# FURTHERING PERSPECTIVES

## Anthropological Views of the World

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**Editor's Note**

Dear Readers,

It is with great pleasure that I present to you the 13th volume of *Furthering Perspectives: Anthropological Views of the World*. *Furthering Perspectives* is a peer-reviewed, graduate student-run academic journal showcasing the diverse anthropological perspectives of Colorado State University anthropology and geography graduate and undergraduate students. In this volume, you will find articles that explore a wide range of topics, from the archaeology of entanglements between humans and material agents, to cultural conceptions of food and food insecurity, to evolution and the behaviors of our primate relatives. I extend my thanks to the authors who have entrusted us with their work, and the hardworking editors who contributed their time and energy to making this journal a reality. I hope that the articles in this issue of *Furthering Perspectives* will inspire, provoke thought, and stimulate further inquiry. I welcome your feedback and encourage you to engage with the ideas presented here.

- Thomas Chittenden



**Cover Picture**
Ouray Saloon Bottle
From "Imbibing Identity: A New Materialist Approach to Consumption and Identity in a Colorado Saloon" by Ben Shirey

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**Research Papers**

**Predator Type Alters Fear Response in Three Primate Taxa: Possible Adaptive Reasons**

Janie Christensen

**Abstract**

Predation is considered a powerful force of natural selection, though it is understudied and occasionally overlooked in primates. Though primates have many adaptations to combat predation, the most quintessential aspect of anti-predator behavior involves the sympatric nervous system and the fight, flight, and freeze response. In primates, this predator response is built upon to create complex social behaviors like mobbing and alarm calling. Although the fight/flight/freeze is highly conserved in all vertebrates, the degree to which each response is expressed and when it is triggered is evolutionarily malleable. Because different predators hunt with different strategies, it is likely that this response is adaptively tailored to both prey species and predator species. Understanding the predator's "perspective", its hunting strategies, learning, and energetics, is very important in understanding the adaptive nature of anti-predator responses. By observing strepsirrhines and small arboreal primates, including tarsiers and Callitrichidae, it appears that across the primate lineages, primates use freezing against visual predators like birds, but not against predators that use other senses, such as mammals and snakes. Mammal predators evoked much more varied responses, within and between primate species and for different predator species. Snakes, on the other hand, evoke an extremely consistent and intense response: mobbing. This is perhaps adaptive due to large-bodied constrictors being ambush predators that rely on stealth, and their infrequent need for food and makes them quick to give up a hunt. However, the mobbing response towards snakes potentially locks primates, including humans, in a maladaptive co-evolutionary arms race with venomous snakes, long after there is no longer a predator-prey relationship. Fear is both highly conserved evolutionarily and has a high non-genetic learned component, complicating the study of its evolution, but the consistent patterns in predator responses indicate that it is shaped by natural selection.

**Introduction**

Predation is a powerful selective force on primates, as in other animals. Primates have many adaptations to avoid predation, including group living, foraging and activity patterns, vigilance, sensory adaptations, and more (Hart 2005; Fichtel 2012). In this paper, I focus on the sympathetic nervous system and emotion-based behaviors that occur when in contact with a potential predator: the fight, flight, or freeze response.

In the past, psychologists described fear as behaviors that occur in anticipation of negative stimuli, ruled by conditioning (Pankstepp 1998). Later models emphasize that fear is an emotion, not just a subset of behaviors, and that the fear response has unique neurological underpinnings that are distinct from other behaviors or emotions. Pankstepp (1998) describes seven primary emotions in mammal behavior, which are highly conserved

across species and can be localized in the brain by electrical stimulation that incites a behavioral and physiological (e.g., hormonal) response. One of those is FEAR, and it is localized in the amygdala (like the other emotions, he stylistically capitalizes it to differentiate the neurological definition from common language). Pankstepp (1998) argues that a moderate triggering of the FEAR system (capitalized to specify a particular neurological definition of the word) leads to the freeze response, while a more extreme trigger leads to flight. He states that defensive aggression, or the "fight" response, is likely a combination of the FEAR and RAGE systems, and states that the RAGE system is often triggered by placing the animal in a situation where its movement and escape is inhibited, such as capture by a predator. Other researchers argue that differences in whether fight, flight, or freeze are triggered has to do with the ambiguity, distance, and escapability of the threat. Animals fight in the most discrete danger, flee with the most escapable danger, and fight or freeze in inescapable danger (Blanchard et al. 2001). However, the behaviors that help an animal escape a predator depend on the hunting behavior and niche of the predator; therefore, if the fear responses deviate from these predictions, there could be an adaptive reason.

Another framework for understanding fear behaviors is to consider it in the context of evolution, and the adaptive purposes of the fight, flight, and freeze response (Ohman 2001). Even though learning or conditioning can impact fear, animals are inherently more sensitive to stimuli that were dangerous in the evolutionary past and were advantageous for their ancestors to avoid (Barros 2002; Kuwai et al. 2020; Ohman, 2001; Thompson, 2020). This indicates an impact of natural selection on fear behavior.

The adaptive underpinnings for fight, flight, and freeze responses have been studied in both primates and other animals (see Figure 2 for a list of hypotheses and definitions). In primates and other social animals, a fourth response occurs as well- the alarm call. Flight is perhaps the most obvious in its adaptive purpose. It physically increases the distance from the predator and gets the prey animal to a protected place, and in more intense situations the prey animal will initiate flight at a farther distance from the predator (Stankowich and Blumstein 2005). Freezing prevents detection when an animal identifies a predator before the predator sees it, and it also seems to increase perception and identification of the threat (Lojowska et al. 2015). In primates, the fight response is mostly expressed as mobbing, which are aggressive displays done in a group, and may not involve physical fighting but is still certainly motivated by aggression (Crofoot 2012).

There are many hypotheses as to why mobbing occurs, which are not necessarily mutually exclusive. Mobbing is hypothesized to act as a predator deterrent (Zuberbühler et al. 1999) or even for cultural transmission of teaching young what predators to fear (Short 2019). It may cause confusion that makes it more difficult for a predator to hunt, enhance the selfish herd effect (where the individual prey animal benefits from a predator taking a neighbor instead of itself), force the predator to move to a new area, attract conspecifics for protection (attract the mightier hypothesis), alert other prey species of the predator's presence, and teach the predator to fear or avoid that primate species (Curio et al. 1978;

Crofoot 2012; Gursky 2005; Gursky 2006). Mobbing is well studied in birds and multiple hypotheses are supported in the literature. Curio et al. found that blackbirds mob for the purposes of cultural transmission: teaching young which predators to avoid (1978). When small birds mob kestrels, the kestrels move to a new area (Pettifor 1990). In some birds, mobbing may even be influenced by sexual selection: males show off to females through mobbing less dangerous predators, which could also be the case in primates (Crofoot 2012; de Cunha et al 2017). Mobbing can occur at any point in the predation sequence, from when the predator isn't actively hunting (Ferrari and Ferrari 1990), to rescue behavior, which is when a group mobs in aid of one individual that has been captured by a predator (Ebberle and Kappeler 2008; Gardner 2015; Teixeira et al. 2016). Ebberle and Kappeler (2008) focus on rescue behavior and argue that mobbing is costly to primates, so it is done to protect conspecifics out of kin selection.

The adaptive purposes of alarm calling is also highly debated, with many similar hypotheses as those proposed for mobbing. Some studies indicate that alarm calling is done to warn conspecifics as a form of kin selection, therefore, it can be detrimental to the caller (Sherman 1985). Other studies conclude that alarm calling is beneficial for the caller because it lets ambush predators know that they have been spotted, and is therefore not altruistic (Adams et al. 2018, Zuberbühler et al. 1999).

The type of predator matters in determining if a fear-based behavior is adaptive. In ground squirrel alarm calls, trills occurred more often for mammalian predators and whistles for avian predators (Sherman 1985). Additionally, trills seemed to be a product of kin selection as they were only expressed around relatives, and increased the chance of the caller being attacked. This supports the kin selection hypothesis because it was both detrimental to the caller and only used when relatives were nearby, not in service of non-related individuals. Whistles, however, seemed to protect the caller and were done with no relationship to surrounding conspecifics, supporting the predator deterrent hypothesis (Sherman 1985). This difference suggests that hawks, ambush predators, are deterred by the call, while terrestrial predators in the open areas where these ground squirrels live are not relying on stealth to hunt, and are, therefore, unaffected. In order for any fear responses to be adaptive, they should be effective against a particular predator's hunting style and sensory adaptations. I hypothesize that primates will use different fear-based predator responses (mobbing, flight, freezing, and alarm calling) for different predator types, for adaptive reasons. The link between predator type and primate behavior can be best understood by looking for behaviors that are universal across primate taxa.

**II. Behavioral Responses to Different Predators in Three Primate Taxa**

This paper focuses on the three most basal groups of primates: Strepsirrhines, tarsiers, and Platyrhinnes (Herlyn 2016). Strepsirrhines, which include lemurs, are the most basal group of primates, and early primate fossils resemble strepsirrhines. They are the sister group to the haplorrhines, which includes tarsiers, monkeys, and apes. Tarsiers are the least derived haplorhines, as the earliest haplorhine fossils resemble them. Platyrrhines (new world

monkeys) are the most basal branch of monkeys, sister group to catarrhines (old world monkeys and apes). These taxa are small and arboreal, resembling the ancestral condition of primates. Examining these taxa provides a wide diversity, providing a large sample size. See Table 1 for summary of anti-predator behavior by taxon.

**A. Tarsiers**

Tarsiers are small, nocturnal basal haplorhines from southeast Asia. Potential predators include snakes, birds, civets, and even monitor lizards. With experiments using model predators, it appears spectral tarsiers (*Tarsius spectrum*) do indeed vary their response depending on the type of predator, likely for adaptive reasons (Gursky 2003; 2005; 2006; 2007).

