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# Using niche construction theory to generate testable foraging hypotheses at Liang Bua

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## Abstract

Niche construction theory (NCT) has emerged as a promising theoretical tool for interpreting zooarchaeological material. However, its juxtaposition against more established frameworks like optimal foraging theory (OFT) has raised important criticism around the testability of NCT for interpreting hominin foraging behavior. Here, we present an optimization foraging model with NCT features designed to consider the destructive realities of the archaeological record after providing a brief review of OFT and NCT. Our model was designed to consider a foragers decision to exploit an environment given predation risk, mortality, and payoff ratios between different ecologies, like more-open or more-forested environments. We then discuss how the model can be used with zooarchaeological data for inferring environmental exploitation by a primitive hominin, *Homo floresiensis*, from the island of Flores in Southeast Asia. Our example demonstrates that NCT can be used in combination with OFT principles to generate testable foraging hypotheses suitable for zooarchaeological research.

KEYWORDS
archaeological theory, extended evolutionary synthesis, foraging theory, *Homo floresiensis*, optimal foraging theory, zooarchaeology

## 1 | INTRODUCTION

Understanding the evolutionary outcomes of hominin dietary and foraging behavior is central to paleoanthropological research.[1–4] Decades of zooarchaeological analyses suggests that ~2-3 million years ago our hominin ancestors began to rely on consuming fatty and calorically dense nutrients from hunting and/or scavenging big game using advanced cognitive, social, and technical abilities.[1,4–6] Theoretical frameworks such as middle range theory[7–9] and optimal foraging theory (OFT)[10–13] have refined our interpretations of hominin-butchery assemblages by guiding inferences for hominin foraging processes (accumulating food) from their static derivatives (cut marked bone). More recently, niche construction theory (NCT) has entered the literature as a promising theoretical tool for archaeology.[14–18] However, its juxtaposition against more established theoretical frameworks, such as OFT, highlights its difficulty in testing NCT in zooarchaeological contexts.[19] Here, we explore the literature surrounding the debate on the utility of OFT and NCT and provide an integrated optimization foraging model to generate foraging hypotheses for *H. floresiensis*, an extinct human relative from Liang Bua, Flores, Indonesia.

## 2 | OFT AND NCT WITHIN ZOOARCHAEOLOGY

Within archaeological scholarship, NCT is often critiqued against optimal foraging theory (OFT), which falls under the broader human behavioral ecology umbrella.[10,20] Critical reviews of and between OFT and NCT within archaeology are extensive[12,13,21–23] and often include statements of exclusivity, but their methodological toolkits overlap and both approaches offer benefits for interpreting hominin subsistence practices.[19,24] Nevertheless, the two approaches may be better suited for different kinds of inquiry, depending on the temporal and spatial resolution of an assemblage(s) (i.e., the degree to which material is attributable to specific actions in the past),[7] as well as the research goals of the investigator.[16,19,25] Specifically, OFT may be better suited for investigating short term adaptation whereas NCT emphasizes longer time-scales of co-evolution.[19]

## 2.1 | Optimal foraging theory (OFT)

OFT applies the concepts of optimization and evolutionary theory to the study of human behavior by generating formal predictive models of how organisms behave while searching for food,[11] and is frequently applied to zooarchaeological assemblages to interpret species representation, skeletal element abundances, and fragmentation patterns of accumulated vertebrate fauna.[10,12,13,20,26–28] This theoretical framework operates under several core assumptions, including: (a) behavior *while* foraging affects fitness; (b) foraging behavior is heritable (but not necessarily genetically fixed; this can include gene-by-environment interactions and learning); (c) relationships between foraging behavior and fitness is known; (d) the evolution of foraging behavior is unaffected by genetic constraints; (e) a foragers anatomical or technological features are known and "fixed"; and (f) foragers aim to maximize expected fitness.[22] While there are numerous predictive models available under OFT (e.g. diet breadth, prey choice, patch choice, marginal value theorem, etc.), the most commonly used in zooarchaeology are diet breadth models.[23,29,30]

