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Although social transmission mechanisms of animal cultures are well studied, little is known about the origins of behavioral innovations, even in established tool users such as chimpanzees. Previous work has suggested that wild chimpanzees are especially prone to engaging with tools during extended periods of low food availability and after long travel, supporting the hypothesis that cultural innovation is facilitated by necessity revealing opportunities. Here, we tested this hypothesis with a field experiment that directly compared subjects’ immediate variation in measures of current energy balance with their interest in a novel foraging problem, liquid honey enclosed in an apparatus accessible by tool use. We found that the previous distance traveled directly predicted subjects’ manipulations of both the apparatus and the tool, whereas previous feeding time was negatively correlated to manipulation time. We conclude that “necessity” augments chimpanzees’ likelihood of engaging with ecological “opportunities,” suggesting that both factors are scaffolding foraging innovation in this and potentially other species.

Key words: foraging innovation, necessity, opportunity, chimpanzees, energy balance.

Energy constraints are a major driver in behavior evolution (Aiello and Wheeler 1995). This is especially true for habitats in which ecological conditions fluctuate, which tends to increase the capacity for behavioral plasticity (Sol et al. 2005; Clavel et al. 2011). One manifestation of behavioral plasticity is the ability to “innovate” (Reader and Laland 2001), that is, to flexibly respond to environmental changes with novel behavioral patterns. Particularly relevant are innovations that enhance foraging efficiency and the ability to cope with food shortages (Sol et al. 2005; Morand-Ferron et al. 2011). Although rainforests are considered relatively stable habitats with high levels of fruit production (Marshall and Wrangham 2007), fruiting patterns can fluctuate considerably, which can result in temporary food shortages with corresponding selection pressures on species that strongly depend on fruit (Wrangham et al. 1991; Yamakoshi 1998; Janmaat et al. 2006; Gruber et al. 2012; Janmaat et al. 2012; Gruber 2013; Lee and Moura 2015).

Although chimpanzees (Pan troglodytes) are typical rainforest dwellers (Boesch and Boesch-Achermann 2000), they are also found in the savannah (Pruetz and Bertolani 2009), suggesting that they have been under selection pressure to deal with ecological oscillations. One possible adaptation is their fission–fusion social system (Moscovice et al. 2007), which allows group size and activity patterns to be adjusted to changes in food availability (Chapman et al. 1995), which minimizes travel costs (N’guessan et al. 2009). Chimpanzees are also known for their behavioral diversity and flexibility (Whiten et al. 1999) and the fact that they are habitual innovators (Reader and Laland 2001; Hobaiter et al. 2014) with a large repertoire of foraging-related tool-use behaviors to access otherwise inaccessible food resources (Sanz and Morgan 2013). This has been compellingly illustrated by large differences in behavioral profiles across chimpanzee communities, including tool use (Whiten et al. 1999).

In some chimpanzee communities, tool use is observed during periods of food shortage, suggesting that it serves as a backup strategy, similar to consuming “fall-back” foods (Bulindi: McLennan 2015; Kahuzi: Yamagiwa and Rasabose 2009; Bossou: Yamakoshi 1998). In a meta-analysis on primate innovation, Reader and Laland (2001) found that in 47% (N = 36) of all relevant studies, “innovation was prompted by ecological challenges, such as periods of food shortage, dry seasons, or habitat degradation.” Innovation in chimpanzees and other animals, in this view, is borne out of the need to acquire nutrients as stated by the “necessity” hypothesis (Fox et al. 1999). Further support for the necessity

Reader and Laland (2001)
hypothesis comes from energy-deprived guppies that were more likely to locate novel food sources than control animals (Laland and Reader 1999). Additionally, Sol et al. (2005) found that foraging innovations in wild bird species were more common in the winter, again suggesting that energy needs are an important driving factor. Similarly, in common mynas (Acridotheres tristis), individuals with high feeding motivation (and low neophobia) were more likely to engage and solve an experimental task that required operations than controls (Sol et al. 2012). Necessity also appears to have an effect within groups of animals because subordinates often experience higher necessity than dominant individuals due to reduced access to resources, and this tends to make them better innovators (Reader and Laland 2001; Griffin and Guez 2014).

