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A multicomponent approach to studying cultural propensities during foraging in the wild

Kelly Ray Mannion[1], Elizabeth F. Ballare[1], Markus Marks[2,3], Thibaud Gruber[1,4]

[1] Swiss Center for Affective Sciences, University of Geneva, Geneva, Switzerland

[2] Institute of Neuroinformatics, Swiss Federal Institute of Technology (ETH Zurich)

[3]Division of Engineering and Applied Science, California Institute of Technology, Pasadena, United States

[4] Faculty of Psychology and Educational Sciences, University of Geneva, Geneva, Switzerland

Correspondence to: Kelly Ray Mannion (kellyray7891@gmail.com) and Thibaud Gruber (thibaud.gruber@unige.ch), Chemin des Mines, 9, Campus Biotech, Swiss Center for Affective Sciences, Geneva, 1202.

Abstract

1. Determining the cultural propensities or cultural behaviours of a species during foraging entails an investigation of underlying drivers and motivations.

2. In this article, we propose a multi-component approach involving behaviour, ecology, and physiology to accelerate the study of cultural propensities in the wild.

3. We propose as the first component the use of field experiments that simulate natural contexts, such as foraging behaviours and tool use opportunities, to explore social learning and cultural tendencies in a variety of species. To further accelerate this component, we discuss and advocate for the use of modern machine learning video analysis tools.

4. In conjunction, we examine non-invasive methods to measure ecological influences on foraging such as phenology, fruit availability, dietary intake; and physiological influences such as stress, protein balance, energetics, and metabolism. We feature non-invasive urine sampling to investigate urea, creatinine, ketone bodies, the thyroid hormone triiodothyronine (T3), cortisol and Connecting peptides of insulin.

5. To conclude, we highlight the benefits of combining ecological and physiological conditions with behavioural field experiments. This can be done across wild species, and provides the framework needed to test ecological hypotheses related to cultural behaviour.

Keywords: cultural behaviour, field experiments, foraging ecology, physiology, tool use

Introduction

The topic of culture in animals has fascinated researchers for several decades, but largely gained momentum, with the publication of seminal articles and book chapters on primate cultures two decades ago (Fragaszy & Perry, 2003; van Schaik et al., 2003; Whiten et al., 1999). Culture involves the social learning and transmission of traditions in multiple individuals of a group that persists over time (Fragaszy & Perry, 2003). Although most notably attributed as a human or primate characteristic (van Schaik et al., 2003; Whiten et al., 1999; Whiten & van Schaik, 2007), cultural behaviour has also been documented in the foraging behaviours and vocalisations of multiple avian and mammalian species (Allen et al., 2013; Aplin et al., 2015; Garland et al., 2017; Whitehead et al., 2004), as well as the mating behaviours of insects such as *Drosophila* (Danchin et al., 2018).

It remains possible that many proposed animal cultural behaviours may be acquired by animals with little social influence, relying on mechanisms such as local or stimulus enhancement (see Tennie et al., 2020), making animal cultures a very different phenomenon from human cultures. However, the last two decades have allowed characterizing of the social learning mechanisms that come into play in the transmission of cultural behaviour; for instance, who an individual is paying attention to and needs to be aware of, or the opportunities they have for social learning (see Kendal et al. 2018; Whiten 2019; Gruber et al., 2021; Schuppli & van Schaik, 2019 for reviews). The matter of culture is not limited to social learning. It is multifaceted, and challenges researchers to devise studies that can consider the three major influences of behaviour: genetics, ecology, and sociality (Whiten et al., 1999). These studies may be devised for animals in the wild or in captivity. Captive studies can typically control what animals are exposed to; instead, field studies, while more ecologically valid, must contend with a range of additional factors. Because of this, they have mostly been limited to excluding competing explanations to social learning such as genetic and ecological variation, a method known as 'the method of exclusion' (see Table 1, Krützen et al., 2007).

Criticisms to the exclusion method (Table 1, Laland & Janik, 2006) have fostered a debate, particularly on the ecological aspects of cultural behaviours related to foraging. One interesting formulation of this criticism is to argue that the impressive behavioural repertoire that some species exhibit depend both on internal and external factors that cannot be easily excluded, but should rather be jointly considered while studying these behaviours' origins. Internal factors such as hormones, steroids, and enzymes, can provide evidence to tease apart the motivation behind behaviours. They also help determine the physical, physiological and/or psychological stress an individual may be experiencing at that time. External factors such as surrounding habitat, resources, temperature, humidity, diet availability, and conspecifics are also crucial components in understanding behaviours and their influences. A long dry season, for example, coupled with low food availability may lead to the innovation of novel behaviours in order to access a necessary resource (Grund et al., 2019). Thus, when investigating why particular behaviours do or do not occur, it is important to include as many influencing factors as possible to establish clear motivations.