Diet breadth models within zooarchaeology assume that foragers will preferentially collect higher ranked resources that yield greater net return rates compared to lower ranked ones as they are encountered within a homogenous landscape.[26] High net return rates can include a combination of low search and handling time for smaller returns (e.g., small prey items with a large and predictable distribution) or high search and handling times for large returns (e.g., large and risky prey items). The resulting combination of prey items that were of greatest profitability given environmental and behavioral contexts can be interpreted as diet breadth—fewer and higher *rank* types in the diet indicate resource abundance while greater and lower *rank* types indicates resource depletion.[30] This is assuming that a foragers goal was to maximize caloric intake—a goal that is frequently assumed in human OFT models in lieu of other foraging goals, such as balancing diet, taste preference, or social stigmas.[31,32] In doing so, many models have created a false notion that body-size based abundance indices reflects foraging efficiency—known as the body-size proxy.[33–36]

Testing hypotheses generated from OFT models comes with a unique set of challenges.[20] Because of the cumulative nature of the archaeological record and the indirect means of reconstructing paleoenvironments, parameters such as prey availability, abundance, heterogeneity, and distribution, are not always known[12,37] or cannot be represented accurately using modern analogs.[38] One way to overcome this challenge is to apply parameter values estimated from modern human foraging societies, such as search and handling times and energetic returns for individual prey items.[39,40] But even when such approximations are possible, the destructive nature of archaeological assemblages often fail to reliably reflect the culmination of foraging events, particularly for small animals.[41–43] In addressing these taphonomic realities, a more nuanced approach that utilizes a broader ecological framework may be better suited for interpreting hominin subsistence behaviors within a particular environment.

## 2.2 | Niche construction theory (NCT)

NCT places an emphasis on how organisms, through their actions and/or behavior, change their own selective environments and act as co-directors of evolution.[44–48] Actions such as environmental modification are expected to serve as an additional source of non-genetic inheritance for organisms that engage in niche constructive behaviors because they directly affect resource availability for themselves, other members of their species, and other conspecific organisms in their environment over generations ("ecological inheritance").[44] Any traits created through these processes are now considered evolutionarily significant under the Extended Evolutionary Synthesis (EES).[44,49] In this view, the environment does not merely "pose the problem" and organisms "posit solutions," but the decision to modify can be a cultural or behavioral response to an unsuitable habitat where selection then favors those that modify to survive.[45]

The evolutionary "success" of *Homo sapiens* has been dependent upon our species' ability to not only modify its environment, but to transfer knowledge from one generation to the next.[45,50,51] By accumulating culture through high-fidelity social learning and cooperation, humans are able to directly influence the selective environments of future generations.[45,52–56] For example, habitual fire-use opened a new dietary niche for Middle and Late Pleistocene hominins that left broad-scale effects on the environment as well as future generations.[24,57] Fire management also became an important social tool for fostering imaginative phenomena like story-telling, dancing, and singing, while also reinforcing cooperation and trust by conveying social networks and group identity.[54,58] Additionally, the development of stone tools opened a new niche for early hominins to exploit resources in an environment that might have otherwise been unavailable to them.[2] By simultaneously constructing, improving, maintaining, and teaching future generations how to use and develop stone artifacts, this early form of culture likely had a substantial impact on subsequent hominin evolution than natural selection alone.[44,45]

The main critique of NCT is its tautological approach to interpreting archaeological phenomena.[10,19] A theoretical tool is meant to provide a logical basis, or concept, that is supported through rigorous hypothesis-testing of observed phenomena.[20] For some, NCT fails to accomplish this and provides, instead, merely a post hoc explanatory approach for describing changes in human behavior.[19] Other proposed limitations of NCT are a matter of scale for measuring behavioral phenomenon, where NCT is more suitable for interpreting the effects of emergent phenomena across generations.[43] Regardless, any theoretical tool that is used to explain past human subsistence behavior is limited by the survival of material culture and the destruction from taphonomic processses.[27]

Stiner and Kuhn[19] originally argued that OFT and NCT can complement each other in interpreting archaeological phenomena: "Integrating research on niche construction in humans with testable individual (agent) decision models really can provide us with some of the tools we desperately need for understanding complex co-evolutionary processes." (182). We extend their argument by presenting an integrated decision-based foraging model designed with NCT concepts to generate testable hypotheses relevant for archaeological research.