Though it may be surprising for their small size, spectral tarsiers are proficient mobbers. In an experimental presentation of model predators, the tarsiers mobbed birds (47% of encounters) and civets (13.6%), but not monitor lizards (Gursky 2007). Gursky (2007) suggests that mobbing is done for perception advertisement, so tarsiers mob ambush predators like snakes and falcons more than pursuit predators like civets and monitor lizards. Gursky (2005) reports that snakes are the most consistently and often mobbed predators, not only for primates, but for non-primate animals like chipmunks and ground squirrels. There is only one known observed event of successful snake predation on tarsiers, described by Gursky (2002): a reticulated python (*Malayopython reticulatus*) constricted a tarsier, and its family group responded by mobbing and alarm calling, while two neighboring groups also traveled to the vicinity and mobbed and alarm called at the snake. Tarsiers occasionally prey on snakes (Gursky 2003), but reticulated pythons are no primate snack: they can grow to 22 feet long and are the only snake known to habitually prey on humans (Headland and Greene, 2011). And while a tiny five-ounce spectral tarsier acting aggressively towards a giant snake that can successfully consume an adult male human may seem ludicrous, it can be effective considering snake biology. The main snake predators of tarsiers are large constrictors like reticulated pythons, which are ambush predators (Glaudas et al. 2019) so the snake will likely abandon the hunt and not attack when it doesn't have the advantage of surprise. Additionally, snakes are ectotherms (cold-blooded) and do not need to eat often, so there is less cost to giving up the hunt than for a bird or mammal. The snakes never attacked, and retreated 72% of the time, indicating little risk for the tarsiers from mobbing (Gursky 2005). This shows that mobbing is not about overpowering or fighting the predator, it is simply about becoming less attractive as prey and too energetically expensive to be worth hunting, as well as encouraging the snake to leave the area to prevent future encounters. This is supported by the fact that tarsiers mobbed models of large constrictors more often than models of non-constrictors. The same was true for natural snake encounters (Gursky 2024, email message personal communication). The author suggests this is possibly due to size (Gursky 2005), but tarsiers likely use other cues in determining if a snake should be mobbed. The snake models were easily available toy snakes, not accurate models of native species, and were based on a *Boa constrictor*, a New World coral snake (either *Micruroides*

or *Micurus* genus), and an Australian green tree snake, *Dendrelaphis punctulatus* (Gursky 2024, email message personal communication). The *Boa constrictor* model would have been similar in size and shape to a *Malaopython reticulatus,* the constrictor species described previously, which the tarsiers mobbed most often. The tarsiers may have interpreted the other two models either as venomous or as harmless types of snakes that rarely prey on them. The coral snake model would have shown aposematism in the form of brightly colored banding, which advertises its toxic nature, much like venomous kraits (genus *Bungarus*) that live in Sulawesi (Gursky 2024, email message personal communication). Perhaps tarsiers avoid mobbing venomous snakes that show aposematism to avoid deadly retaliation. Meanwhile, the green tree snake has a dark back and yellow belly, resembling the members of its genus (*Dendrelaphis*) that are native to Indonesia and rarely ever prey on mammals, making them non-dangerous to tarsiers (Magdua et al. 2021). As tarsiers sometimes prey on snakes, (Gursky 2005), perhaps they are better at distinguishing different types of snakes than other primates, helping them not to mob indiscriminately.

Spectral tarsiers also use alarm calling, and use different alarm calls for different predators (Gursky 2003; Gursky 2007). Alarm calling was their main defense against the wooden civet model, used 35 times compared to mobbing which was used only 10 times. Different calls for each predator suggest it is done for intraspecific communication. Also, mother tarsiers were more likely to respond to their young's calls if it was the correct match to the correct model predator, indicating it could perhaps be used to help young tarsiers learn what to fear and how to communicate sighting of a predator, supporting the cultural learning hypothesis (Gursky 2003). However, the nature of alarm calling differed depending on the predator: Alarm calling towards birds was always combined with mobbing, but for civets and monitor lizards, alarm calling was done independently of mobbing (Gursky 2007). This could be because it functions as calling conspecifics in birds but serves other purposes for civets and monitor lizards.

The freeze response appears to be used by tarsiers as well, but only against birds. In Gursky's 2007 experiment, tarsiers froze upon encountering bird models 53% of the time, and 0% of the time for other predators. By a small margin, it was the most used strategy against birds, followed by mobbing (47%). This supports the idea that fear response differs depending on the predator's sensory abilities and hunting style, as birds are visual predators. Although flight wasn't used as a category in Gursky's (2007) experiments, the author noted that tarsiers created distance from predators. They moved higher up in trees when in response to terrestrial predators and down in trees when encountering aerial predators. So although flight occurs in tarsiers, it is safe to say that the leaping mechanism in tarsiers does not appear to be the *main* predator defense, as predicted by some researchers like Terborgh and Janson (1986). Perhaps if encountered with a predator who is directly attacking, the tarsiers would flee.

**B. Strepsirrhines**

Goodman and Landgrand (1993) found that lemurs are preyed upon by mammalian, snake, and bird predators. Birds and mammalian predators appear to be the most serious threats, including Euplerids (fossa and its smaller relatives such as the ring-tailed mongoose), and nocturnal and diurnal raptors. As in tarsiers, constricting snakes are the primary serpentine predators, though some deaths have been recorded for venomous species.

Whether a lemur showed mobbing or fleeing behavior depends on the type of predator and species of lemur. In an experiment comparing captive red ruffed lemurs (*Varecia rubra*) with ring-tailed lemurs (*Lemur catta*), red ruffed lemurs showed more mobbing behavior than ring-tailed lemurs towards birds (Macedonia 1993). Ring-tailed lemurs mobbed perched birds but fled from flying birds. Red ruffed lemurs also mobbed both perched and flying birds, one individual even leaped up to attack a swooping flying bird model as it neared the ground. When it comes to mammalian predators, both lemur species were similar in their behavior in that they were likely to flee to trees, though they still mobbed smaller predators occasionally. Some red-ruffed lemur individuals remained on the ground and approached large mammalian carnivores. Yet in a higher intensity situation, when surprised with a mammalian predator jumping out from behind a screen, both species of lemurs always fled silently, then made mobbing vocalizations only when safely up a tree. These differences between species are likely due to size. Adult red ruffed lemurs are nearly 3 times the size of ring-tailed lemurs, so they are less threatened by avian predators and small mammalian predators. However, the threat posed to juveniles still necessitates a response. Lemurs likely only mob in situations where it is somewhat safe, which can also explain the differences between responses to birds and mammals. Adult red ruffed lemurs mobbed more intensely at birds because but were more likely to flee and kept their distance from large mammalian predators. This may have to do with the level of danger, as large mammalian predators like fossa (*Cryptoprocta ferox*) can prey upon adult red ruffed lemurs, unlike birds (Goodman and Landgrand 1993). Mobbing behavior towards snakes, however, remains consistent across species, regardless of size. Small gray mouse lemurs (*Microcebus murinus*) show more confrontational behavior towards snakes compared to other predators in general, as they tended to approach snake predator models more than models of mammals or birds: 12% of the time compared to 2% of the time for a fossa model and 0% of the time for a flying bird model (Rahlfs and Fichtel 2010). Much like tarsiers, the gray mouse lemur has been observed attempting to rescue caught conspecifics from snake predation by mobbing and biting the snake (Ebberle and Kappeler 2008). This was also observed in the much larger lemur, Coquerel's sifaka (*Propithecus coquerel*i), which not only was successful in freeing the caught primate but also led to the later death of the snake (Gardner et al. 2015). Much like the tarsiers, nearby lemurs came to the vicinity of the attacked conspecific upon hearing mobbing calls, supporting the attract the mightier hypothesis.

Mobbing and the fight response aren't just dependent on size, however, it also depends on parenting behavior. Mobbing correlates with parking behaviors, as both large red ruffed lemurs and tiny tarsiers park their young (leave them behind while traveling) and are similarly very likely to mob predators. Ring-tailed lemurs carry young on their backs and

would locate young and pick them up before fleeing, which was their primary response to both bird and mammal predators. Red ruffed lemurs, on the other hand, park young in trees before mobbing or approaching predators. Because they don't carry their young on their backs, fleeing would leave young vulnerable and is not a viable option. Red ruffed lemur matriarchs also showed a unique new behavior, which involved approaching large mammalian predators (dogs), and even physically attacking smaller ones (raccoons). After approaching, they retreated, trying to get the predator to chase them, to lead the predator away from the parked young. This behavior also occurs in birds (Macedonia 1993) and other animals (deer, coyotes) also may approach predators that come near parked young.

Rahlfs and Fichtel (2010) conducted an experiment with gray mouse lemurs and found that they froze 18% of the time for raptor predators and never for any and occurred for all subjects while it occurred only for one subject when presented with the control. The Pereira and Macedonia (1993) experiment did not describe freezing behavior, but the lemurs were on the ground when presented with the models, getting food left out by researchers, so that may have had an impact: if freezing is about crypsis, as would indicate if it is only used against sharp-eyed avian predators, it is likely only useful when the primate is in a tree with some cover.

Flight is a common strategy used by lemurs, though it differs by species and situation. Both red ruffed lemurs and ring-tailed lemurs fled when the slowly approaching mammalian predator increased in proximity and when it surprised them by jumping out from behind a screen. The ring-tailed lemurs also fled from a flying bird model, unlike red ruffed lemurs who again were not in as much danger and had to defend parked young (Pereira and Macedonia 1990). In this experiment, the lemurs began on the ground and fled to the trees, which is safer and has more cover. In the wild, sifakas will drop from the canopy when encountered with bird predators and climb higher to get away from terrestrial predators (Wright 1998). Flight in lemurs is therefore less about creating distance from the predator and more about reaching safer areas. The type of predator therefore impacts the direction of flight. Type of predator also matters for whether flight is used- lemurs only fled from mammals and soaring birds, not snakes and perched birds. Flight seems highly dependent on proximity to the predator, level of danger, and availability of safe places within flight distance.

Additionally, Lemurs show alarm call behavior, with different alarm calls for different predators and different stages of threat. Some calls act as alerts, and some that are highly coordinated and serve as mobbing after the lemurs have already fled (Macedonia 1993). Alarm calling also differed between species, as red ruffed lemurs called for much longer periods of time, particularly at mammalian predators. This persistent calling, up to forty minutes after the predator was no longer visible, was likely done to drive away the predator in order to protect parked young, as it would no longer be useful as warnings to conspecifics (Macedonia 1993).

