack of variety in captive diets can be difficult, depending on the availability and cost of foods locally. Nevertheless, providing a diet which matches the dietary composition of wild conspecifics more closely will improve their overall health (Cabana et al., 2018), and potentially maintain the composition of their wild-type microbiome (Clayton, Al-Ghalith, et al., 2018), reducing their

need for veterinary intervention. In humans, evidence of the importance of the microbiome in resilience to illness or infection is steadily building (Carter et al., 2021; see Young, 2017 for a recent review), and points to similar relationships in non-human primates (Clayton, Al-Ghalith, et al., 2018). Thus, diet can play a key role in reducing the risk of zoonotic disease (and therefore transmission) between human and non-human apes.

Improvements can be made to captive ape diets by focusing more on obtaining vegetables and unripe fruits (in as great a variety as possible) and minimizing the use of ripe fruits, thus reducing sugar and increasing fiber intake (Britt et al., 2015). Providing foods whole where possible (such as on the mesh roof of the enclosure) increases the variety of parts of the food which the ape can consume and increases processing time (Bloomsmith et al., 1988). Providing more browse (cut from ape-safe plants growing locally) also increases the amount of fiber available in the diet and again increases processing time (Birke, 2002; Cassella et al., 2012). Browse has multiple potential uses, as apes may also use it to make tools (e.g., by stripping leaves to use a stem as a probe to access out-of-reach food items) or as nesting material if sufficient quantities are provided (Thorpe and Chappell, personal observation). If centers routinely cut back vegetation around the perimeter of outdoor enclosures to protect the integrity of electric fences and prevent saplings from being used as ladders for escapes, the trimmed vegetation can be given to the apes as foraging or nesting material (again, providing the plants are known to be safe).

1.14 | Increase opportunity for species-typical nesting behavior

Encouraging more natural nesting behaviors (and therefore presumably better quality of rest: Anderson et al., 2019; Pruetz & McGrew, 2001) in captive apes requires three elements: (1) provision of suitable locations to support a nest structure and material with which to construct a nest; (2) removal of at least some off-ground flat platforms to encourage apes to make more natural nests; and (3) opportunity for apes to learn (from humans or other apes) the skills needed to build nests.

If it is safe for centers to allow their apes to remain in forested outdoor enclosures at night, and there are sufficient living trees for the number of individuals in the enclosure, apes can construct arboreal nests using natural vegetation in the tree of their choice. However, if apes are housed in cages (either 24 h per day, or only during the night) to prevent escapes from outdoor enclosures, encouraging natural nest-building behavior is more difficult. Ideally, the number of solid, arboreal flat wooden platforms should be reduced, and alternative nesting places and nesting material provided. Metal 'baskets' attached to cage walls can provide a suitable nest-building base (Anderson et al., 2019) (see Figure 2b). The nest base needs to balance providing sufficiently firm structural support for a nest platform to be constructed on it by the ape (Anderson et al., 2019), while not being so comfortable that the ape will rest in it without nesting material. Natural vegetation is ideal for nesting material if it

can be provided in sufficient quantities. If this is not possible, man-made materials such as lengths of fire hose, browse or webbing straps attached permanently at one end to the basket can be used. These materials provide one layer of nesting material which the ape can arrange, enabling a smaller quantity of leafy branches and vegetation to be provided. These materials can be used by the apes to bend and weave into a comfortable and secure nest. A disadvantage of metal nest baskets is that they can take up a lot of space in small cages and reduce the opportunities for care staff to change the enclosure furniture over time to increase temporal change for the apes. In such situations it is possible to make suspended hammocks from woven fire hose or webbing (see Figure 2d), leaving straps hanging that the apes can use to weave through holes in the hammock.

While ideally all individuals should be encouraged to build natural nests, space constraints or physical limitations on individuals (because of age or injury) may limit this. Thus, a variety of nesting locations and types should be provided. If necessary, some arboreal platforms may be retained to accommodate old or less mobile individuals, or the suspended hammocks made from woven fire hose or webbing may provide a good alternative. Implementing similar foraging and nest building modifications in our orangutan rehabilitation center doubled the amount of time the orangutans spent manipulating food, nests, and other objects from 19% to 39%, and elicited complex bending and weaving behaviors needed to construct wild-type nests, that had been absent before the project (Thorpe et al., 2021). Enabling apes to sleep comfortably off the ground should provide them with similar benefits to nesting in the wild (Koops et al., 2012) as outlined above, improving their physical and mental health. In addition, nest-building itself provides focused activity for apes, engagement with their environment (Mellor et al., 2020), and a physical problem to solve. Multiple nesting spaces can also provide opportunities for friends to be together, helping build strong bonds between individuals by emulating “social” nesting opportunities in the wild (e.g., in orangutans: van Noordwijk & van Schaik, 2005).

1.15 | Improve social interactions

Since most centers have little control over the age/sex profile of the population in their care, they may ultimately need to work towards having larger, naturally forested enclosures or islands, which may enable groups a degree of freedom to fission-fuse and individuals to choose with whom they associate (Pruetz & McGrew, 2001). However, this may not be a realistic prospect in the short term, given constraints of space and funding, or where there are many adult male orangutans housed singly.