Finally, animal body size has been central to discussions of OFT and NCT applications due to the emergence of small game exploitation in the Mediterranean Basin that defined the Broad-Spectrum Revolution.[21,35,46,59] In order to avoid body size proxy, we chose the Indonesian archaeological site of Liang Bua as an alternative location for discussing hominin diets where small and large game are each readily available. In addition, the stratigraphic resolution at Liang Bua is reasonably high, at which features from both OFT and NCT can be concomitantly applied.

## 3 | THEORETICAL APPLICATIONS AT LIANG BUA

Liang Bua is a Middle to Late Pleistocene and Holocene archaeological cave site located on the Indonesian island of Flores (Figure 1) and is better known as the discovery site of *Homo floresiensis*.[60–62] Skeletal evidence of this taxon (~100–60 ka) was recovered alongside four other animals larger than ~3 kg—Stegodon (*Stegodon florensis insularis*), giant marabou stork (*Leptoptilos robustus*), vulture (*Trigonoceps* sp.), and Komodo dragon (*Varanus komodoensis*) from deposits ranging from ~190–50 ka (Table 1).[68] Previous paleoecological reconstructions suggest that Liang Bua was exposed to more-open terrain from ~190–60 ka before shifting to more-closed environments at ~60 ka.[63,69] The abrupt disappearance of all five of these larger animals from the Liang Bua stratigraphic sequence, including *H. floresiensis*, at ~60 ka suggests a type of ecological relationship existed among these taxa (e.g., a sole herbivore surrounded by a scavenging guild) preferring the more-open savanna ecosystems.[63,70]

The most abundant animal at Liang Bua are murine rodents (rats), which comprise ~75% of the total faunal assemblage.[68] They are taxonomically and ecologically diverse, with at least eight endemic species (four extant, four extinct) ranging in average body size from ~50 g to ~2,500 g and specializing in either more-open or more-forested habitats (Table 1).[63,71,72]

The diet of *H. floresiensis* likely consisted of some combination of animal (vertebrates and invertebrates) and plant matter. On Flores, the only terrestrial mammalian prey available to *H. floresiensis* would have been *Stegodon* and rats.[63] *Stegodon* in particular would have been a significant source of fatty nutrients for *H. floresiensis*,[1] but the degree to which hominins were hunting individuals and/or scavenging carrion is still unknown. Either way, competition with scavenging birds and Komodo dragons in an open environment would have put *H. floresiensis* under greater predation risk than in a forested one (i.e., hunting rats). There are a number of scenarios that can be modeled given their encounter and success rates, the encounter rates of competing predators, their means of obtaining *Stegodon* meat (hunting and/or scavenging), and the order of access with other competing scavengers—but all of these values are unknown and/or unattainable. An alternative way to model the foraging behavior of *H. floresiensis* is to consider the basic types of environments available to them, the relative payoffs provided by each habitat type, and a means to estimate why (i.e., what form of niche construction) hominins would behave under these circumstances (Figure 2).