**C. Platyrrhines**

Researchers have observed mobbing in Platyrrhines both in natural observations and experiments with predator models. In the wild, buffy-headed marmosets (*Callithrix flaviceps)* were observed mobbing a tayra (*Eira barbara)* until it descended the tree and fled. With snakes, their mobbing calls were quieter and behavior more intense, with the entire group coming down from the tree to emit soft mobbing calls, fleeing at any movements (usually not movements of the snake, but of other marmosets). Young marmosets were involved in mobbing snakes, but kept their distance for tayra, which only adults mobbed (Ferrari and Ferrari 1990). The authors (Ferrari and Ferrari 1990) suspect that this could be a cultural practice teaching young marmosets to fear snakes, and is probably lower risk than mobbing tayra, while mobbing for the tayra may be more practical and about preventing the predator from attacking at that moment. Mobbing the tayra also caused it to move to a new area. In the wild, red titi monkeys (*Plecturocebus cupreus*) were also observed mobbing ocelots, perched raptors, snakes, and tayra, but the titis would often leave before the predator, not successful in driving the predator to a new area, suggesting that this may not always be successful (Dolotovskaya et al. 2019). Also, much like tarsiers and lemurs, platyrrhines show rescue mobbing behavior when a snake has caught a conspecific (Teixeira et al. 2016). Unlike snakes, titi monkeys did not attempt rescue behavior when a juvenile was caught and eaten by a capuchin monkey (Sampaio and Ferrari 2005).

Alarm call behavior in other platyrrhines is also well documented. Titi monkeys (family Callicebinae) have specific alarm calls for different types of predators (Berthet 2022; Casar 2012). This suggests they may be used for communication with conspecifics to identify and warn of a predator. But it is also very clear that alarm calls serve a predator deterrent purpose as shown in one impressive experiment: Ocelots, an ambush predator, can distinguish titi monkey alarm calls from other calls, and will move away from potential prey upon hearing an alarm call (Adams and Kitchen 2018). Ferrari and Ferrari (1990) report that *Callithrix flaviceps* responded with low intensity (alarm calling that induced conspecifics to look up) to flying birds 1086 times, over 11 times per day, which didn't always induce fleeing, which happened 33 times per day. Calls directed at birds therefore occurred more often than calls towards other predators and were sometimes false alarms. The marmosets also made alarm calls at terrestrial predators, which were phonetically distinct and while they occurred less frequently (only 62 times), they produced more intense reactions, leading to some kind of anti-predator behavior 24% of the time compared to only 3% of the time as in birds (Ferrari and Ferrari 1990). Mammalian-directed calls were made by the whole group, not just the individual that sighted the predator, and were always associated with mobbing. Therefore, alarm calling in *Callithrix flaviceps* occurs often for birds and seems to have a purpose as a warning to conspecifics, while for terrestrial predators it was described as "piercing" in sound and for the purpose of driving away the predator. It is not clear if alarm calling has a deterrent function for birds, as Dolotovskaya et al. (2019) reported that a hawk attacked a titi monkey after it alarm called, though it was unsuccessful, and the hawk eventually gave up the hunt. Titi monkeys do not alarm call upon hearing vocalizations of capuchin monkeys (Dolotovskaya et al. 2019), even though they will alarm call upon

hearing raptor vocalizations (Berthet 2022). This is similar to how Old-World monkeys do not alarm call as much when hunted by chimpanzees in comparison to leopards (Zuberbühler et al. 1999) and could be because primate predators use sound to locate their prey.

Freezing, hiding, and fleeing were also observed often in wild platyrrhines. Much like other primates, freezing was only observed in response to birds in wild Buffy-headed marmosets (*Callitrix flaviceps*) and was used in addition to hiding and fleeing by dropping out of trees (Ferrari and Ferrari 1990). For wild Titi monkeys (*Plecturocebus cupreus)* observed by Dolotovskaya et al. (2019), the monkeys mobbed and drove away a tayra early in the day that was in a nearby tree. When encountering the same tayra hours later in the same tree they were in, they fled and alarm called rather than moved towards the tayra as they had done earlier, possibly as a result of being more surprised or the tayra, in this case, being actively hunting rather than resting in the nearby tree. Like the lemurs, whether they approached or fled from a mammalian predator seemed to depend on its distance away when they noticed it and the predator's behavior. Fleeing and hiding was the main defense titi monkeys used against capuchin monkeys (Dolotovskaya et al. 2019), but for other predators, it was used in addition to mobbing and alarm calling.

## III. Discussion

### A. Birds

In all primate taxa, freezing was exclusively used against birds. Birds are highly visual predators, and mammalian and snake predators depend more on smell and hearing/vibrations. Birds have incredible vision, and Jones et al. (2007) describe how birds are more reliant on vision than most other animals, especially diurnal birds of prey. They see both fast and slow movements well, and birds of prey have the highest behavioral acuity (ability to demonstrate detail in vision) among all animals tested. Therefore, freezing is done to visually avoid detection. Across taxa, primates seem inclined to mob perched birds but freeze or flee from soaring birds. Macedonia (1993) suspected this was because birds that are perched are not actively hunting. This is true for some species of birds but not others- some birds perch and wait for unsuspecting prey to come by others hunt on the wing (Jasic and Carothers 1985). Birds are also very flexible when it comes to if they hunt by stealth or persistence. Harpy eagles, which prey on large platyrrhines, prefer to hunt without stealth, and will perch nearby and emit calls to test the defenses of a group of primates with persistence, but if they are unsuccessful, they will move on to another troop and hunt by ambush (Gil-da-Costa 2007). This is likely what was occurring in an observation by Dolotovskaya et al. (2019) when a perched bird attempted to predate on a titi monkey who was alarm-calling. The bird wasn't successful and moved on after more members of the group began to call and its target moved to a protected area. Primates probably mob perched birds but flee from flying birds because primates have the advantage in trees and can clearly see the extent of the threat, while a flying bird is more unpredictable, difficult to identify, and has the advantage of faster movement. For flying birds, which may ram into prey and

stun them with the impact, fighting is likely not a helpful strategy unless the primate is too big to be predated upon by a bird, and is defending its young (Pereira and Macedonia 1990). Fleeing is likely helpful when primates can drop through trees to be inaccessible to birds, and freezing is likely helpful when the primate is already in a protected space. Birds were the only type of predator to warrant the use of all four responses, even in the same species of primate, indicating they require intense flexibility and ability to discriminate. Taken together, all of this indicates that bird predators require different fear responses than other predators, but they still must be adaptable to the specific situation.

**B. Mammals**

Whether primates mobbed or fled from a mammalian predator depends on the situation. The same predator can elicit different responses in the same group of primates, such as the titi monkeys fleeing when they noticed a tayra in the same tree as them but mobbing it when it was in a different tree (Dolotovskaya et al. 2019). Mobbing occasionally caused the predator to leave. This indicates fleeing is probably a last resort for mammalian predators, done when the primates are convinced the predator is in active pursuit or has successfully ambushed them. Mobbing, on the other hand, occurred often for predators that were not actively hunting, and for smaller predators that pose less danger. This supports the idea that the fight-flight-freeze response is dependent on different levels of danger, but it is different than what is predicted by Blanchard et al. (2001) who suggested that fleeing should occur first, and fighting only as a last resort. Mobbing is done in low-stakes situations, and fleeing in intense ones. In cases where a mammalian predator is not yet actively hunting, fleeing is a poor strategy as it may cause the predator to give chase, as most mammalian predators are attracted to movement, just as a dog chases a ball or a cat attacks a string. Standing one's ground, such as by mobbing, is the best defense against a mammal that is not in pursuit yet, but fleeing is best once the situation intensifies.

Alarm calling was a very common response against mammalian predators, occurring in all cases except in the caged mouse lemurs in the Rahlfs and Fitchtel (2010) experiment, but it is likely done for multiple purposes. In Ferrari and Ferrari (1990), marmosets alarm call at tayra as a part of mobbing. Other times, it seems to be about warning conspecifics, as the alarm call contains information about the predator (Berthet 2022; Gursky 2007). For mammals that are ambush predators, like cats, it can serve as a deterrent. Adams and Kitchen (2018) followed ocelots and found that they moved towards general titi monkey calls, but away from titi monkey alarm calls, indicating that they lose interest in hunting: clear support for a predator deterrent function of alarm calls. The hypothesis that alarm calling and mobbing teaches young to fear the predator also seems unlikely, as captive predator naive marmosets had a stronger instinctual recognition and fear of oncilla than bird and snake models (Barros et al. 2002), and young kept their distance from mobbing events of tayra, unlike snakes (Ferrari and Ferrari 1990).

The specific type of mammalian predator matters, but more research is needed as to why. Alarm calling and mobbing occurred for Carnivora, but primate predators only

produced fleeing, even if the predatory primate wasn't actively hunting (Dolotovskaya et al. 2019). Zuberbuhler et al. (1999) suggested that primates tend to be persistence predators that don't rely on stealth, and so are less affected by alarm calls. However, civets and tayra are also persistence predators (Galef et al. 1973; Gursky 2007) and are deterred by mobbing and alarm calling, so something else must separate carnivores from primate predators. Perhaps mammalian predators find noisy primate vocalizations to be noxious, or they disrupt their ability to hunt other prey in the area, but primate predators like capuchins and chimpanzees are undeterred.

Hunting behavior and the choices predators make is a very understudied field, especially for small Carnivora living in tropical forests that prey on primates. Even though mammalian predators can be a leading cause of death in a group of primates, primatologists may observe them for years and never see the predation event in progress because fossa, civets, and other small carnivores tend to avoid humans and hunt at night (Gursky 2007; Wright 1998). To better understand the predator-prey relationship between primates and their mammalian predators, more research should be done about the way predators hunt and respond to anti-predator tactics, as only this way can any adaptive reasons for anti-predator behavior be determined.

**C. Snakes**

By far, the most consistent anti-predator behaviors across primate taxa are in response to snakes. It is almost entirely mobbing behavior and alarm calls, and primates across taxa were dramatically more likely to confront and approach snakes than avoid them. This is perhaps the most fascinating finding of this paper, especially because it seems to be maladaptive in the larger and more derived primates, including humans. Also, this behavior seems to have in turn influenced snake evolution.