However, there are alternative hypotheses to explain the presence of tool use. Specifically, some studies failed to find significant correlations between tool behavior and reduced food availability (Koops et al. 2013; Sanz and Morgan 2013), suggesting that other mechanisms may be at work, alternatively or simultaneously. One such idea, the “opportunity” hypothesis, proposes that behavioral innovations, such as tool use in chimpanzees, are better explained by individuals being exposed to specific environmental conditions, specifically encountering a resource in the presence of potential tool material (Koops et al. 2014). In Sumatran orangutans (Pongo abelii), for instance, differences in tool-based insectivory correlate with site differences in insect abundance but not with changes in the availability of preferred foods (Fox et al. 2004). Another example is found in the chimpanzees of the Goualougo Triangle (Republic of Congo) where no increase in stick-based foraging was observed during periods of fruit shortage (Sanz and Morgan 2013).

Beyond opportunity and necessity, additional hypotheses have been discussed. For example, Rutz and St Clair (2012) have proposed the “relative profitability hypothesis” to explain disparities in tool use within and between crow species. Here, the idea is that tool use occurs if it is relatively more profitable than alternative non-tool-based foraging strategies. In sum, despite large interest, the current literature is inconclusive about what drives behavioral innovations and the emergence of tool use in animals.

The Sonso chimpanzee community is interesting to test hypotheses of tool innovation and use, as members of this group do not use tools to extract food other than liquids, in contrast to other well-studied chimpanzee communities (Whiten et al. 1999). In previous experiments, we let individuals encounter natural liquid honey, presented in an artificial cavity dug in a large, fallen tree, designed to foster tool use (Gruber et al. 2009). Strikingly, some individuals manufactured a tool, a leaf sponge, to access the honey, but there was much variance in how long individuals engaged with the task and whether they used a tool (Gruber et al. 2011). Leaf-sponges are used community-wide to access water from tree holes, puddles, and clay pits, suggesting that the honey-sponging individuals applied an “old solution to a new problem” (Kummer and Goodall 1985).

Subsequent research on the same community showed that periods with much traveling and low fruit consumption resulted in extended problem-solving efforts with different honey-provisioning devices (Gruber et al. 2016), suggesting that an unfavorable energy balance increases chimpanzees’ interest in difficult, out-of-reach food resources. Interest was highest after extended unfavorable conditions, whereas actual tool use was best predicted by extensive travel effort before an experiment. Although relevant, this study was hampered by the fact that estimates of both travel and feeding efforts were only indirect and patchy, as they were assessed via long-term data from behavioral scans. The relative paucity of scans also prevented us from investigating immediate effects on explorative and tool-interaction behavior, although such data are crucial for theories of tool innovation.

In this study, we readdressed the role of necessity and opportunity in chimpanzee tool use and cultural behavior more generally by experimentally exposing subjects in a standardized way to a foraging problem while simultaneously measuring participants’ immediate prior travel effort and food intake. To this end, we followed subjects during their daily foraging, sampling their feeding activities and movements in their home range over a roughly 24-h period before presenting them with a portable apparatus that contained encased liquid honey. Although we could not directly measure metabolic data (or “energy balance”), we were able to assess them indirectly via food intake and physical activity (e.g. Hoyt et al. 2006). This protocol thus allowed us to relate the energy balance of subjects to their interest in problem-solving behavior when encountering artificially provided honey. As in previous experiments, subjects had to engage with a specific mechanism to access the honey, this time by manipulating a stick in a predetermined way (Figure 1). Based on previous results (Gruber et al. 2016), we expected that individuals who had traveled more and/or fed less over the previous 24-h period and between groups of animals would engage more with both the apparatus and the tool when encountering the experimentally provided feeding opportunity.

METHODS

Study site and community

The study was conducted with the Sonso community whose home range includes the “Budongo Conservation Field Station” (Reynolds 2005) in Western Uganda from January 2016 to May 2016. The Sonso chimpanzees have previously taken part in other field experiments involving encased honey (Gruber et al. 2012, 2016; Gruber 2016).