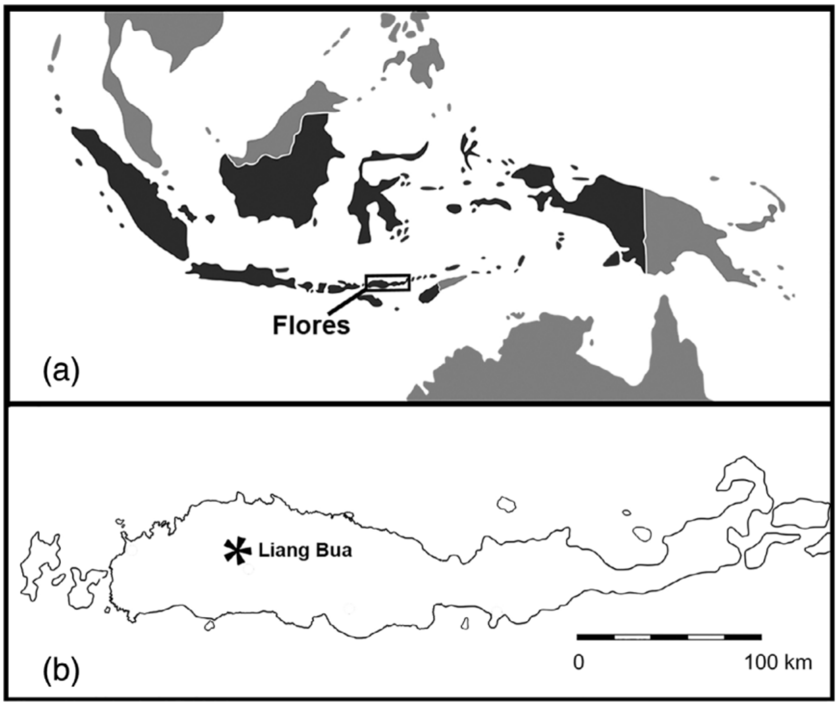

FIGURE 1 Map showing the location of Flores within Indonesia (A) and the location of Liang Bua on Flores (B). Image modified from Veatch et al. (2019)

TABLE 1 Summary of Liang Bua fauna by body size and habitat type

| Taxon | Classification | Body mass (g)[a] | Murine body Size[a] | Habitat type |
|---|---|---|---|---|
| *Papagomys armandvillei* | Murine | 1,200–2,500 | Giant | Closed |
| *Papagomys theodorverhoeveni* | Murine | 600–1,600 | Huge | Closed |
| *Spelaeomys florensis* | Murine | 600–1,600 | Huge | Closed |
| *Paulamys naso* | Murine | 100–200 | Medium | Closed |
| *Rattus hainaldi* | Murine | 40–100 | Small | Closed |
| *Hooijeromys nusatenggara* | Murine | 300–600 | Large | Open |
| *Komodomys rintjanus* | Murine | 100–200 | Medium | Open |
| *Stegodon florensis insularis* | Proboscidean | 569,000[b] | N/A | Open |
| *Leptoptilos robustus* | Stork | 16,000[c] | N/A | Open |
| *Trigonoceps* sp. | Vulture | 3,000[d] | N/A | Open |
| *Varanus komodoensis* | Varanid | 70,000[e] | N/A | Open |

[a] Murine body size estimates and categories summarized from Veatch et al.[63]
[b] Body size estimated from a regression based on limb bone length.[64]
[c] Body weight estimated from the tibiotarsus recovered from Liang Bua.[65]
[d] Body weight estimated from skeletal remains at Liang Bua.[66]
[e] Body weight averaged from living Komodo dragons on Flores.[67]

## 3.1 | Hominin NCT foraging model

Odling-Smee and colleagues[73] originally proposed two binary forms of niche construction resulting in four behavioral categories with relevance to archaeology (Table 2).[45] The first two categories are ways in which organisms change the selection pressures between themselves and the environment: *perturbation* and *relocation*. The former occurs when organisms physically change aspects of their currently inhabited environment, while the latter occurs when organisms choose to migrate to other locations exposing themselves and future generations to different environments. The other two forms of niche construction focus on whether organisms initiate (*inceptive*) or respond (*counteractive*) to a change in their environment.[24]

Counteractive relocation (moving to a different, presumably more suitable environment due to climate change) is one form of niche construction relevant to Liang Bua. Given the shifting availability of prey species from more-open to more-closed environments at ~60 ka, *H. floresiensis* would have either (a) migrated in response to changing foraging returns, or (b) remained in the region and adapted to a different environment. In OFT, the decision to leave an environment (or "patch") where returns diminish over time due to depletion by the forager is often represented using the Patch Choice Model (i.e., Charnov's Marginal Value Theorem).[74] In contrast, we are interested in (a) how tradeoffs between foraging returns and predation risk affected hominin behavior, and (b) how foragers respond to long-term (years or generations) exogenous change in the abundance of high-value prey species. Optimal foraging in this scenario may involve *counteractively relocating* to a more favorable environment, depending on the degree of both ecological change and mortality risk. Here, we present a model based on first-principles broad enough to apply data attainable for zooarchaeological research (i.e., omitting handling times, travel time, patch heterogeneity, predator encounter rates, etc.). We make the following modeling assumptions (Figure 2):