Small arboreal primates appear to be preyed on primarily by large-bodied constrictors in the Boidae or Pythonidae families, though some reports of venomous snake attacks can be found (Dolotovskaya et al. 2019; Ebberle and Kappeler 2008; Garder et al. 2015; Goodman and Landgrand 1993; Gursky 2003; Gursky 2005; Teixeira et al. 2016). These constrictors are sit-and-wait, or ambush predators, that conserve energy, do not eat often (as little as once every few months) and take a wide variety of prey that comes within striking distance (Glaudas et al. 2019). Coiled snakes waiting for prey strike about half their body length, and so the best strategy to avoid snake predation is to detect them, which has influenced primate evolution so that many primates, including humans, are born adept at visually detecting snakes more so than detecting other objects (Jacky 2022; Kawai and Qiu 2020). Considering the numerous successful rescues described in this paper, it seems that mobbing for rescue purposes is a low-cost and high-reward cooperative behavior when employed against snakes. Because snakes, being ectothermic, generally attempt to conserve energy and do not need to eat often, they can probably afford to not hunt when encountering a primate more so than a bird or mammal predator can. Due to a lack of limbs, their only weapon is their jaws, which are engaged with the potential prey during the rescue behavior,

so they can't easily hurt the rescuers, and they can't flee without spitting out the prey. This may explain why rescue behavior occurs for snakes but not for other predators as in Sampaio and Ferrari (2005). Nonetheless, this snake rescue behavior is a remarkable example of cooperation that occurs even in solitary foraging, less social primates. Mobbing when a snake has not yet attacked any primates may likewise be adaptive by driving the snake to a new area, teaching it to avoid primates, or discouraging any subsequent attacks, much like for mammalian ambush predators. Snakes can learn what prey is dangerous (Phillips and Shine 2006), so an individual snake that experiences unpleasant mobbing is unlikely to attack that species of primate in the future. When Gardener et al. (2015) described one of these rescues, the rescued sifaka, though scarred from the snake bite, survived, and gave birth to an infant several months later, while the snake died of a broken mandible several weeks later. This goes to demonstrate the intense selective pressure predation puts upon both the prey and the predator.

Mobbing snakes is complicated due to the impacts of cultural learning. A mild fear of snakes appears to be innate, as young tarsiers alarm call at them soon after they're born (Gursky 2005) and human babies exhibit pupil dilation when looking at pictures of snakes (Hoehl et al. 2017). But while fear of snakes is innate or at least more easily conditioned than for other objects, actual mobbing behavior has a learned or cultural component. It doesn't occur in captive-born predator-naive marmosets or other primates such as Vervet monkeys (Cagni et al. 2011; Fitchel 2012). This has strange implications. Mobbing appears in *all* primate taxa studied, very consistently, which most would assume is genetically ingrained through evolution as a result of natural selection. And yet, it is (at least in part), a learned behavior. This is very unusual, as learned behaviors are usually not thought of as being long-lasting or conserved. If snake mobbing is truly a product of social learning, it is perhaps the oldest cultural practice, stemming from the very first primates and persisting into humans today, after being passed from parent to offspring and within social groups for millions of years.

Furthermore, one of the more fascinating aspects of snake mobbing behavior, especially when compared to other predators, is that it is often *maladaptive*. Many venomous snakes will bite in self-defense. This is why differing behavior based on the type of snake due to learning may be important. Only one rare snake, the reticulated python, can regularly consume humans, and even so, it is very rare, and yet fear and aggression towards snakes persists in our species. In the U.S., many people erroneously believe that "the only good snake is a dead snake" and will actively go out of their way to kill not only venomous snakes, but also the many snakes that are mistaken for them. Many rural communities host rattlesnake killing contests, stating that it will protect people, but in reality, is a sensationalist sport killing activity (Cummins 2021). Meanwhile, in Arizona, researchers state that more than half of rattlesnake bites would have been avoided if the person had simply moved away from the snake upon encountering it (Curry et al. 1989). Clearly, the desire to approach and engage snakes is rooted in fear and aggression, much like mobbing behavior in primates. It is an evolutionary anachronism that persists in humans past its usefulness.

So much has this persisted in the hominin lineage that it has influenced snake evolution (Mueller 2023). Spitting cobras have venom that has specifically evolved to cause intense pain and not to kill, much different than most venom in snakes meant to incapacitate their small prey. It can be deployed at a distance, as a defensive maneuver, and this type of venom's evolution is dated to 6 million years ago, when the hominin lineage split from other apes, and in Asia, 2 million years ago, when hominins arrived, both because snakes were being killed at such high rates by weapon-wielding hominins. By being defensive at a distance, the snakes could avoid being killed by hominin mobbing with weapons, and by being non-lethal, avoiding the spitting snakes could become a cultural practice spread by communication. The evolution of snakes and primates is intertwined in fascinating and surprising ways. In the recent past and present, humans and our ancestors could have avoided many issues simply by leaving snakes alone, but our ancestral tendency to mob has inhibited this. For the safety of ourselves and the welfare of the other animals we share the Earth with, it is important to study ancestral anti-predator behavior in primates.

**IV. Conclusion:**

All primates studied varied their response to predators based on predator species, likely for adaptive reasons, but also due to previous adaptations that are now maladaptive. And across the primate taxa, due to either convergence or conserved ancestral states, there are similarities to primate's reactions based on the type of predator. Freezing was only found in reactions to birds, and no other predator types. Mobbing was the main strategy found for snakes, done with particular intensity, and possibly related to cultural learning. All other strategies seem to be found in some situations for mammalian and bird taxa, but how and when they were used varied by predator type. There wasn't just one response to one predator type: it varied depending on factors such as infant care behavior, intensity of the threat, and many other factors. It is the flexibility of responses that perhaps is most important to primates' survival. To fully understand if any of these responses are adaptive and how future research should focus on examining these strategies from the predator's point of view. Primatologists must work with zoologists to truly understand predation on primates. Studying predation on primates not only informs us about the delicate co-evolution between primates and their predators but can inform us about human behavior.

**Appendix.**

Figure 1.

| | Birds | Snakes | Mammals |
|---|---|---|---|
| Tarsiers | Freeze for flying birds, mob perched birds, alarm call | Mobbing, alarm calling | Mob, flee, alarm call. Alarm used most against civet |

| | | | |
|---|---|---|---|
| Lemurs | Freeze for flying birds, mob perched birds, Alarm call, Fleeing only n species where young carried on back. Mobbing only in species where young are parked. | Mobbing, alarm calling | Mob, flee, alarm call. Flight used most against domestic dog. Will flee if surprised. Mobbing only n species where young are parked. |
| Platyrrhines | Freezing, fleeing, and mobbing | Mobbing | Mob, flee, alarm call Mobbing used most against tayra. Alarm call discourages ocelot attacks. Will flee if surprised |

Figure 2. List of hypotheses about how fear response behavior is adaptive.

| Hypothesis | Behavior Type | Definition | Defining Literature |
|---|---|---|---|
| Distance/Protection | Flight | Fleeing increases distance from the predator or gets the animal to a hiding place, allowing escape. Depends on threat level and starting distance to the predator | Stankowich and Blumstein 2005 |
| Crypsis | Freeze | Freezing prevents the predator from visually detecting the prey animal's movement | Lojowska et al. 2015 |

| | | | |
|---|---|---|---|
| Perception of threat | Freeze | Freezing helps the prey identify the threat and assess the situation before acting | Lojowska et al. 2015 |
| Conspecific Communication | Alarm calling | Alarm calls are used to warn group members of a predator, often including information about what type of predator and where. | Sherman 1985; Berthet 2022 |
| Predator Deterrent | Mobbing (fight), alarm calling | Mobbing or alarm calling advertises to the predator that the prey animal is not suitable or easy prey. | Crofoot 2012; Zuberbühler et al, 1999 |
| Perception advertisement | Mobbing (fight), alarm calling | A type of predator deterrent in which the prey animal indicates to an ambush predator that it has been spotted and lost the element of surprise. | Sherman 1985; Zuberbühler et al, 1999 |
| Selfish Herd Effect | Mobbing | An individual benefits from the predator having other potential targets within its social group | Crofoot 2012; Curio et al. 1978 |
| Cultural learning/transmission | Mobbing, alarm calling | Young prey animals learn which predators to fear by watching adults mob. | Crofoot, 2012; Short, 2019 |

| | | | |
|---|---|---|---|
| Move on hypothesis | Mobbing | By being noxious to the predator, the prey forces it to move on to a new area. | Crofoot 2012; Pettifor 1990 |
| Display to conspecifics/sexual selection | Mobbing | Mobbing demonstrates fitness to potential sexual or coalition partners | Crofoot, 2012; de Cunha et al, 2017 |
| Predator learning | Mobbing | The predator learns that this prey item is too dangerous or not worth the effort, and avoids them in the future. | Crofoot et al, 2012 |
| Attract the mightier hypothesis | Mobbing | Mobbing attracts stronger conspecifics in greater numbers to aid in defending against a predator. | Crofoot et al, 2012; Gursky 2006 |

Fig 3. Ethogram/Glossary

| | |
|---|---|
| Parking | Leaving an infant behind while the mother forages, as opposed to carrying it. |
| Kin selection | Any behavior that is altruistic that aids related individuals. |
| Altruism | Any behavior that aids others but harms the actor. |
| Mobbing | Moving towards a predator in a group while exhibiting behavior that is considered aggressive for that primate species, including vocalizations, posture, facial expressions, biting, hitting, or mock charges. Considered part of the **fight response** in this paper. |
| Rescue behavior | Mobbing that occurs when a conspecific is caught by a predator |
| Crypsis | Avoiding detection by a predator, often through staying motionless (**freeze response)**. |
| Flight/fleeing | Behaviors such as running or moving away that increase distance between the predator and the actor |

| | |
|---|---|
| Alarm calling | Vocalizations that occur immediately on sight of a predator. |

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# Conceptualizing Food Security on the Pine Ridge Reservation

Cameron Kacsh

**Abstract**

Food insecurity is an enduring issue on the Pine Ridge Reservation, tracing its roots to the establishment of the reservation in 1868. Early federal food assistance programs consisted of low-quality and culturally inappropriate foods that created intergenerational health issues. While the implementation of the Federal Distribution on Indian Reservations (FDPIR) in the late 1970s has improved the quality and quantity of federal food assistance, it has not made a long-term impact on food insecurity. Using a political economy approach that integrates quantitative data with historical and cultural context, this paper advocates for a nuanced approach that aligns health and nutrition with cultural integrity and resilience to create a more effective and sustainable framework for alleviating food insecurity on the Pine Ridge Reservation.