Experimental apparatus

The experimental device consisted of a 40-cm-long natural wooden log with a 23-cm radius and a 17-cm-deep cavity that could carry a plastic receptacle filled 10-cm deep with liquid honey (Figure 1). The only possible way to access the honey was by operating a stick that protruded through a 1-cm-wide hole in the cavity’s lid. The stick could be freely moved within the cavity, which allowed subjects to extract honey by pulling the stick out from the honey pool. However, as the stick was blocked at one end, it was not possible to remove it completely from the apparatus. This made it impossible for subjects to discard the stick and to search for alternative tool solutions as they have done in previous experiments (for a review, see Gruber 2016). Hence, the current device differed from previously used ones in the diameters of the hole and stick as well as the fact that the stick was permanently connected to the device, which prevented subjects from exploring other solutions. This allowed us to directly compare motivation of subjects. Conversely, the lack of payoff could also drive them away quickly if they were not successful in obtaining honey (see Results).

Subjects

At the time of the study, the Sonso community consisted of 68 individuals (12 adult males and 23 adult females with their
Figure 1
Components of the experimental device supplying liquid honey by tool use. (a) Lower part of the log with cavity carved out to fit a plastic receptacle containing liquid honey; (b) tool-retaining mechanism of the receptacle: a metal spring (relaxed) was coiled around a cone-shaped stick, whose wide (>1 cm) end prevented removal through the 1-cm hole in the lid. During each trial, the receptacle was filled with liquid honey to a depth of 10 cm; (c) receptacle with closed lid and protruding stick; the metal spring inside the receptacle slightly compressed; (d) receptacle inserted into the artificial cavity of the log; (e) experimental log completely assembled. As soon as a subject pulled the stick out of the receptacle, honey became accessible at its lower end (~3 cm). As soon as a subject released the stick, it retracted back into the cavity by the mechanical force of the compressed spring, replenishing it for another round of manipulation.

Day 1
Start 8 am 6 pm 7 am Night (stationary) Day 2 Experiment

Figure 2
Time frame for estimating travel effort and feeding behavior. The experiment consisted of 2-day focal animal follows, terminated by the presentation of the apparatus on day 2. Individuals were left in the evening after they built their nests and were thus assumed to have remained stationary overnight (i.e., from 18:00 to 07:00 local time the following day). Presentation of the apparatus on day 2 varied depending on the opportunities to run an experimental trial.

offspring). We carried out focal animal follows on \( \mathcal{N} = 6 \) individuals selected due to previously demonstrated interest in similar experiments (2009-2015; Supplementary Table S1; see also Gruber et al. 2016). Prior to these experiments, none of the subjects was ever observed using a stick in a natural or experimental foraging context. Because we did not aim to influence party composition, subjects never encountered the device alone, such that \( \mathcal{N} = 16 \) further individuals participated in the experiment in addition to the \( \mathcal{N} = 6 \) subjects. All encounters were filmed and analyzed by C.G. with BORIS v 2.981 software (Friard and Gamba 2016). Behavioral activity and interactions of individuals were coded following a predefined ethogram (Supplementary Table S2).

Experimental design
To investigate the relationship between travel distance, foraging success, and propensity to innovate, we conducted our field experiment with the following design. Each trial lasted 2 days (Figure 2). On day 1, we located 1 of the 6 focal animals in the morning and tried to follow it until it nested in the evening (“day 1 focal follows”). On day 2, we localized the same individual early in the morning and continued to follow it until a good opportunity for

an experimental trial arose (“day 2 focal follows”). During all focal follows, GPS data were collected using a GARMIN 64s, whereas behavioral data were collected using continuous focal animal sampling (Altmann 1974). For every feeding event, we noted the type of food consumed (fruit, leaves, flowers, bark, wood, meat, termite soil, others) and (whenever possible) the food species.