1. At each time $t$, foragers choose to exploit either an open or forest environment. Both types of environment are equally available and accessible.
2. The payoff from forest foraging, characterized by small- and giant-body sized murines, is a constant $x(\text{Forest}) = 1$ assuming the greater reproductive rates of murines (more $K$-selected) compared with *Stegodon* (more $r$-selected).
3. The payoff from open foraging, characterized by *Stegodon* and medium- to large-body sized murines is a variable $p$ (for example, $p = 2$ implies that the open environment has twice the payoff as the forest environment). The pay-off ratio between the two environments is constant when the open habitat is not depleted over time ($\delta = 1$).
4. After making their decision, foragers are subject to a stochastic survival event (N). $\mu$ is the background mortality rate, which is *extrinsic*, or independent of the foraging decision. $\mu$ can be estimated from comparative datasets (see Table 3). If the forager choses to exploit an open environment, they incur some additional mortality risk $\theta$ due to predation. Predation risk is a common feature in non-human OFT models but is often omitted when applied to humans.[82,83] $\theta$ and $\mu$ are additive.
5. Individuals that survive at the end of time $t$ repeat the decision problem indefinitely until their death.
6. Open environments may be subject to depletion over time (which is exogenous, i.e., not dependent on the foraging decision), as represented by the payoff modifier $0 < \delta \leq 1$. This can be thought of as over predation by other predators like Komodo Dragons that reduce the availability of *Stegodon* for hominins, or exogenous climate change. The payoff for open foraging thus varies with time: $x(\text{Open}, t) = p\delta^t$.

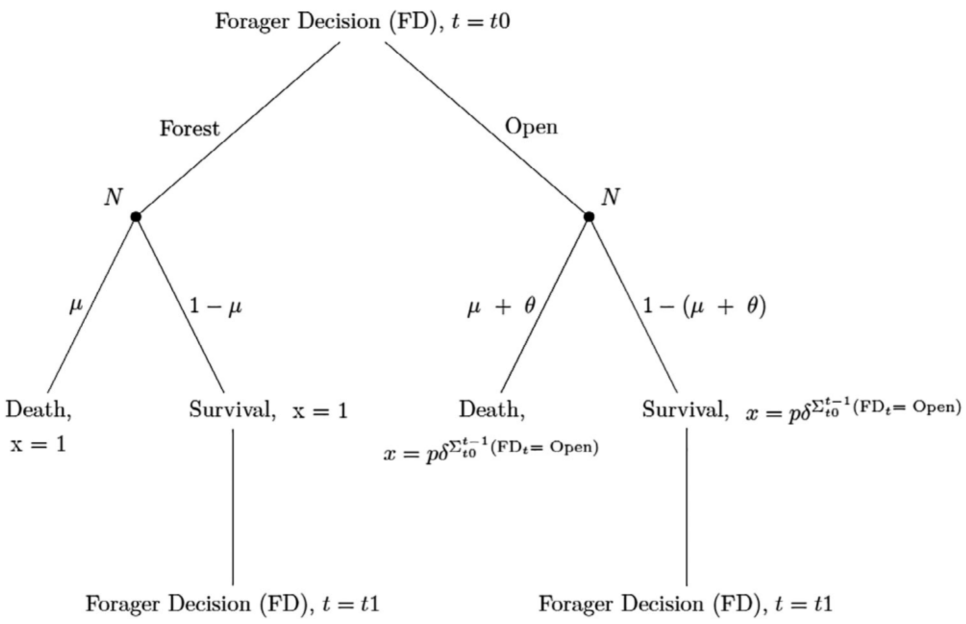

FIGURE 2 Decision tree representation of the foraging model. $t$ = start time. $N$ = stochastic survival event. $\mu$ = background mortality rate. $\theta$ = additional mortality rate incurred in open environments due to predation risk