Table 1: Keywords and concepts discussed.

Keyword	Definition
Culture	all behaviours and knowledge that are acquired and passed on within and between generations through social learning (van Schaik et al., 2003; Boyd & Richerson, 1985)
social learning	learning (*e.g.,* behaviour such as tool use or vocalizations; or abstract ideas such as values) through associating with or interacting with other individuals or their products (Heyes, 2012)
innovation	behaviours that have originally been brought into the population through individual invention (van Schaik et al., 2016)
cultural species	species that have been previously studied and described as having social learning and traditions continuing over time (Whiten & van Schaik, 2007)

conformity	an individual displays a particular behaviour because it is the most frequent the individual witnessed in others (Claidière & Whiten 2012)
Zone of Latent Solutions (ZLS)	animal cultural behaviours may be re-innovated by animals with little social input (Tennie et al., 2020)
method of exclusion	used to identify the presence of culture in wild animals; to be cultural, differences in behaviour should be caused by social learning and not by differences in genetics, ecology, or individual learning (Krützen et al., 2007). For criticisms, see Laland & Janik, 2006
necessity hypothesis	tool use behaviour arises as a response to food scarcity e.g., individuals use tools when there is not enough food available, and the tool provides access to a resource (Fox et al., 1999)
opportunity hypothesis	tool use behaviour emerges due to the frequency of encountering materials needed to make a tool or the resources for which an individual would use the tools (Fox et al., 1999)
consumer-centric method	determines what is truly available to the animal by incorporating the individuals' selective foraging behaviour (Wessling et al., 2021)
geometric framework for nutrition	the relationship of dietary macro- and micro-nutrient composition patterns with health and disease (Cohen & Raubenheimer, 2020)

With these considerations in mind, the goal of this review is to generate a multi-component approach to study culture in wild species, that incorporates variations in internal and external factors. While the principles of our proposed approach are applicable across species, and we incorporate different species, many examples in this review focus on primates partly due to our expertise and partly due to the vast research available. In Section 1, we highlight how field experiments can bring meaningful answers to the debates surrounding the emergence and maintenance of cultural behaviour. In Section 2, we address how engagement in experiments depends on some of the very factors highlighted by the debates on the method of exclusion. In Section 2.1, we discuss how to assess and incorporate ecological variation that may or may not motivate an individual to engage with an experiment. In Section 2.2, we then discuss the use of non-invasively collected urine samples to determine how protein and energy balance can be studied in conjunction with behaviour, to represent the internal state of an individual. Finally, we discuss how applicable such multicomponent paradigms are, notably with species known to display culture, as well as other species with the potential to do so.

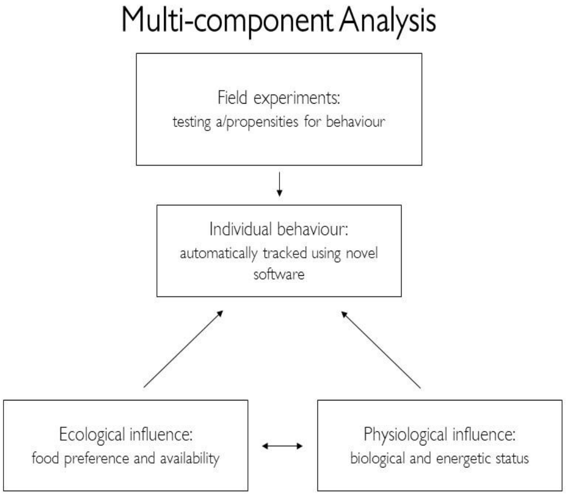

Figure 1: We advocate for multi-component analysis in studies exploring cultural behaviour or propensities in wild species. Field experiments can be used in combination with novel video analysis software to document individual behaviour and engagement. In order to fully understand behaviour, it is necessary to study the impact and interplay of both ecological and physiological factors.