## Introduction

The Pine Ridge Reservation is a poignant example of Indigenous resilience in North America and a reminder of the complex challenges many Indigenous communities face. Situated between Badlands National Park in southwest South Dakota and the Nebraska state line, the reservation's landscape is largely open prairie dissected by the White River, with dry badlands in the north and scattered coniferous forests and sandhills in the south (Raymond et al. 1976). It is home to the Oglala Sioux Tribe, a Nation with about 47,000 enrolled members, of whom fewer than half are estimated to live on the reservation (Bureau of Indian Affairs 2023; U.S. Census Bureau 2017). Since its establishment, Pine Ridge has been plagued by a disproportionally high prevalence of food insecurity compared to the general U.S. population, making it one of the most pressing issues on the reservation.

The United States Department of Agriculture (USDA) defines food insecurity as “the limited or uncertain availability of nutritionally adequate and safe foods, or limited or uncertain ability to acquire acceptable foods in socially acceptable ways” (2023). The USDA currently uses six indicators to assess household-level food insecurity: anxiety about running out of food or money to buy food, running out of food and not being able to buy more, perceptions of a poor-quality diet, and reduced food intake or experiences of hunger in adults or children. Coping behaviors, non-economic sources of food insecurity, and other phenomena associated with food insecurity are not represented in data gathered by the USDA (Bickel et al., 2000).

There have been many different types of efforts to establish food security on Pine Ridge throughout its history; the Federal Distribution Program on Indian Reservations (FDPIR) is the most recent federal assistance program designed specifically to address the needs of low-income households living on or near reservations (Pindus et al. 2016). The program supports food-insecure households by providing monthly boxes of USDA-approved

supplementary food to enrolled households, picked up by participating individuals at local distribution centers or delivered directly to homes (U.S. Federal Government n.d.). These boxes often include educational pamphlets, books, and worksheets that provide nutrition and health information (U.S. Federal Government n.d.). The program has significantly improved the quantity and quality of food provided by the federal government to reservations, but, as this paper will demonstrate, it is held back by differences in how federal and Tribal definitions conceptualize food security. While the USDA measures food security by adequate access to enough quality fruit, vegetables, grains, dairy, and protein to ensure a healthy lifestyle, based primarily on caloric value, this paper problematizes the metrics used to assess food insecurity (Food and Nutrition Service 2020). The Pine Ridge Reservation as a case study establishes the importance of an integrated approach to address food insecurity, which is not merely a matter of providing access to food but careful consideration of the broader social, cultural, economic, and environmental factors that shape a community's relationship with food.

**Acknowledgment**
As a non-Indigenous author, I recognize the importance of acknowledging the limitations of my positionality. Due to the intersecting factors that contribute to food insecurity, it is an issue that benefits from interdisciplinary and intercultural collaboration. However, my understanding of this topic is shaped by my background as a European-American, and I am accountable for any potential biases associated with my lived experience. These acknowledgments are not yet standard in the academic field, but anthropology has historically contributed to the dispossession, exploitation, and stereotyping of Indigenous people (Deloria 1988). To address this historical power imbalance, I have drawn upon scholarship from Indigenous authors from within the federal government, within Tribal governments, and within academia to inform my conclusions and portray the complexities of food insecurity with humility and respect for the sovereignty of the Oglala Lakota people.

**Terminology**
The choice of terminology can be complex and politicized. The Oglala Sioux Tribe is the official name of the Tribal government, and how the Tribe has been historically recognized in diplomatic relations with the United States. FDPIR exists because of treaty obligations the United States has with the Oglala Sioux Tribe, among many others, which recognize Tribal governments as sovereign nations. Given this context, I have chosen to use *Oglala Sioux* when referring to the Tribe as a political entity. *Sioux* has historically been used to refer to the Oceti Ŝakowin, or Seven Council Fires, both collective terms for the Lakota, Dakota, and Nakota peoples, who are connected by language and kinship, with the Oglala being one of the seven divisions of the Lakota. (Flute 2022; Hämäläinen 2019; South Dakota Office of Indian Education 2018). However, while still commonly used, the word *Sioux* is considered an offensive term derived from the Ojibwe word for *snake* by many contemporary people who belong to these three groups (Hämäläinen 2019). For this reason, I have used *Oglala*

*Lakota* and *Lakota* in all other contexts, as this is the preferred language of the Tribe (Oglala Lakota College 2024). Similarly, *buffalo* and *bison* are often used interchangeably to refer to the same animal, but *buffalo* is the term used by Indigenous peoples in North America with specific cultural significance and implications attached to this word (Schneider 2023). Finally, the word *Indigenous* is used globally, but here I use it to refer specifically to the Indigenous peoples of North America. The term is deliberately capitalized to affirm Indigenous sovereignty and legitimacy (Younging 2018). Out of respect for Indigenous peoples, and specifically the Oglala Lakota, I am careful to use precise terminology attributed to them as original knowledge creators on these subjects.

**Methods**

This paper involves a comprehensive literature review and an analysis of food insecurity data from the non-profit organization Feeding America to disaggregate food insecurity levels by county (including counties within the reservation) and state compared to national datasets. Compared to other federal food assistance programs, the amount of substantial literature on the Federal Distribution Program on Indian Reservations is noticeably lacking. As representation of Indigenous people in state and federal government agencies has improved in the last few decades, it is reasonable to expect that this gap in literature will shrink in the future. There is a need for research on a localized level, as much of the existing literature on FDPIR does not explore the unique challenges and needs of individual communities. Acknowledging the diversity of Indigenous experiences within the context of these greater issues is essential to better serve communities. The experiences of the Oglala Lakota do not represent all Indigenous peoples in the United States, and Indigenous people who live on reservations also face different challenges than those who live outside reservations. Nevertheless, the Pine Ridge Reservation offers a valuable case study for understanding how approaches to addressing the basic needs of Indigenous communities can be contextualized and improved upon. It is necessary for these needs to be addressed on a culturally specific and localized scale that acknowledges the variety of experiences across Nations, reservations, and households. There is no one-size-fits-all model to create food security, and differences in needs impact the effectiveness of food assistance programs. Therefore, the conclusions drawn in this paper should not be taken alone but instead used within more expansive and inclusive work on the subject.

In this paper, I use a political economy framework that primarily draws upon the ideas of anthropologist Eric Wolf. In *Europe and the People Without History* (2010), Wolf emphasizes the need to understand Indigenous societies as part of an interconnected system of global processes, economics, and power relations. All societies are shaped by social, economic, and political forces on a local and global scale, and these factors influence the cultural experiences of people living in these societies; political economy is the theoretical framework that examines how these intersecting forces shape societies and the production, distribution, and consumption of resources (Wolf 2010).

**Background on the Oglala Lakota and the Pine Ridge Reservation**

Historically the most mobile of the Oceti Ŝakowin, the Oglala Lakota consider the Great Lakes region, the Great Plains, and the Black Hills their ancestral homelands (Robertson 2002; South Dakota Office of Indian Education 2018). Bands, typically consisting of about 20 households, formed permanent groups that moved together throughout the year, maintaining a defined homeland while being highly mobile and flexible (Hämäläinen 2019). This allowed them to freely move between other Oceti Ŝakowin groups for trade, communal living, and occasional conflict (Hämäläinen 2019). The shared cultural traditions of the Oceti Ŝakowin, as well as the vast territory that covered diverse ecosystems and abundant resources, ensured that the Oglala Lakota could move to meet their needs while always being among kin (Hämäläinen 2019; South Dakota Office of Indian Education 2018). During the warm months, migrating schools of fish, wild grains like oats and rice, fruits, nuts, and tubers ensured that food was plentiful (Hämäläinen 2019). The abundance of deer, elk, and waterfowl around the Great Lakes, as well as large buffalo herds on the Plains, offered ample hunting opportunities (Hämäläinen 2019). In winter, the Lakota followed the buffalo into the Black Hills, where they lived comfortably through the cold months (Hämäläinen 2019). Small-scale corn farming supplemented food reserves for times of scarcity (Hämäläinen 2019). This mixed subsistence approach enabled the Lakota to be flexible and mobile while sustaining a diet that nutritionists would consider well-balanced and high-quality (Hämäläinen 2019).

The role of the buffalo in culture, social relations, and survival in Oglala Lakota traditions is a prime example of the multidimensional facets of food, which go beyond mere subsistence. One oral tradition describes how the buffalo are the direct relatives of the Lakota, who preceded the Lakota on Earth to lead them to everything they needed to survive, providing food, clothing, shelter, and knowledge of water sources (Bear Eagle 2018). The buffalo's symbolic importance transcends its material value; it is a sacred animal, which is recognized for continuously offering itself and its knowledge to ensure the survival and security of Lakota peoples (Birchfield 2014; Hämäläinen 2019; Nauman 2020; Williams 2020). The buffalo is a reminder of the connection between the Lakota and the natural world as part of the same interconnected system, not separate, and is an affirmation of cultural heritage and ancestral ties to the land (Bear Eagle 2018; Nauman 2020; Schneider 2023).

Colonial expansion into the Great Plains led to the disruption of Lakota foodways and traditions. The construction of the Transcontinental Railroad was a pivotal event that split the Great Plains in half, disrupting animal migration and the food systems of Tribes throughout the region (Hämäläinen 2019; Schneider 2023). The trade of firearms and commercial buffalo hunting led to the overhunting and near-extinction of the animals, primarily at the hands of white settlers who moved into the area (Hämäläinen 2019; Williams 2020). The decimation of buffalo herds caused widespread famine among the Lakota, as well as diseases brought to the Plains by settlers and miners after gold was discovered in the Black Hills (Hämäläinen 2019; Williams 2020). The United States imposed policies of forced relocation and assimilation beginning in the 19th century, which

disrupted traditional food systems, cultural transmission, and access to ancestral lands and resources (Hämäläinen 2019; Reinhardt 2007; Schneider 2023).