TABLE 2 Categorization of niche constructing behaviors modified from Laland and O'Brien[45] and Odling-Smee and colleagues[73] with examples reflecting behaviors observed in the Paleolithic

| | Perturbation | Relocation |
|---|---|---|
| Inceptive | Organisms initiate a change in their selective environment by physically modifying their surroundings, for example, *stone tool production* | Organisms expose themselves to a novel selective environment by moving to or growing into a new place, for example, *invasion of new habitat* |
| Counteractive | Organisms counteract a prior change in the environment by physically modifying their surroundings, for example, *fire management* | Organisms respond to a change in the environment by moving to or growing into a more suitable place, for example, *migration due to climate change* |

The long-run expectations of forest and open foraging strategies are conditional on both resource value and mortality risk. Following the geometric distribution, expected time until death is:

$$E[t_{\mathrm{Death}} | \mathrm{FD} = \mathrm{Forest}] = \frac{1}{\mu}$$

$$E[t_{\mathrm{Death}} | \mathrm{FD} = \mathrm{Open}] = \frac{1}{\mu + \theta}$$

Now consider the pure strategy of exclusive forest foraging, $S_{\mathrm{Forest}}$: $\mathrm{FD}_t$ = Open for all $t$ in $[t_0, t_\infty]$. Because the payoff from forest foraging is always 1, $E[S_{\mathrm{Forest}}] = E[t_{\mathrm{Death}} | \mathrm{FD} = \mathrm{Forest}] \times 1 = 1/\mu$. The pure strategy of exclusive open foraging is defined as $S_{\mathrm{Open}}$: $\mathrm{FD}_t$ = Open for all $t$ in $[t0, t_\infty]$. Thus,

$$E[S_{\mathrm{Open}}] = p\frac{1 - \delta^{\frac{1}{\mu + \theta}}}{1 - \delta}$$

We calculated the conditions in which open foraging has a higher expected payoff than forest foraging, given different values of $\mu$ (background mortality rate) and $\delta$ (depletion rate of large prey), as visualized in Figure 3.

Thus far, we have only considered pure strategies (i.e., always forest or always open). When $\delta = 1$, the pure strategies are unimprovable by mixing between forest and open because the ratio of mortality to payoff is constant for all time steps. However, when $\delta < 1$, $S_{\mathrm{Open}}$ can be improved by adopting a more flexible strategy where the forager initially exploits in open environments and then switches at some time $t_\phi$ to forest—similar to the patch choice OFT model. Once again, in niche construction terms, this is an example of *counteractive relocation*. For $\delta < 1$, we can define this optimal switching threshold as the number of time periods to pursue open foraging before switching to exclusive forest foraging.

$$t_\phi = \log_\delta\left(\frac{\mu + \theta}{\mu p}\right)$$

$$\begin{aligned} S_{\text{Counteractive Relocation}} : FD_t &= \text{Open for all } t \text{ in } [t_0, t_\phi), FD_t \\ &= \text{Forest for all } t \text{ in } [t_\phi, t_\infty] \end{aligned}$$

Figure 4 illustrates the mechanics of the counteractive relocation strategy across different levels of open-habitat depletion ($\delta$), holding constant $p = 2$, $\mu = 0.02$, and $\theta = 0.01$.

TABLE 3 Description of model parameters

| Model parameter | Description | Empirical data sources | Citation example |
|---|---|---|---|
| *p* | Payoff ratio of open/forest foraging | Zooarchaeological and taphonomical data | Roberts et al.[75] |
| μ | Background mortality rate | Comparative analyses, that is, phylogenetic regression of primate adult mortality rate conditional on body size. | Bronikowski et al.[76–78] |
| θ | Predation rate in open patches | Comparative analyses of hunter-gatherer and/or primate predation rates given similar ecological contexts | Hill et al.[79–81] |