Section 1: Identifying and studying potential cultural behaviours

1.1 Field experiments

Studies, especially those involving experiments, see an imbalance in research in the wild vs in captivity: a more substantial amount of research has been conducted in captivity to dissect social learning (Mesoudi et al., (2008); Whiten et al., (2016); Bandini & Harrison, 2020; Whiten et al., 2022). Although innovation is not rare in the wild, with many species having been documented innovating behaviours (Nishida et al., 2009; Perry et al., 2017), it is only recently that the social transmission and continuance of behaviours becoming traditions has been described in detail in the literature (however, see Terkel, 1996). Indeed, the 2010s have seen the development of studies in the wild that directly tackle the social learning aspect of culture, either through statistical analysis of social networks (Allen et al., 2013; Hobaiter et al., 2014), field experiments (van de Waal et al., 2013) or a combination of both (Aplin et al. 2015). Yet, questions remain as to why particular behaviours survive to become traditions over others (Grund et al., 2019). Field experiments allow opportunities for such behaviour to develop, while bringing as much control as possible in the field (Gruber et al., 2010). While this article is a review and does not require ethical approval, all proposed experiments should be reviewed by the relevant ethical bodies, even when deemed non-invasive to the study animals (Gruber, 2022). Here, we consider two classes of field experiments focused on cultural tendencies such as foraging behaviour, which is easily studied in many species and explores social learning and conformity. Additionally, experiments offering tool use opportunities can also foster manifestations of cultural behaviour.

1.1. *1 Foraging behaviour experiments*

To understand how foraging behaviour can be socially learned, researchers have altered food sources (van de Waal et al., 2013), or altered how an individual would obtain the food item (Aplin et al., 2015) in a natural setting. In one such study, wild vervets exhibited social learning and conformity in field experiments whereby a food item was offered in two different colours. During training, one colour was sweet, the other was bitter, then, during the test, the different colour options were the same because the bitter was removed. The vervets kept their colour preference acquired during training (i.e., only picking one colour while the other is now palatable). This study highlights how important social learning and conformity are, and that even if a behaviour is not adaptive, individuals will continue to perform their acquired behaviour (van de Waal et al., 2013). Similar information diffusion via social learning and conformity occurs in sub-populations of wild great tits (see also Wild et al., this issue). Aplin et al., (2015) first trained individuals from multiple sub-populations with a different method to solve a puzzle box that contained food by sliding a door with their bill specifically to the left or right. Individuals in each sub-population solved the puzzle boxes in the same manner as their respective trained models despite having both sides as possibilities to open the door (Aplin et al., 2015). Such foraging field experiments can be used to test a variety of species for their tendencies to learn and transmit information socially and ultimately provide more information on how diffusion and traditions can occur in populations.

1.1.2 Tool use experiments

Tool use can be a popular and exciting animal cultural behaviour particularly in our quest to reconstruct the last common ancestor of modern humans with their closest relatives the great apes (Gruber & Clay, 2016). A practical method to investigate tool use behaviours in the field consists of providing opportunities for tool use and observing what wild animals make of them. An example of such an experiment is the honey-trap experiment, which provides a log filled with honey accessible only through a small opening, a high-energy food for chimpanzees, on a likely travelling path (Gruber et al., 2009, 2011). The honey-trap experiment allows researchers to control the amount (Gruber et al., 2009), occurrence (Gruber et al., 2016) and possible recipient (Gruber et al., 2011) of an ecological opportunity to extract or forage for honey while being non-invasive in nature.

Figure 2: The honey-trap experiment set up in Bugoma Forest Reserve, Uganda with motion sensing camera-traps. Picture: Kelly Ray Mannion

Similarly, to investigate stone tool use behaviours, Koops et al. (2022) set up experiments providing both potential tools and food source (i.e., rocks and nuts). Findings in the two field experiments offer support for the need for social learning and transmission because chimpanzees were unable to re-innovate stick-using (Gruber, 2016; Gruber et al., 2011) or nut-cracking behaviours (Koops et al., 2022), despite opportunities offered by field experiments. However, when chimpanzees were proposed with known material for tool manufacturing, they displayed the behaviour, exhibiting intracommunity differences based on their knowledge of the different materials to fabricate the tools (Lamon et al. 2018). Simply put, with field experiments, researchers can determine the presence or absence of tool use behaviours by simulating natural contexts and then more extensively investigating curiosity, cognition, and exploration with experiment engagement.