The modifications to enclosures suggested in the previous sections will have the effect of increasing activity in general and foraging time in particular, which has been shown to reduce aggressive behavior in primate species (see Honess & Marin, 2006 for a review). In addition, we have also found that the webbing grid network helps when dominant chimpanzees try to charge others: the horizontal

straps at the lowest level (see Figure 2a) slow down the dominant individual's charge, and the vertical elements allow subordinate individuals to escape to higher levels (Thorpe and Chappell, personal observation). Providing opportunities for high-ranking males to express their dominance on enclosure furniture, rather than other chimpanzees, can also mitigate social tension (Thorpe and Chappell, personal observation). For chimpanzees, for example, threading large plastic barrels onto securely attached chains enables displaying males to hit the barrel in a similar way to drumming on buttress roots in the wild (Arcadi et al., 1998). Hanging items such as tires, boomer balls, and pots for pulling, banging, and making noise provides other ways for them to express dominance and relieve tension. In relatively small cages, it may be impossible for individuals to split up into parties, but we have found that hanging “curtains” made of strips of fire hose or webbing in strategically placed spots provides areas where individuals can associate with others, or be alone, with some level of privacy. Similar measures have been shown to reduce aggression in monkeys (Honess & Marin, 2006; Reinhardt & Reinhardt, 1991). This kind of “permeable” barrier keeps them out of direct sight of others in the group, but also prevents individuals becoming pinned up against a solid barrier in the event of aggression. In orangutans, similar barriers can be woven into an area of mesh between adjoining cages so that neighboring individuals (particularly adult males housed in adjoining cages) can rest out of sight of other individuals. We have found that these measures reduced the rate of attacks (with physical contact) in a chimpanzee sanctuary group from 0.32 to 0.07 per hour of observation (60 attacks and threats combined, of which 12 were attacks before modifications; 14 attacks and threats combined, of which 3 were attacks after modifications), a more than fourfold decrease (Thorpe et al., 2021). Wrangham et al. (2006) calculated that adult male chimpanzees at Gombe attacked at a rate of 0.02 attacks per hour (2301 attacks over 100,000 h). While the rate we observed after modification cages was still slightly higher than this figure, it is much closer to the rate experienced by wild chimpanzees, reducing the risk of injury and therefore the need for veterinary intervention.

These examples show how it is possible to make significant changes to the apes' behavioral profiles and habitat challenge, choice, and complexity on relatively small budgets with readily available materials. To optimize the impact of the process centers need to apply these principles to provide complex enclosures from each ape's arrival through to its departure, enabling the physical and cognitive challenges presented to the ape to be built up gradually. In this way, we can radically improve how well-prepared rehabilitant apes are for release into natural habitat, as well as improving the quality of apes' lives in rehabilitation centers.

2 | DISCUSSION

The interventions outlined above are examples that combine to ensure that the fit between apes and their environment is as close as possible to that defined by evolution, thereby increasing the health of the individual ape, the population of re-introduced apes into which

he/she was released, the ecosystem he/she inhabits and the humans who share his/her range. While we have shown positive effects of these interventions on the behavior of captive orangutans and chimpanzees in sanctuaries and rehabilitation centers, work on evaluating whether these interventions result in positive changes to One Health is still in progress. One of our next tasks is to test the extent to which the EDT can instigate these cascading effects in post-release individuals, improve the tool further, and then extend it to other ape species, contributing to evidence-based husbandry and management decisions. There are some difficult issues that we have not yet addressed with the EDT, which are part of ongoing projects. For example, orangutans may have only learnt that supports can break under their weight in the final stages of their preparation for release, such as in prerelease islands or the early stages of a soft release. Prolonged experience of the conditions under which this might happen would be very beneficial, and we are working to replicate this in captivity, but of course, there are ethical issues to address. Similarly, orangutans will not have experienced prolonged hunger in the center, but they need to be able to deal with this, both physically and cognitively, after they are released. If they have learnt about fallback foods then this will help, but building their capacity to switch behavioral strategy in periods of low food availability will increase their chances of being able to "bounce back" after difficult times (Schuppli, Forss et al., 2016).

The cascading effects of small changes in behavior on One Health sketched out in Figure 1 could work to our advantage during the rehabilitation process: a seemingly small behavioral change (spending more time off the ground) could have positive effects that ripple through multiple aspects of a re-introduced orangutan's individual behavior, social interactions, physical and mental health, interactions with humans, and habitat use, reinforcing their resilience and ability to adapt to life in the wild. It also shows that behavioral ecology is intricately intertwined with One Health and has an important role to play in creating integrated and lasting solutions. Furthermore, it reiterates the insight of the One Health movement that these difficult and seemingly intractable problems can only be tackled by taking an integrated and systems-based approach to individuals, populations, and the ecosystems of which they are part.

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ETHICS STATEMENT

No new data were collected for this review paper, thus ethical approval was not required. Ethical statements for the referenced studies can be found within the referenced publications.

AUTHOR CONTRIBUTIONS

Jackie Chappell: conceptualization (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (supporting); visualization (equal); writing original draft (lead); writing review & editing (equal). Susannah Thorpe: conceptualization (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (lead); visualization (equal); writing original draft (supporting); writing review & editing (equal).

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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SUPPORTING INFORMATION

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