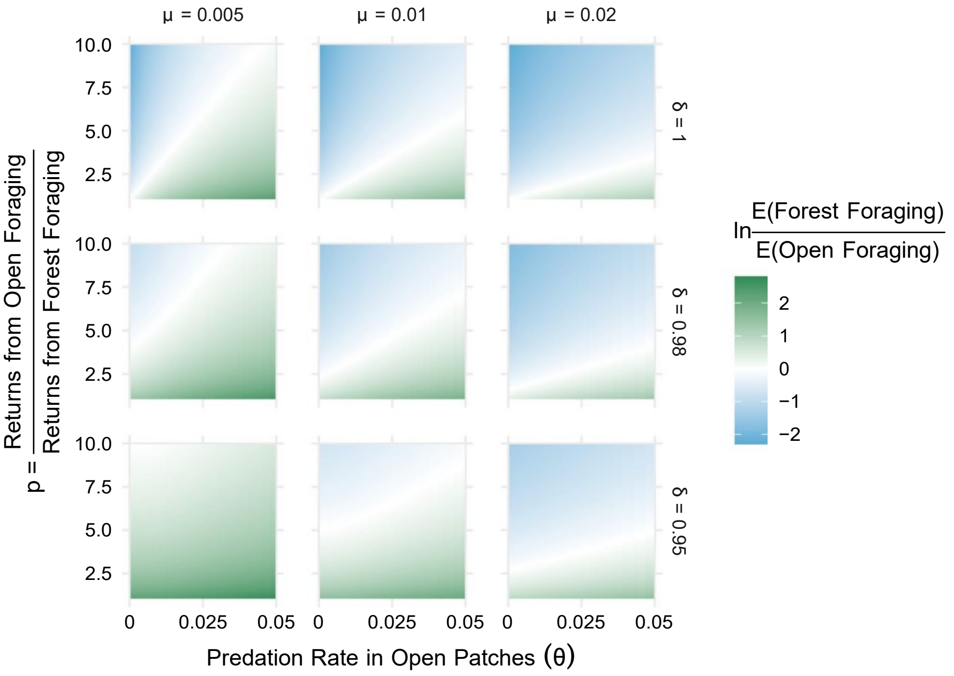

FIGURE 3 Model simulations showing proportion of mixed-habitat foraging (Natural log of $E[S_{\text{Forest}}]/E[S_{\text{Open}}]$) for given values of μ (background mortality rate), θ (additional mortality rate incurred in open environments due to predation risk), *p* (payoff for open foraging), and δ (diminishing return in open environments). Blue indicates open foraging favored and green indicates forest foraging favored

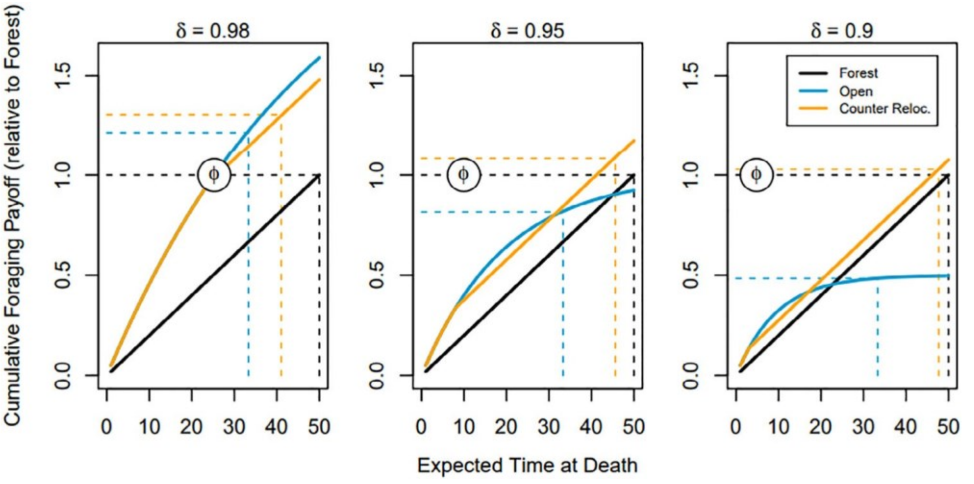

FIGURE 4 Foraging payoffs over time from pure open foraging $S_{\text{Open}}$ and counteractive relocation $S_{\text{Counteractive Relocation}}$, relative to the constant payoffs from forest foraging (represented by the solid black line). ;is the time when $S_{\text{Counteractive Relocation}}$ switches from open to forest environments. Vertical dashed lines denote expected time at death for each strategy, horizontal dashed lines represent expected payoff at time of death. We hold constant $p = 2$, $\mu = 0.02$, and $\theta = 0.01$

## 3.2 | Model results and discussion

Assuming technologies remain static (i.e., no fire-use, stone tool innovation, etc.) and given the composition of assemblages under different ecological scenarios, we can hypothesize how *H. floresiensis* will forage within their environment and why.