Much of the resulting experimental data are in the form of videos that need processing, with contemporary research methods relying more and more on automated processes (see Supplementary Information, and Schofield et al. this issue for more information). For example, to overcome challenges associated with analysing videos of individuals in the wild, Marks et al., (2022) have developed an analysis pipeline based on deep learning called SIPEC that automatically detects, Segments (outlines), Identifies individual primates, performs Pose Estimation, and Classifies their behaviour and interactions in a naturalistic environment. The neural network architectures of SIPEC are developed particularly for use on primates behaving in complex scenes by utilizing raw video pixels (Fig. 3) while requiring less annotated frames for training than other methods. Thus, SIPEC has the potential to streamline field experiment video data organization and analysis across field sites (see Supplementary Information). While being developed for primates, the methods employed in SIPEC could be applied to other species.

Figure 3: SIPEC: SegNet analysed video-frame segmenting a chimpanzee in Bugoma Forest, Uganda.

Findings by Gruber, Koops, and collaborators highlight that simply providing an experimental opportunity for tool use is not sufficient to foster the behaviour, disputing claims that cultural behaviour can be easily triggered in wild animals. Yet, it is equally interesting to understand why the behaviours are not triggered. Therefore, additional factors must be considered, which we tackle in Section 2.

Section 2: Influencing Factors

2.1 Ecological Evaluation

Once experimental data have been processed, the results must be embedded within the general context of the experiment. For foraging behaviour, ecological factors are crucial, and data such as fruit availability and intake are necessary to determine whether animals will ultimately engage with an experiment or not. Adding an ecological layer to the evaluation thus helps in accounting for a more precise assessment of cultural behaviour in wild populations. This is also true in the context of tool use, which has been hypothesized to emerge from various factors and pressures. The necessity hypothesis first introduced by Fox et al. (1999) proposes that tool use is a response to food scarcity, while the opportunity hypothesis states that tool use emerges due to the frequency of encountering materials needed for a tool or the resources for which one would use the tools. For example, the honey-trap experiment directly tests the opportunity hypothesis because individuals are confronted with a task that requires them to identify and/or use the tool that is available (Gruber et al., 2012). Recent articles have attempted to offer various frameworks, e.g. insisting on the role of opportunity (Koops et al., 2014), drawing a framework of relative benefit (Rutz & St Clair, 2012), or redefining the role of necessity by focusing on variations in energetic balance and motivation to engage with an opportunity (Gruber et al., 2016; Grund et al., 2019).

These frameworks, which were originally defined for tool use but applicable for any type of foraging experiment, highlight the need to carefully assess the context in which experiments are conducted as well as the potential effects of diet on animal behaviour during the experiment. For example, the diet of stick using and non-stick using Ugandan chimpanzee communities differs significantly (Gruber et al., 2012). The Sonso chimpanzee community, which does not display stick-using in the honey-trap experiment, consumes a large variety of food items and may not experience the necessity to acquire honey with sticks, which may have led to the loss of this behaviour over time (Grund et al., 2019). However, to test such a scenario, it is important to assess feeding ecology (Sanz et al., 2014; Sanz & Morgan, 2013; Koops et al., 2013), therefore, allowing the characterisation of both the studied community's feeding ecology, and the current context of a given experiment (i.e. what the animal was offered in the week or so before an experiment, what it ate, and whether this had an impact on its overall engagement with the experiment, Gruber et al. 2016).

2.1.1 Food Availability and dietary intake

There are several methods that can be used to better understand variation in food availability and how this might affect the presence or absence of behaviours. Long-term phenology is necessary to understand the relationship of food availability and seasonality. It provides researchers with an understanding of the value of available foods, and of the potential effects that seasonality has on a given population (Sanz & Morgan, 2013). Although long-term phenology collection is the standard, new methods are being implemented to further detail the availability of food species and items such as the geometric framework for nutrition, which explores the relationship of dietary nutrient composition patterns with health and disease (Cohen & Raubenheimer, 2020), and the consumer-centric method (Wessling et al., 2021), which narrows the scope from the general habitat area in determining what is truly available to the animal by incorporating the individuals' selective foraging behaviour. These methods compile dietary and ecological information to show periods of low- or high- nutrient availability and therefore the effort required to meet caloric and nutritional demands. Essentially, these methods show what is "on the menu"; nevertheless, they do not reveal what an individual chooses to eat nor why.