The Pine Ridge Reservation, then called the Great Sioux Reservation, was established by the 1868 Treaty of Fort Laramie in an effort to secure Lakota sovereignty over their ancestral lands, particularly the sacred Black Hills ("Treaty with the Sioux-Brule, Oglala, Miniconjou, Yanktonai, Hunkpapa, Blackfeet, Cuthead, Two Kettle, San Arcs, and Santee-and Arapaho" 1868; Schneider 2023). The terms of this treaty also established the responsibility of the United States to provide food to the Lakota and other Tribes as reparations for the damage caused to traditional food systems as a result of American expansion ("Treaty with the Sioux-Brule, Oglala, Miniconjou, Yanktonai, Hunkpapa, Blackfeet, Cuthead, Two Kettle, San Arcs, and Santee-and Arapaho" 1868; Usha Maillacheruvu 2022). This treaty was violated as the Lakota were gradually removed from resource-rich areas desired by American farmers and miners, including the sacred Black Hills, into infertile environments (Hämäläinen 2019; Schneider 2023). These areas suffer from ecological degradation and pollution due to commercial exploitation of natural resources, including uranium mining (Birchfield 2014; Hämäläinen 2019; Williams 2020). Relocation and the lack of ecological abundance on the Pine Ridge Reservation disconnected the Oglala Lakota from vital resources, including buffalo herds and fertile lands. This undermined the community's ability to sustain itself economically, culturally, and spiritually, contributing to diminished access to food.

**Overview of the Food Distribution Program on Indian Reservations**

The Food Distribution Program on Indian Reservations (FDPIR) is a federal assistance program that provides food for low-income households on or near reservations as well as throughout the entire state of Oklahoma on the condition that the residence houses at least one individual who is a registered member of a federally recognized Tribe. It is offered as a more accessible alternative to other federal programs, such as the Supplemental Nutrition Assistance Program (SNAP), because many reservations do not have SNAP program offices or stores that accept SNAP benefits. While these programs are not exclusive from one another, households can only use the benefits from one federal assistance program each month (USDA 2020).

In most cases, Indian Tribal Organizations (ITOs) execute the program locally, acting as liaisons between Tribal members and the Food and Nutrition Service that heads FDPIR nationally (USDA 2020). FDPIR eligibility is assessed on a household level; to qualify for benefits, households must apply through these ITOs and meet residency, income, and Tribal membership requirements, reassessed at least once a year (USDA 2020). Once accepted into the program, households can select a certain number of foods from a preapproved list according to their dietary preferences, household size, and what is available through their dedicated ITO (Byker Shanks et al. 2016). The program differs from SNAP in that foods that have been ordered from all eligible households within a Tribal community are shipped from the USDA to these ITOs, who store the food and fulfill orders for pick up from

an ITO distribution center (USDA 2020; Pindus et al. 2016). Some ITOs also offer delivery services (Pindus et al. 2016). ITOs may also apply for funding for additional services they can provide to their respective communities, which may include cooking classes, nutrition counseling, and cookbooks (USDA 2020).

**Program Impacts**

*Food Insecurity Rates*

Feeding America, a nonprofit organization that collects localized information on food insecurity in the United States, provided the datasets initially used in this research. Until 2022, the organization did not collect information on race or ethnicity, and as of 2023, there remains no signifier for Indigenous people in the data, which creates challenges for disaggregating this information. However, two counties (Bennett and Oglala Lakota) lie entirely within the designated area of the Pine Ridge Reservation, along with approximately half of Jackson County. Comparing the data for these three counties to state and national averages offers important insights into food insecurity rates on the reservation. While a small portion of Pine Ridge extends into Nebraska, this data was excluded because it was not possible to differentiate between data collected from households living on and outside the reservation.

Comparing the data from Bennett, Oglala Lakota, and Jackson Counties to national data from the Economic Research Service reveals a startling trend. First, the food insecurity rate in the state of South Dakota has experienced a steady decrease from 13% in 2011 to 8% in 2021 (Gundersen et al. 2013; Hake et al. 2023). This is consistent with national averages, which dropped from 15% in 2011 to 10% in 2021 (Economic Research Service 2022). Trends after 2021 are not yet well understood, as the COVID-19 pandemic disrupted global food systems and data collection on food access and availability.

Despite an overall decline in the state's food insecurity rate over the past decade, food insecurity rates in Bennett County, Jackson County, and Oglala Lakota County have not seen any statistically significant changes. The average cost of food has risen in the state and all three counties. In Bennett County, food insecurity rates were at 18% in 2011 and 2016, and 17% in 2021 (Gundersen et al. 2013; 2018; Hake et al. 2023). Jackson County saw a modest increase in food insecurity from 18% in 2011, 19% in 2016, to 20% in 2021 (Gundersen et al. 2013; 2018; Hake et al. 2023). Oglala Lakota County, which has the largest population and the most food insecure households, has particularly high food insecurity rates: 28% in 2011, 27% in 2016, and 26% in 2021 (Gundersen et al. 2013; 2018; Hake et al. 2023). This data demonstrates that FDPIR has not had a significant long-term impact on food insecurity in a ten-year period.

*Household Participation in FDPIR*

In 2013, the USDA contracted a report titled "Study of the Food Distribution Program on Indian Reservations (FDPIR)", which was the first nationally comprehensive study on this subject since 1989 (Pindus et al. 2016, xii). Twenty-three Tribes participated, including the

Oglala Sioux Tribe. Although the data was not disaggregated, the study provides valuable insights into the program's reach, how households incorporated it into their food practices, and areas for improvement as identified by participating households.

The report provided a demographic overview of the participating Tribes. In 2013, about half of all households served by FDPIR were composed of single adults with no children (Pindus et al. 2016). The second most common household composition was a single parent with one or more children, followed by married couples with children (Pindus et al. 2016). Most households were headed by women (62% women compared to 38% men). Between 1989 and 2013, there was a shift in the ages of participants; in 1989, 37% were under the age of 18, 48.2% were between the ages of 18-59, and 14.8% were 60 or older. This is in contrast to 2013, when 30.6% were under the age of 18, 48% were 18-59, and 21.4% were 60 or older (Pindus et al. 2016). Average household income from all sources ranged from $0-1,144 per month. Approximately a quarter of households having at least one wage earner, 11% with no income source, and over three-quarters receiving various forms of financial assistance, such as Social Security and Supplemental Security Income benefits (Pindus et al. 2016). Households participating in the FDPIR were "four times as likely… to experience low and very low food security" compared to national averages (Pindus et al. 2016, 82). Although FDPIR is designed as a supplemental food program, over a third of households use it as their primary or only food source. The Pine Ridge Reservation has one of the highest participation rates, with over 1,000 households enrolled in the program (Pindus et al. 2016). Despite participating households' heavy reliance on FDPIR as their primary or only food source, the majority (93.1%) were satisfied with the nutritional adequacy of food received through the program (Pindus et al. 2016). Fresh produce and frozen meat, which had not been available to households under previous programs, were cited as the most important food types provided through FDPIR (Pindus et al. 2016). There was a general consensus that the quality, variety, and freshness of the food had improved since the early 2000s (Pindus et al. 2016).

While participants were generally satisfied with the program, they also identified many opportunities for improvement. Although the availability of fresh products has generally improved over the past 10 to 15 years, a greater variety of fresh fruits, vegetables, and meats was one of the most common suggestions (Pindus et al. 2016). Participants emphasized the importance of increasing access to traditional foods, as the foods currently available do not adequately represent the diversity of Indigenous foods and preferences; only one-third of participants felt that FDPIR offered relevant "cultural or traditional" foods (Pindus et al. 2016, 161). For example, buffalo meat was preferred by people who identify it as a traditional food source, but not for those who do not share the cultural traditions of buffalo hunting (Pindus et al. 2016). Canned salmon was equally unpopular in areas with direct access to fresh salmon (Pindus et al. 2016). The type of traditional food offered was important; hominy is similarly traditional in some areas, but some Tribes prefer white hominy, while yellow hominy is preferred by others (Pindus et al. 2016). This demonstrates the need for specific culturally relevant foods, and that people strongly prefer foods that are

traditional to their own Tribe. In some instances, there are existing Tribal food production systems that are not incorporated into FDPIR packages, and there was strong interest in expanding these systems and acquiring FDPIR food products directly from Tribal sources (Pindus et al. 2016).

The most common reasons why needs were unmet included specific dietary requirements, as associated with health conditions like diabetes, and the desire for larger portions and more fresh produce (Pindus et al. 2016). This is likely because those with no other food source do not receive enough from FDPIR to adequately sustain themselves. There was a clear desire for a greater variety of fresh and frozen food options (Pindus et al. 2016). While the program changes between 1989 and 2013 were well-received, there remains a tension between FDPIR providing nutritious food, ensuring the quantity and quality of food items, and the need to include culturally relevant foods.

**Adapting the Program to Meet Community Needs**

Historically, food provided by the federal government has been surplus, low-cost, and highly processed foods with limited nutritional value (Byker Shanks et al. 2016). These foods were often made from ingredients that did not exist in the ancestral diets of North American Indigenous peoples, such as wheat, dairy, and sugar (Byker Shanks et al. 2016). The forced introduction of these foods has been directly linked to the high prevalence of diet-related health issues, such as diabetes, in Indigenous communities today (Maillacheruvu 2022; Talahongva 2018). Thankfully, the efforts of Indigenous advocacy groups, ITOs, and federal and Tribal health professionals have led to reforms in the program and integration of traditional foods (Maillacheruvu 2022; USDA 2023). The impact of these efforts is evident in the 2024 FDPIR food list, which now includes a wider variety of foods than have previously been available, evidenced through the introduction of items such as buffalo, wild rice, and wild-caught fish (USDA 2023).