To calculate travel effort and feeding behavior prior to an experiment, we first determined the subject’s travel speed (number of meters traveled per hour of observation time) and the proportion of time it spent feeding (feeding time per hour of observation time) on day 1. We subsequently extrapolated the obtained travel speeds and feeding proportions to 10 h (Figure 2; 8 AM–6 PM), resulting in a given subject’s “day 1 feeding time and travel distance.” The experiment was carried out on day 2 at different times, depending on opportunities (range 07:16–13:38 local time). As a consequence, observation times on day 2 varied accordingly (average 3.5 h). For better comparability, we used the average observation time to calculate the “day 2 feeding time and travel distance” of each subject, extrapolating its day 2 travel distances and feeding proportions to 3.5 h. Overall, travel distance and feeding behavior were assessed over both days by adding the calculated travel distances and feeding times of day 1 and day 2, referred to as “estimated travel effort” and “estimated feeding time,” respectively. Once a subject was given the opportunity to interact with the apparatus, other individuals were usually also present such that several individuals could sometimes be tested during the same trial. We analyzed their behaviors separately, provided individuals had unconstrained access to the apparatus.

Once a subject encountered the apparatus on day 2, we recorded its behavior on video. The subject’s behavior was subsequently coded by C.G. First, we calculated the “device engagement time” as an expression of an individual’s motivation to access the encased honey (Supplementary Table S2): “Device engagement time” included all the subject’s physical contacts with the apparatus, including licking leaked honey, touching the apparatus and licking the fingers, or
manipulating the apparatus or stick. From this, we then extracted the “stick touching time” as an expression of an individual’s propensity to engage with the only suitable tool, a precondition to successfully solving the task. Engagement with the log or stick was considered as terminated when the individual let go of the apparatus or tool and left the experimental setup. We managed to conduct a total of \( N = 16 \) successful trials over a period of 3.5 months between January and May 2016, involving \( N = 22 \) individuals, some of which encountered the log more than once (see Supplementary Table S3). From these trials, we managed to extract \( N = 8 \) trials, for which we also had focal follow data (see below).

### Statistical analyses

We conducted focal follows for \( N = 6 \) individuals, who subsequently contributed to \( N = 8 \) experimental trials, that is, providing both data on previous travel effort and feeding history and subsequent performance at the apparatus. This resulted in a final data set of \( N = 9 \) data points because in 1 of 8 experimental trials, we had focal data on the previous behavior of 2 present individuals, KC and KX. We entered them as separate data points because both subjects took turns in accessing the device without any visible signs of tension.

Given the low sample size, we analyzed the data with univariate, nonparametric procedures instead of generalized linear mixed models. We carried out 2 sets of analyses. In the results section, we used the full \( N = 9 \) data set, whereas in the supplement, we present additional analyses with each individual represented only once.

## RESULTS

### Behavioral responses

In 8 of 16 experimental trials, we could estimate the previous traveling and feeding activities of at least 1 of the participating individuals (for 1 trial we had previous focal data on 2 individuals; range of individuals with or without focal data engaging with the device in these 8 experimental trials: 0–4, see Supplementary Table S3). The mean engagement time with the apparatus in the 8 experiments was 10 s (range: 1–61 s, including individuals with and without focal data). In 7 of the 8 trials, engagement included some form of stick contact by 1 or 2 individuals (see Supplementary Table S3), mainly touching and pulling the stick. Mean stick interaction time during instances of log engagement in the 8 experiments was 11 s (range: 0–43 s, including individuals with and without focal data). In 2 cases, stick use was successful insofar as subjects managed to extract honey (KB, KU; Supplementary Table S3). Here, both individuals pulled out the stick to lick honey pasted to its lower end (Figure 3), which led to the highest stick touching times (KU: 31 s; KB: 45 s) of all trials. Remarkably, however, no individual solved the problem in the sense that it showed repeated, controlled up-and-down movements of the stick by hand (or foot) to access the honey.

### Travel and feeding history and interest in honey

For \( N = 9 \) cases, we were able to estimate the subjects’ previous travel effort and feeding time as part of \( N = 8 \) experimental trials (Table 1). “Estimated travel effort” ranged from 1.0–4.4 km, whereas “estimated feeding time” ranged from 1.8–11.0 h. Mean device engagement time was 19 s (range: 0–50 s) and mean stick touching time was 13 s (range 0–45 s; see Table 1).