Knowing what an individual "chooses" to eat means first understanding variation in foraging effort and dietary intake. Variation in overall food and fruit availability can be assessed via direct observations (e.g. feeding data collected by researchers during habituation and daily follows) (Altmann, 1974) or by examining dung samples, which provide information about food items already consumed (McGrew et al., 2009). This and subsequent nutritional analyses reveal the major species consumed daily, the caloric density and nutritional content of food items, and the percent of time spent eating each. Examining dung samples is especially important when studying ecology in communities that are not fully habituated or when researchers encounter difficulties with logistics that make it impossible to collect dietary information from daily follows (Basabose, 2002; Doran et al., 2002). Examining dung also verifies the species and food parts that individuals were observed consuming and enables recording species that were eaten outside of follow times (Matthews et al., 2020; McLennan, 2013). Both direct and indirect observations are important as they provide information about an individual's choice of diet.

Finally, with the increasingly documented impact of humans on animal cultures (Brakes et al., 2021), studies should also consider how neighbouring human settlements may be affecting behavioural variation in animal communities. This is particularly true when wildlife engage in crop-foraging, an activity shown to be a significant generator of new cultural variants in both primate and non-primate species (Gruber et al., 2019). Determining the access to these additional food sources is particularly essential when analysing how food variation impacts cultural tendencies like tool use. In this context, individuals likely employ less effort to meet dietary needs when they have more access to crops. This is a potential negative force in keeping a cultural behaviour (e.g., using sticks to forage for honey if a human-constructed hive is available and easily breakable). Overall, it is important to know how the increased proximity between wild animals and humans, as well as access to additional food sources will alter their physiology (e.g. energy balance) and the cultural behaviour of wild animals.

2.2: Underlying Physiology

As illustrated above, foraging behaviours expressed by an individual are influenced by both the foods available to them and their choices in consuming specific food items. To understand why those items are chosen, an individual's physiological state can be examined, investigating how energetic needs drive an individual's foraging effort and dietary intake. This allows the assessment of underlying constraints such as physical, psychological, and dietary stressors amongst others. For example, Nitrogen stable isotopes, used to differentiate between the excretion of exogenous and endogenous N sources (i.e., dietary or body protein; $\delta^{15}N$), increase in arctic ungulates during the dry winter months (Barboza & Parker, 2006; 2008). This increase positively correlates with the consumption of lichens, a low-N food, and muscle catabolism, which provides energy to the body by using body protein stores, the latter having been connected to reproductive success (Barboza & Parker, 2006, 2008). Here, the physiological measurement of nitrogen determined at least one reason for individuals choosing to consume certain foods according to seasons and reproductive status, thereby providing a substantial improvement over behavioural observations that only determined which foods were consumed more often.

Finding and consuming adequate food and the right balance of nutritious resources is crucial to an animal's survival because diet provides the biochemicals necessary for DNA replication, growth and development, reproduction, immune-responsiveness, and reproduction (Karasov & Martínez del Río, 2007). As highlighted in the previous section, both finding food and consuming the adequate calories and nutrients depends largely on food availability, as well as other daily environmental factors including temperature, rainfall, seasonality, reproductive status, illness, and injury. To deal with these variations while maintaining internal homeostasis, individuals are continuously adjusting their physiological, endocrinological, and immunological systems. These adjustments can be measured in response to or alongside observations of adjusted behaviour (Emery Thompson, 2017). Investigating physiological biomarkers along with behavioural and dietary observations also enables the examination of the effect of different environments on the same species. In central Bornean orangutans, for example, urea decreased with decreasing fruit availability in a masting forest, likely because both protein and non-protein energy intake decline when fruit is scarce (Vogel et al., 2012a; 2012b). Nevertheless, such results may not generalize to all populations, so the ecological context must be considered.