When open habitats are more abundant and predation risk is low, we expect assemblages to reflect a pure open habitat foraging strategy. For example (see Figure 3), foraging in an open environment is profitable when large game is abundant (δ = 1) and background mortality rates are highest (μ = 0.02). If large game becomes depleted (δ = 0.95), an open environment may still be a more suitable niche to exploit given the same mortality rate. Note that we interpret μ as annual mortality rate, 0.02 is typical for modern human foragers.[84,85] When mortality rate is high, foraging in an open environment maximizes payoffs even when under relatively high rates of predation. For a smaller-bodied hominin like *H. floresiensis*, background mortality rates may have been even higher, favoring more risky foraging strategies. Therefore, if *H. floresiensis* favors a more-open habitat foraging strategy (i.e., hunting predominantly *Stegodon* and open-habitat adapted murines), we could hypothesize (a) that competition with or risk of predation by Komodo dragons was low, and (b) background mortality rates were potentially high.

If background mortality rates are low, we expect assemblages to reflect a pure closed-habitat foraging strategy, regardless of open-habitat resource availability. According to our model, foraging in a forested environment is profitable when open environmental resources are low ($\delta = 0.95$) or unavailable, and background mortality rates are low ($\mu = 0.01$ and $0.005$). In this scenario, we can interpret that forested environments are a steady and reliable food source for a stable population of *H. floresiensis*. Therefore, if the archaeological record reflects a greater proportion of close-habitat foraging when more-open environments were available, we could interpret that *H. floresiensis* favored a low-risk foraging strategy.

If the ratio between open-habitat and forest-habitat resource availability changes, we expect assemblages to reflect a mixed-habitat foraging strategy. According to our model, this is more likely to occur when open habitat resources are depleted ($\delta = 0.95$ or lower) and the open habitats are only modestly more profitable than forest habitats. In other words, as open environments become unavailable (i.e., climate change and/or predator-driven prey depletion), we would predict *H. floresiensis* to follow the more-open environments (counteractive relocation) while also exploiting the more stable forested resources.

The model highlights the importance of understanding ecological factors impacting hominin behavior, such as predation risk and habitat depletion. Like all models, there is an innate simplicity to how these scenarios are generated with limitations in reflecting real life situations. The archaeological record, for example, will rarely show a "pure" foraging strategy, but these models help to better understand how hominins could react under certain circumstances, and why. While we focused on modeling counteractive relocation, other models containing perturbational niche construction could provide additional insight into the ecological conditions of hominin behaviors, especially for modern humans. Overall, modeling hominin foraging behaviors is an extremely complex endeavor and is unlikely to reflect every decision made, but there is still value in quantitatively interrogating our assumptions about the costs and benefits of different hominin foraging strategies over time.

## 4 | CONCLUDING REMARKS

It is imperative that theoretical frameworks provide a means for generating testable hypotheses. In contrast to the more frequently used agent based OFT models, NCT has been critiqued as being a post hoc explanatory tool, and thus, uninstructive for testing niche constructive behaviors in the past.[19] Here, we provided an example of an integrated NCT decision-based model for hominin resource exploitation suitable for archaeological research. We demonstrate how NCT and OFT principles can generate several foraging scenarios for *H. floresiensis* that can be directly tested using zooarchaeological data. By considering what ecologies are available to *H. floresiensis* we can thereby predict where individuals will forage while considering various rates of mortality, predation, and habitat depletion. While few applications of NCT involve non-modern human hominins, we hope to have provided a tool to explore these more simple forms of niche construction for more ancient hominins, and how we may attempt to uncover the complexity of hominin behavior.

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## DATA AVAILABILITY STATEMENT

The R code for generating the NCT foraging model is provided in the supplementary material.

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