Despite these improvements, FDPIR still has some shortcomings that could be addressed. The current list of traditional foods is limited and does not represent the diversity of Indigenous cultures. Careful consideration of the cultural integrity of traditional foods, particularly animal products, is essential. Including buffalo meat in the FDPIR offerings is particularly significant for the Lakota, as the buffalo holds a crucial role in their traditions, spirituality, and identity (Lulka 2006). However, concerns have been expressed about the potential cultural decontextualization of the buffalo through the commercial production system (Lulka 2006). Many buffalo today have been interbred with cattle for generations, are managed by non-Indigenous ranchers, and are fed primarily grain, therefore existing in entirely different conditions than ancestral herds did (Lulka 2006). Oglala Lakota people value animals that are managed by Tribes and are as genetically and behaviorally as close to ancestral herds as possible for cultural and health reasons (Lulka 2006). The inclusion of traditional foods and Tribal involvement in food procurement practices is not just about the reinstating of traditions but a path to “collective continuance” and “a matter of investing in a form of Indigenous resilience” (Schneider 2023, 805). Careful consideration of the role of

the buffalo in Oglala Lakota society and meaningful collaboration to integrate this role into FDPIR offers the opportunity to provide not only nutritious food but cultural and spiritual significance, economic opportunities that can help remediate the commercialization of buffalo in FDPIR, and a foundation for future collaborative efforts. It is also a way to honor Indigenous knowledge and cultural transmission (Schneider 2023).

Access to fresh produce remains an issue. Concerns from the 2016 study participants highlighted issues related to package pick-ups later in the month, when fruits and vegetables may be depleted or of lower quality and freshness (Pindus et al. 2016). It is important to acknowledge that many people living on reservations lack access to electricity and refrigerators, so canned, dried, and powdered goods are essential parts of a complete FDPIR package and must not be devalued (Pindus et al. 2016). In addition to integrating a greater variety of traditional foods, sourcing products through local and Tribal channels has the potential to enhance consistency in the quality of foods received by households and save funds for other areas of the program by shortening transport times and distances (Pindus et al. 2016). Examining the many dimensions of food within Oglala Lakota society demonstrates how food insecurity is not an isolated issue but is shaped by intersecting social, political, and economic forces. Therefore, to make a meaningful long-term impact on the well-being of people living on the Pine Ridge Reservation, the USDA must reframe its metrics for what it means for Indigenous communities to achieve food security within this broader context.

**Conclusion**

To understand and address food insecurity on the Pine Ridge Reservation today, it is essential to contextualize the issue within colonialism and the structural inequalities that come with it to identify the root causes of the issue. Land dispossession and ecological desecration, particularly of buffalo herds on the Great Plains, have limited the ability of the Oglala Lakota to produce their own food, and therefore, many are dependent on the United States federal government to fulfill their basic needs. Capitalist market forces have disconnected traditional foods and knowledge from their original contexts, and persistent poverty and limited economic opportunities on reservations heighten vulnerability to food insecurity (Lulka 2006; Ricart 2019). Food insecurity is a symptom of broader systemic forces, and the path to creating long-term solutions is by identifying these contributing factors.

While FDPIR is an essential resource for many households living on the Pine Ridge Reservation, there are many areas for improvement within the program. This study shows that the Pine Ridge Reservation has a disproportionately high rate of food-insecure households, and some food-related needs are not being met. Where there is a disconnect between community needs and resources provided by FDPIR, these gaps can be attributed to misaligned conceptions of what food security should look like for the Pine Ridge Reservation. For the USDA, food security involves caloric quantity, quality, and variety. While these factors are also valued at a community level, food security for the Oglala

Lakota requires the ability to access and use traditional foods within cultural contexts, the ability for Tribal members to care for each other, and avenues to build resilient communities around cultural values. Food practices are deeply engrained in social, cultural, and environmental relationships, and true food security requires not just enough food to survive, but active engagement and cultural integrity. All aspects of food must be integrated into the conceptualization of food insecurity to create long-term solutions and resilient communities. This disconnect in approaches can be bridged by fostering increased collaboration between Tribal and federal agencies that prioritize meeting the nutritional and cultural needs of communities participating in FDPIR. In this regard, some progress has been made, but a deeper level of collaboration with each Tribe and expansion of the resources and funding available for projects is needed. In some cases, local food production already exists, but is not being fully integrated into FDPIR. The Oglala Lakota, for example, manage a buffalo herd on the Pine Ridge Reservation, but FDPIR still obtains most buffalo meat from non-Indigenous sources. The program could purchase buffalo meat from Tribal sources, maintaining the cultural integrity of the animal and contributing to the investment in and growth of the herds. This collaborative approach has the potential to bridge existing gaps and ensure that FDPIR not only addresses immediate nutritional needs but also aligns with the cultural fabric and goals of Indigenous communities.

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**Occurrences of Extinct Viverravidae Carnivora & Omomyidae Primates in Lower Eocene Localities (~56-53 Ma), Willwood Fm, Bighorn Basin, WY**

Jason Kapernekas

**Abstract:**
The ecological relationship between faunivorous mammals within an ecosystem provides insights on intraspecies and interspecies competition and niche partitioning. I report on the results of frequency analyses of relative occurrences of faunivores who are extinct members of the Order Primates (Omomyidae) and the Order Carnivora (Viverravidae) within lower Eocene (56-53 Ma) CSU localities of the Willwood Formation, Bighorn Basin, WY. Focusing on predators (primate, carnivoran) of similar body mass, my hypotheses concern relative predator abundances over time (proxy = meter level). If relative abundances are similar over time, it may indicate predator relative success. If the relationships change over time, it may be indicative of prey loss or an ecological variable. My investigation is grounded in Modern Evolutionary Theory and is relevant to adaptive questions within Vertebrate Paleontology, Primate Paleontology, Paleoecology, Biological Anthropology, Primate Evolutionary Biology, & Zoology.

**Introduction:**
The ecological relationship between faunivorous mammals within an ecosystem provides insights on intraspecies and interspecies competition and niche partitioning (Simpson 1949). This paper reports on the results of frequency analyses of relative occurrences of faunivores who are extinct members of the Order Carnivora (Viverravidae) and Order Primates (Omomyidae) within the lower Eocene (56-53 Ma) CSU localities of the Willwood Formation, Bighorn Basin, WY. Focusing on predators (primate, carnivoran) of similar body mass, my hypotheses concern relative predator abundances over time (proxy = meter level). If relative abundances are similar over time, it may indicate predator relative success. If the relationships change over time, it may be indicative of prey loss or an ecological variable. Through this study, the analysis of relative occurrences between extinct faunivores can help illustrate past ecosystems as well as possible interactions between species.

**Hypotheses**
Hypothesis 1: Percent frequency of faunivores (Omomyidae, Viverravidae) relative to total faunal population, varies through time *(e.g.*, meter level). Null Hypothesis: There is no variation. When looking at faunivore abundance over time, variation of frequency in occurrences could help illustrate predator success levels, prey loss or even an ecological variable (Simpson 1949).

Hypothesis 2: Percent frequency of faunivores (Omomyidae, Viverravidae) relative to each other, varies through time. Null Hypothesis: There is no variation. When comparing

frequency of faunivores to one another the possibility of competition and niche partitioning can be seen within the data (Simpson 1949).

**Methods**

Study fossils were obtained from the CSU Primate Origins Lab fossil collection. These fossils were collected from 135 Localities (2013-2022 ANTH 470 field seasons), and catalogued into the DMNS Vertebrate Paleontology Department. The 115 Omomyidae (Order Primates) specimens belong to the two genera *Teilhardina,* and *Tetonius.* The 34 Vivveravidae (Order Carnivora) specimens belong to the genus *Vivveravu*s. The remaining taxa within this sample contained 2,600 other fossil mammal specimens from various genera.

Using this data, specimens of the study faunivores were graphed as a percentage of total number of specimens in the vertebrate fauna. This was done by meter level grouping (0-200 meters; 201-400 meters; 401-460 meters). Meter level is used as a proxy for time. Following this graph, expected (no variation) vs. observed occurrences for faunivores were determined by meter level grouping. Running this statistical analyses provides possible correlations. To add to this, Chi-Square ($X^2$) tests were administered to determine the significance of differences between expected and observed frequencies (VanPool and Leonard 2010).

**Results:**

The data indicate statistically significant differences in faunivore (Omomyidae, Viverravidae) distribution as a percent of total fauna over time (*Table 1*). Each p-value is less than 0.05 therefore provides a statistically significant difference in the correlation of occurences of faunivore groups. The null hypothesis of no variation is unsupported.

Youngest 53 Ma

| Meter Level 401-460 | Chi-Squared | p-value |
|---|---|---|
| All-group data | 24.676 | 4.38E-06 |
| Faunivore Only | 24.482 | 7.50E-07 |
| **Meter Level 201-400** | **Chi-Squared** | **p-value** |
| All-group data | 5.018 | 0.081 |
| Faunivore Only | 4.794 | 0.029 |
| **Meter level 0-200** | **Chi-Squared** | **p-value** |
| All-group data | 24.741 | 4.24E-06 |
| Faunivore Only | 24.264 | 8.40E-07 |

Oldest 56 Ma

***Table 1.*** Statistical tests, correlations of occurrences in ML 401-460, ML 201-400, ML 0-200.

The data also indicate statistically significant differences in faunivore (Omomyidae, Viverravidae) distribution relative to each other over time (*Table 2*). The observed data is different than the expected data, therefore the null hypothesis of no variation is unsupported.

Youngest 53 Ma

| Meter Level 401-460 | Observed | Expected |
|---|---|---|
| Omomyidae | 0.00% | 4.18% |
| Viverravus | 3.29% | 1.24% |
| **Meter Level 201-400** | **Observed** | **Expected** |
| Omomyidae | 2.68% | 4.18% |
| Viverravus | 1.19% | 1.24% |
| **Meter level 0-200** | **Observed** | **Expected** |
| Omomyidae | 5.47% | 4.18% |
| Viverravus | 0.90% | 1.24% |

Oldest 56 Ma

***Table 2.*** Observed and Expected data of occurrences per ML grouping.

**Summary of Results:**

The results of the statistical tests indicate a significant difference between expected and

observed relative abundances of faunivores. Instead of remaining stable over time, frequency changes occur in both taxa but in different ways. (*Figure 1*) In the lowest part of the section (0-200 meters), the sample sizes of both faunivores are the greatest. However, whereas the percentage of Viverravidae falls short of the expected value, the percentage of Omomyidae is higher than expected. (*Figure 2*) In the 201- 400 meter section, Viverravidae is near the expected frequency, but Omomyidae is lower than expected and disappear above the 370 meter level. (*Figure 3*) In the highest part of the section (401-460 meters), Omomyidae is absent and the frequency of Viverravidae is higher than expected.