Many biomarkers can be measured in an individual through the analysis of samples collected via invasive and/or non-invasive methods. This includes blood plasma and serum, saliva, urine, faeces, hair, fingernails and semen (Novak et al., 2013; Higham, 2016; Behringer et al., 2018). Each biological sample is used when answering different questions pertaining to time (e.g., saliva provides information about changes to analytes within seconds to minutes; hair in weeks to months) (Novak et al., 2013); and to the facts that not every biomarker can be measured in each sample matrix (Higham, 2016), or that some biomarkers and their metabolites cannot be detected by in-house or commercially made assays yet (Higham, 2016; Behringer et al., 2018). These biomarkers include but are not limited to glucocorticoids, steroid hormones, growth factors, luteinizing hormone, CPK, adreno-corticotropic hormone, neopterin, cytokines, dopamine, oxytocin, and ghrelin. For in-depth reviews, see Behringer et al., 2018; Behringer & Deschner, 2017; Deschner et al., 2020; Higham, 2016; Novak et al., 2013; Emery Thompson, 2017. Because this paper focuses on the motivations behind the use of foraging strategies, we highlight analytes of energy balance and what their quantification can offer to controlled experiments in wild settings. Specifically, these include cortisol (response to a stressor; Novak et al., 2013; Preis et al., 2019), C-Peptides (energy balance; Polonsky et al., 1986; Emery Thompson, 2017), ketone bodies (fat catabolism; Knott, 1998; Naumenko et al., 2019), creatinine (muscle mass and lean body mass; Miller et al., 2004; Emery Thompson et al., 2012, 2020; O'Connell et al., 2021), urea (nitrogen balance and protein energy; Vogel et al., 2012a, 2012b), and T3 (metabolism; Behringer et al., 2018; Deschner et al., 2020; Emery Thompson, 2017).

In terms of energy balance, cortisol, C-peptides, ketone bodies, creatinine, urea, and T3 are most related by the Krebs Cycle which involves gluconeogenesis, lipogenesis, ketogenesis, the production of muscle protein (i.e., Amino Acids) and the subsequent Urea Cycle (release of an amine group) (Watford, 2003; Karasov & Martínez del Río, 2007). It is also connected to insulin regulation and C-peptide production, metabolism (i.e., the hypothalamus-pituitary-thyroid (HPT) axis), and cortisol regulation (i.e., hypothalamus-pituitary-adrenal (HPA) axis), which itself has a positive effect on glycogenolysis (Karasov & Martinez del Rio, 2007; Novack et al., 2013; Behringer et al., 2018). Thus, each measure reveals a different aspect of the internal state of an individual, especially when measured in conjunction with others. For example, wild great tits that exhibited less exploratory behaviour in a test chamber post-capture had a faster onset of the glucocorticoid response exhibited by their increased plasma cortisol levels. However, levels of an associated hormone also showed that this was independent of adrenal capacity and more associated with individual reactivity (Baugh et al., 2017). Overall, the increase in cortisol and HPA activation was attributed to personality (e.g., risk taking), which could influence whether an individual would try a new method to obtain a food resource.

As with all physiological processes, none of the aforementioned analytes operate in total isolation. Several of them cross-talk, making their production and subsequent effects plastic and adaptive in stressful environments. For example, the activation of the HPA axis and glucocorticoid production in non-mammalian vertebrates increases HPT axis activity and thus thyroid hormone production. In frogs, this increase, in combination with an increase in corticotropin-releasing hormone (growth) promotes the rate of metamorphosis (Bonett et al., 2010). Conversely, in mammalian vertebrates, glucocorticoids (cortisol) typically inhibit thyroid (T3) production during a stressor. However, because the thyroid hormone T3 performs other important functions in the body (e.g., thermoregulation), it can increase or decrease independently of other analytes. During periods of low energy intake, for example, low T3 (decreasing metabolic rate) can be found in conjunction with high levels of cortisol (mobilizing energy during a physiological stressor) (Novak et al., 2013; Behringer et al., 2018). If an individual experienced a sudden increase in energetic demands (e.g., predation, reproduction), both T3 and cortisol would likely be high to meet new energetic requirements (Behringer et al., 2018). Similarly, T3 and UCP are expected to perform positively as both are indicators of energy intake, although much variation remains (Emery Thompson, 2017; Behringer et al., 2018). UCP's have also been tied directly to carbohydrate consumption (Emery Thompson, 2017) and thus it is possible that a high protein, low carbohydrate diet produces an increase in T3 but not in UCP's.

Despite the outlined variation, together, the relationships among urea, creatinine, ketone bodies, UCPs, cortisol, and T3 among others can help delineate an individual's energy balance when tracked in individuals and compared across populations to examine variation across age, sex, developmental stage, habitat and diet. Overall, if an individual were ingesting a diet low in non-protein energy but high in protein energy, they would likely exhibit high UCP's, ketones, urea, cortisol, creatinine, and low T3;

however, if an individual were employing gluconeogenesis to convert protein to glucose, low UCP, low cortisol, low creatinine, and high T3 concentrations may be present instead (Figure 4).