### Relationship between previous energy expenditure and interest in device

Individuals showed increased interest in the apparatus with increased distance traveled before a trial (Spearman’s rank correlation \( \rho = 0.85, N = 9 \) trials; Figure 4; Supplementary Table S5). In contrast, “estimated feeding time” was weakly negatively correlated with “engagement time” with the device (Spearman's...
DISCUSSION

In the current study, we investigated whether tool use in wild chimpanzees is a direct consequence of necessity (in terms of food intake and energy spent during travel) or opportunity (in terms of encountering difficult-to-access high-quality food). In particular, we were interested in the short-term effects of individuals’ travel and foraging histories on their subsequent interest in a task that required a tool-based behavioral innovation. We investigated this using a portable apparatus that supplied high-quality food, liquid honey, to subjects in a standardized way. Based on a previous analysis of experimental and long-term observational data (Gruber et al. 2016), we predicted that unfavorable energy balances (i.e., high travel costs, low feeding time) would foster high interest in the device and the proposed tool and, as a consequence, increase the probability of a behavioral innovation.

To this end, we collected focal data from N = 6 subjects over a continuous period covering much of 2 consecutive days. The relationship between our experimental data and the behavioral data acquired for each subject suggested that extended travel and low feeding time prior to encountering a difficult feeding opportunity indeed favored both exploratory and tool-use behavior. Based on our results and previous studies, we first discuss possible drivers of behavioral innovation in wild chimpanzees and then propose a new model of chimpanzee foraging innovation, which scaffolds opportunity and necessity with one another (see also Rutz and St Clair 2012 for a similar framework in New Caledonian crows).

Drivers of behavioral innovations in wild chimpanzees

Chimpanzees are widely considered the most “cultural” of all nonhuman animals, evidenced by behavioral profiles that differ drastically between communities (Whiten et al. 1999). Although much is known about the social learning mechanisms that favor the spread of novel behaviors in chimpanzees (Whiten et al. 2009), very little is known about the mechanisms underlying behavioral innovations (Gruber et al. 2010; Reader et al. 2016). For chimpanzees, the current literature has focused on 2 main scenarios to explain the origins of innovations: opportunity and necessity (Koops et al. 2014). The “opportunity hypothesis” predicts that animals acquire novel behaviors, such as tool use, because they encounter the key ingredients in spatio-temporally favorable conditions. The “necessity hypothesis,” in contrast, predicts that animals become more motivated to solve problems if their favorite staple food is lacking, which forces them to meet their nutritional needs from alternative but typically more difficult-to-access (e.g., embedded) food sources. There is evidence in support of both hypotheses as causal factors of tool innovations, which has triggered an ongoing debate (Koops et al. 2014; Gruber et al. 2016).

Our study was designed to address this impasse and our results suggest that both necessity and opportunity can play a role in interlinked ways, a proposal that, surprisingly, has not received much attention so far (but see Rutz and St Clair 2012). We found that wild chimpanzees that traveled more before an experiment spent more time trying to access high-value food and were more likely to engage with a provided tool the following day than individuals that traveled less, possibly due to the fact that they had spent less energy. Persistence in problem solving is widely thought to be essential for foraging innovations in animals (Benson-Amram and Holekamp 2012; Cauchard et al. 2013). In the present study, we also found that engagement time was above average in trials when subjects successfully retrieved honey using the stick. Necessity, in other words, may drive individuals to explore novel food sources and increase their willingness to devote time to solving unfamiliar problems. This will increase chances of behavior innovations through basic trial-and-error or more complex processes but only if a relevant ecological opportunity is in place.