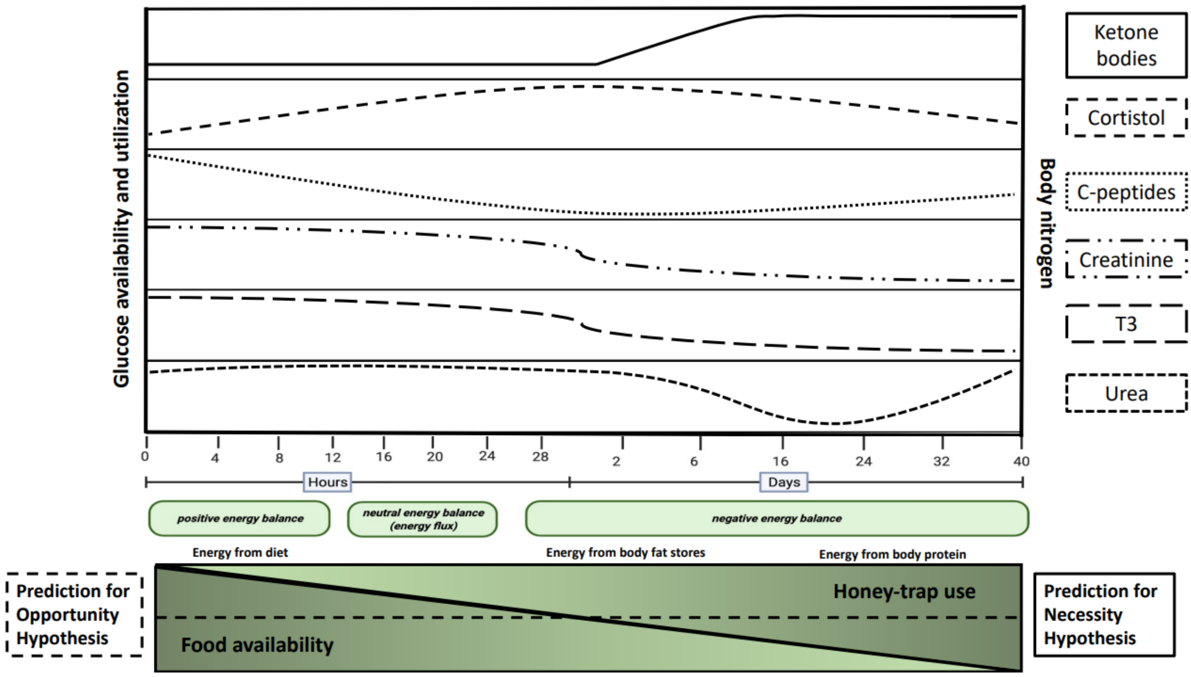

Figure 4. The relationship between food availability, a foraging experiment such as the honey-trap, and energy balance over time in mammals. The left- and right-hand axes represent the expected tendencies of urinary ketone bodies, cortisol, Connecting-peptides of insulin (UCP), creatinine, triiodothyronine (T3) and urea as glucose availability from the diet decreases and energy from body nitrogen increases. If more engagement with a foraging experiment and tool use were seen in conjunction with low food availability and negative energy balance, we would predict that tool use would be motivated by necessity. The opportunity hypothesis predicts engagement independent of energy needs. Thus, it is supported by finding engagement when not predicted by necessity in periods of positive energy balance. This is represented by the horizontal dotted line through the bottom triangles. Figure modified from Karasov & Martínez del Río, 2007 and Vogel et al., 2012a.

Both the quantification of physiological analytes of protein and energy balance and foraging experiments provide ways to gain further insight into the factors that underlie and influence the production of cultural behaviour. Combining the two enables one to answer questions such as *is a given cultural behaviour promoted by differences in food abundance, activity budget, and/or energy balance?* and can add further evidence to aid in disentangling the necessity vs. opportunity debate. For example, if an individual were to exclusively show interest in a tool use foraging experiment during periods of low fruit availability and significant physiological stress (i.e., negative protein and/or energy balance) as quantified by urinary biomarkers, this would provide support for the necessity hypothesis. This would also likely coincide with low UCP, high ketone, low urea, low creatinine, high cortisol and high T3 concentrations. If, however, an individual was to show (more) interest in the experiment during periods of high fruit availability and evidence of physiological health (i.e., positive protein and energy balance), this would provide more support for the opportunity hypothesis. This would also likely coincide with high UCP, low ketone, high urea, high creatinine, low cortisol and low T3 concentrations (Figure 4).

Conclusion

Culture is a biological phenomenon which is not unique to humans. Yet, to truly grasp the presence of culture in wildlife we must examine as many probable factors as possible, as there are both internal and external factors contributing to the behaviours that are performed. Untangling the drivers of these behaviours is challenging but more methods are being developed to better account for possible behavioural influences. Many biomarkers already exist in primates and other animals that can be analysed through non-invasive methods, like urine collection, to compare observed behaviours with energetic statuses. Advances in technology and data collection methods allow more in-depth research than ever and facilitate the study of more elusive species and behaviours. Diet is a component of feeding ecology that can be assessed in terms of both food availability and food preference. Usually measured via phenological methods, new methods like the consumer-centric method are changing how we can assess food availability. The diet availability and the actual diet of an individual should be used together, when possible, to get a broader understanding of how an individual utilizes their environment; coupled with energetics, we can start to understand the “why”.

In addition to observational sampling, we propose bringing as much control to wild studies as possible by implementing field experiments to dissect the occurrence of cultural behaviours and tendencies in natural environments. The key to field experiments is simulating something in nature that can elicit certain behaviours for study. There are many ways to design such field experiments like providing an obstacle, puzzle or sound that would not be out of place in the natural setting, but that researchers can control in terms of timing and placement unbeknownst to the study species, thus remaining non-invasive in essence. The honey-trap experiment is an example of a practical method to explore tool use behaviour in wild populations. The simple design makes it an adaptable experiment to apply to different primate species and facilitate cultural studies across communities and populations. This experiment is versatile in nature and can be further adapted for use in other species, such as corvids.

Similar to how other wild and many captive studies have shown (Gruber et al., 2009, 2011; Koops et al., 2022; Motes-Rodrigo et al., 2019), it is possible to find ways to implement natural experiments to expand our knowledge about different species, although this may be ultimately constrained by their environment. For instance, creating a field experiment to test cetacean cultures in the wild may prove more challenging. However, an experiment set-up in which dolphins can utilize sponges (Krützen et al., 2005; Mann et al., 2008) may be implemented. While we addressed field experiments targeted towards cultural species, such experiments can also be extended to other species. In particular, finding ways to test species depicted in the literature as cognitively cogent like the octopus (Godfrey-Smith, 2016) with natural experiments could lead to interesting findings for innovation and tool use behaviour. Species where object manipulation already occurs in some fashion like sea otters that use rocks to break open prey (Haslam et al., 2019), can be tested and provide more evidence for determining if behaviours originate from necessity or opportunity. Finally, experiments may allow testing the specific factors that can trigger the occurrence of tool use in non-tool using species, if their cognition allows it, or the diffusion of a socially learned behaviour.

Overall, creating more “natural” experiments provides researchers with more opportunities to investigate chosen behaviours and their origins. Still, culture is not limited to tool use, and developing experiments that do not focus on foraging cultural behaviour appears more feasible in some species. Birds and cetaceans have documented evidence of social learning in their vocalizations and song behaviours and experiments have been conducted to further tweeze out the extent of their cultural propensities (Ford, 1991; Garland & McGregor, 2020; Aplin, 2019). For these species, we suggest that combining field experiments such as audio playbacks (see King & Jensen, 2022) with the study of ecological or physiological factors can allow researchers to determine how these factors impact social learning and the transmission of behaviours.

As illustrated above, we recommend that behaviours be investigated in conjunction with as many influencing factors as possible. Ecology and physiology should be an investigative priority because it is these underlying conditions that motivate individuals. For example, the physiological measurement of an individual's energetic status is generally used to provide a picture of the overall health of a community and its adaptations for survival since diet, nutrition, and physiology are key to DNA replication, reproduction, growth and development, and immuno-responsiveness. Yet, by being combined with field experiments, it can also characterize the potential precursors to the behaviours we observe; only by gathering such data can we gain a better understanding of the underlying constraints and biological drivers that influence an individual. As we study more species and populations, our understanding about the drivers of cultural behaviours will grow. Ultimately, this knowledge, having encompassed as many factors and contexts as possible, can be extended to humans and provide further information about how we as a species have developed such extensive cultural propensities. The combination of these three approaches, behaviour, ecology and physiology, also provides the contextual information for cultural innovation and the potential for species to innovate new adaptive behaviour in a changing world. More understanding on how animals develop behaviours is crucial at a time in which the focus of scientific research shifts from the existence of animal cultures towards their conservation.

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