We assumed that travel effort and foraging success have metabolic consequences on what we called “energy balance.” Previous studies in humans (e.g., Plasqui and Westerterp 2004; Hoyt et al. 2006) and nonhuman animals (see review in Ascensio et al. 2009) have linked physical activity with energy balance, despite the fact that the relationship is complex and depends on additional socioecological factors (Clutton-Brock and Janson 2012; Pontzer 2017). For instance, individuals differ in energy requirements depending
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Moreover, quality and size of food patches differ throughout a home range, whereas the size of the travel party will determine the amount of travel effort necessary to obtain sufficient energy (Asensio et al. 2009). For example, N’guessan et al. (2009) found a negative relation between estimated feeding time and device engagement time (N = 6; rho ranging between 0.14 and −0.89; Supplementary Table S5). The same was the case for the negative correlation between estimated feeding time and device engagement time (N = 6; rho ranging between 0.71 and 0.89; see Supplementary Table S5). Reduced food availability also has a direct connection to group size, downregulating the foraging subgroups of a community to a size that still allows the individual to forage efficiently (Matsumoto-Oda 2002; Asensio et al. 2009). As a consequence, subgroup size can be positively correlated with travel time (e.g., long-tail macaques, van Schaik et al. 1983) or food availability (e.g., chimpanzees, Anderson et al. 2002). Although these are all important factors for more informed models of tool innovation and use, the design of our study did not allow us to address any such social correlates of foraging behavior.

A model of behavioral innovation and spread

Based on our findings and the current literature, we propose a 3-step model for foraging-related tool innovations and spread in chimpanzees and possibly other animals more generally (Figure 6). Step 1 describes the innovation process, fostered by both necessity and opportunity; step 2 describes the social spread of an
Disappearance: In our study, 2 individuals successfully...ecological resourcedemonstrators
Positive energy balance

innovation; step 3 describes the maintenance or eventual disappearance of the innovation within a group.

1) Behavioral innovation: Our hypothesis is that foraging-related innovations are directly influenced by resource shortages that render current behavioral coping mechanisms and foraging patterns less effective (Gruber 2013). Based on previous work (e.g., Gruber et al. 2012, 2016), we assume that shortages are either sustained or acutely severe. As a result, individuals are driven to explore alternative resources and, by doing so, they exploit new ecological opportunities that are already present (but so far overlooked) or that have appeared recently because of a change in their environment. Hard-to-access, well-protected, energy-rich foods are likely to be of specific interest (e.g., nuts, larvae, honey; Ungar 2007), a situation modeled by our experiment. Our data suggest that unfavorable energy balances caused by reduced intake and/or high expenditure increase individuals’ motivation to access such a difficult-to-access, high-value food. Necessity, in other words, increases the time and attention an individual directs toward ecological opportunities (substrate and tool material) already present in their environments, and both factors combined increase the likelihood of behavioral innovations. Necessity, in short, creates new opportunities.

2) Community-wide spread: In our study, 2 individuals successfully operated the apparatus by manipulating the stick in the correct way, although there was no indication that they learned the novel tool-use behavior as they did not display the behavior repeatedly. Yet, with more opportunities to engage in trial-and-error exploration, these subjects may have acquired a behavioral innovation that enabled them to access the novel food resource, which would give them an advantage over others in their energy balance. Chimpanzees are remarkable social learners, suggesting that behavioral innovations could spread quickly to other community members (Ramsey et al. 2007; Gruber et al. 2015a; Lamon et al. 2017). If the new behavior persists in the community, it becomes part of the community’s cultural profile, beyond the ecological context in which it originated. If only parts of the community display the behavior, the behavioral innovation can also become part of a subculture, as previously demonstrated for moss-sponging in the Sonso chimpanzee community (Lamon et al. 2018).

3) Maintenance and disappearance: Once subjects have learned socially to exploit a novel food resource, there is no reason why its consumption should be restricted to particular periods of the year, suggesting that “necessity” is less relevant in its maintenance as long as ecological conditions do not change. “Opportunity,” in contrast, is likely to continue playing a key role in maintenance. For example, if there is a reduction in the availability of tool material or food resource, the prediction is that the socially acquired behavioral innovation is likely to disappear again. Disappearance is also predicted by necessity, especially if alternative foraging opportunities appear and provide a stable food supply. Budongo Forest, for example, has been subjected to selective removal of tropical hardwoods, which has benefitted various fig tree species whose fruits are consumed by chimpanzees throughout most of the year (Reynolds 2005). This finding has been interpreted as a potential factor in the loss of stick use in the Budongo chimpanzees (reduced ecological necessity,

Figure 6
Ecological model of the role of “necessity” and “opportunity” in the emergence of foraging-related behavioral innovations and tool use. (a) Individual innovation. Unusually severe food shortages or prolonged periods of food stress cause difficulties for individuals to meet their nutritional requirements (“necessity”) and, as a consequence, increase motivation to explore their surroundings for alternative food resources (“opportunity”). Unfavorable energy balances further increase subjects’ attention and motivation to access previously inaccessible, high-value foods, which is likely to lead to behavioral innovations. (b) Social transmission of the behavior. If a behavioral innovation is advantageous it is likely to spread to other community members through social learning and become part of the community’s cultural repertoire. 3) Maintenance or disappearance of the behavior. Variation in ecological necessity (availability of alternative food options to meet nutritional requirements) and opportunity (availability of tool-accessed resource and tool material as well as social opportunity to witness a behavior being demonstrated) will shape tool use exhibition and maintenance in the community.
In line with previous findings, our field experiment indicates that chimpanzees’ propensities to engage with foraging opportunities may be linked to unfavorable energy balances. Although the current study has focused on the relationship between ecological challenges and behavioral innovations, additional factors need to be taken into account in the future. In addition to the social factors already discussed above, individual variation in curiosity and persistence is likely to influence how individuals respond to necessity, in addition to factors such as age, sex, and social rank, which are also known to influence performance in problem solving (Reader and Laland 2001; Gruber 2016). It may also be argued that the Sonso chimpanzees are unable to represent sticks as a material basis for tools (see discussion in Gruber et al. 2015b; Gruber 2016). Furthermore, the natural availability of honey-providing beehives within the chimpanzees’ home range is likely to influence individual behavior (Sommer et al. 2012; Sanz and Morgan 2013). Future studies may also want to provide more direct measures of energy balance, such as by tracking urinary C-peptide levels (Emery Thompson et al. 2009). A drawback of our study is indeed that we did not have physiological measures of energy balance and had to rely on indirect ways to assess variation. A combination of field experiments with physiological markers would be an important next step in linking internal variables and tool-use behavior. We also acknowledge that we base our conclusions in the current experiment on a small sample size, despite the fact that they confirm an hypothesis drawn from a previously larger indirect study (Gruber et al. 2016). More work is thus needed to disentangle how opportunity and necessity interact together to lead to tool use. In particular, it may be that future work finds different patterns connecting these 2 factors (e.g., more travel and/or less feeding lead to less engagement with a given opportunity). If this happens, an exciting avenue of research will be to compare the various contexts that lead to these effects to understand how variations in the respective weight of each factor can influence tool-use innovation.

In conclusion, experimental problem-solving tasks are a valuable way of assessing the propensity for behavioral innovations in wild animals and can be used to investigate the role of necessity and opportunity. Our experiment focused exclusively on a tool-operated mechanism, but it is also important to explore nontool-based foraging tasks. First, comparing tool and nontool-based foraging tasks may allow isolating pressures that solely act on tool use. Second, nontool-based tasks will also allow testing our model in other environments or with species that have developed alternative strategies to cope with ecological pressures (Snith and Chapman 2008). Both tool and nontool-based experimental tasks will thus lead us to better understand the dynamic interactions between opportunity and necessity in fostering behavioral innovation. It is also important to keep in mind that the current ecological conditions observed by researchers may be different from the conditions in which an innovation originated, suggesting that current conditions are more valuable in understanding the maintenance of cultural behavior than its origins. Foraging experiments, as the one presented in this study, may provide insights into how rare situations can lead to novel behavior, which, if adaptive, may then spread to become established into a cultural repertoire.

**SUPPLEMENTARY MATERIAL**

Supplementary data are available at Behavioral Ecology online.

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