**Discussion:**

At first glance, the disappearance of the Omomyidae would seem to be due to predation by carnivores. What is more likely, is the impact of thermal temperature change (McInerney and Wing 2011). The start of the early Eocene was marked by an event known as the PETM, the Paleocene-Eocene Thermal Maximum (Badgely and Gingerich 1988). This four-million-year climate event is associated with the highest thermal temperatures known to geology (Bown et al. 1994). Throughout the early Eocene, global thermal temperatures decreased through the 0–200-meter levels reaching their low between 200-400 meters. Temperatures are already increasing and continue to do so throughout the 400–460-meter section. Such climate events take a toll on entire biomes.

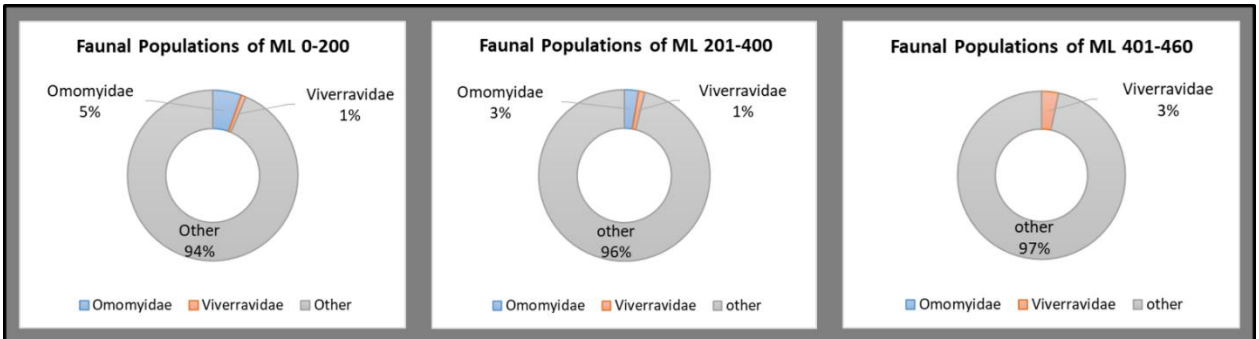


*FIG 1.* Faunal Populations of ML 0-200 *FIG 2.* Faunal Populations of ML 201-400 *FIG 3.* Faunal Populations of ML 401-460

(1) In response to increased thermal temperatures there is a pressure for volume to decrease and surface area to decrease (Bergmann-Allen's Principle). This would allow for a trend in selection for decreased mammalian total body mass through this section. At the same time, increased humidity would encourage higher plant abundance and diversity (McInerney and Wing 2011). In turn, would positively increase primate prey numbers, specifically invertebrates and small vertebrates (Grubbs 2022). With high-pointed dental cusps and small body sizes, Omomyidae would have thrived under these conditions (Fleagle 2013). The higher-than-expected frequency of Omomyidae corresponds with increased temperature. This small-bodied arboreal leaper, much like today's tarsier, would have had plentiful arboreal foods (Fleagle 2013). In contrast, the weasel-bodied semi-terrestrial Viverravidae has lower than expected values due to the temperature increase (Rose 2006).

(2) In the next phase, the middle stratigraphic section, thermal temperatures rapidly decreased, pressuring body volume to increase and surface area to decrease (Bergmann-

Allen's Principle). Therefore, a trend in selection for increased mammalian total body mass throughout this section occurs. Lower thermal temperatures resulted in less humidity and lower plant abundance and diversity (McInerney and Wing 2011). Loss of tropical flora would have placed stress on the Omomyidae due to habitat change in plant and faunal foods. As demonstrated by modern small-bodied faunivorous primates such as the tarsiers, terrestrial locomotion is a nonviable option (Fleagle 2013). The Viverravidae, in contrast, are semi-terrestrial generalists and maintained the same frequencies as before. Simply put, by following food sources on the ground and not relying on life in the trees, *Viverravus* was better adapted to changes in climate (Heinrich and Houde 2006). Further, it retained forelimb and hindlimb adaptations for use of the trees and could hunt in both physical spaces (Heinrich and Houde 2006).

(3) In the final phase, the upper stratigraphic section, Eocene thermal temperatures increased again. Thus, we would expect a repeat of the earliest Eocene responses (Chew 2015). However, by the 370-meter mark, the sample Omomyidae primates are absent. The stress of thermal temperature fluctuation, coupled with competition from a similarly sized more generalized faunivore, could have been too much for specialized faunivorous primates (Kay and Covert 1984). They may even exhibit some range constriction, meaning they would have stayed within more favorable ecosystems.

In summary, as time went on, the changes caused by fluctuations of thermal temperature appear to have been unbearable for *Teilhardina* and *Tetonius*. In contrast, *Viverravus* could withstand these challenges due to adaptive flexibility.

**Future Directions:**

Paleosol maturity, an indicator of relative time taken to form an ancient soil and proximity to water sources, allows us to assess microhabitats in the Willwood Formation. The fauna from this study were obtained from multiple localities ranging in paleosol maturity. Moving forward, it would be beneficial to test hypotheses related to paleoecology preferences by adding analysis of paleosol maturity data to this study. This information would provide further ideas concerning study population frequency within microhabitats.

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# Imbibing Identity: A New Materialist Approach to Consumption and Identity in a Colorado Saloon

Ben Shirey

## Abstract

This article takes a New Materialist approach to consumption at Ouray, Colorado's 220 saloon, examining the identity-creating entanglements generated between human and material agents in acts of consumption. As object-agents, the beverages available in 19th century saloons had the power to imbue their consumer with certain desired qualities by the various material and symbolic attributes bound up in them. Thus, choice of what to consume and what not to in a public drinking establishment was a conspicuous means of identity construction widely engaged by the people of Victorian America. Antczak's and Beaudry's (2019) methodological framework of "assemblages of practice" presents an avenue for incorporating the agency of humans and their beverages in an analysis of identity construction through this communal practice of consumption. I focus on the collection of drinking vessels from the midden associated with the 220 saloon, framing it as the site of an assemblage of practice to make interpretations about the constructed identities this assemblage would have facilitated in this space of communal consumption and the roles that human and non-human agents had in this process.

## Introduction

This project frames Ouray, Colorado's 220 saloon as the site of an assemblage of practice and examines the identity-creating entanglements generated between human and material agents there. New Materialism in archaeology reorients approaches to material objects, drawing from object-oriented ontologies (Olsen and Whitmore 2015, Edgeworth 2016), entanglement theory (Hodder 2012), and Indigenous thought (Cipolla 2017, Cipolla et al. 2019) among other perspectives to understand things as agents in "symmetrical" relationships with humans (Whitmore 2007). Analysis of the human-thing relationships involved in commodity consumption in industrial settings bears promise in this area of theoretical development (Wilson 2008). This paper contends that no 'thing' better demonstrates material agency than alcohol, which interacts with and influences human agents in a number of well-known ways and plays a powerful role in identity construction. The beverages available in 19$^{th}$ century Western saloons, by the various material and symbolic attributes bound up in them, imbued certain desired qualities upon their consumers. Similar to their modern counterparts, Victorian Americans strategically manipulated this power through consumption choice in public drinking establishments to conspicuously construct identity. Antczak's and Beaudry's (2019) methodological framework of "assemblages of practice" presents a new avenue for incorporating the agency of both humans and their beverages into archaeological analysis of identity construction through practices of consumption.

The project focuses on the collection of beverage vessels and drinkware from the midden deposits associated with the 220 saloon and boarding house (Figure 1). I analyze the vessels according to their material and symbolic attributes as active "things" rather than inert objects (Antczak and Beaudry 2019). I place these beverages and their consumers in their historical and social context and describe the attitudes and practices associated with beverage consumption in Victorian saloons using documentary sources. I use this to interpret the identities that arose from the human-thing entanglements that formed this assemblage of practice.

**Identity, Consumption, and Assemblages of Practice**

Social theorists have long associated practices of consumption with self-definition (Mullins 2011, 106). Identity construction involves selective expression of sameness and difference, and human agents interact with materials to strategically signal desired affiliations (Sunseri 2020, 18). In capitalist contexts, this manipulation of material often occurs in the form of publicly visible consumption choices. Consumers' choices of what and how to consume implies more than simple personal preference—it allows them to embody and express desired qualities and form the contours of identity (Mullins 2011, 106). This was especially true during the 19th century, when principles of gentility set high moral standards on character and behavior, including consumption (Praetzellis and Praetzellis 2001). Genteel consumption became deeply ritualized, and Victorians placed high importance on one's choices and manners in this practice as a reflection of character (Mullins 2011, 151). However, human consumers are not the sole possessors of agency in these interactions. Looking at consumerism only in the traditional sense treats objects as inert and misrepresents the social practices in which things participate as active members (Wilson 2008). As Wilson notes, "people manipulate objects and objects manipulate people" in the complex practices surrounding consumption (2008).

Antczak and Beaudry's (2019) concept of "assemblages of practice" provides a framework that links the archaeological assemblages with New Materialist archaeological concepts of shared human and material agency. In this framework, artifacts are not just a means to understand humans; rather, material things are never static or inert but are vibrant participants in social processes alongside humans and live out "itinerant" existences, accruing biographies of their own (Antczak and Beaudry 2019). In an assemblage of practice, humans and things become entangled in processes structured by cultural practice. Artifacts are the remains of these human-thing assemblages, material entities with interconnected histories of participation in physical and social processes. They bear evidence of these processes, and by examining them and their contexts using all available lines of evidence we can reconstruct the nature of their entanglements. The 220 saloon represents an assemblage of drinking practice where the intoxicating beverages, bottles, and drinkware entangled with the patrons and employees of the notorious establishment. Antczak and Beaudry (2019) stop short at noting the entanglement of these entities in their

brief examples, but this project aims to further examine the specific qualities of materials and how they uniquely structured entanglements with humans.

Things, including alcoholic drinks, entangle with humans on the basis of their symbolic and material qualities. Things are bound up with social characteristics and symbolic associations and have the power to imbue consumers with the same (Keane 2005). An oft-cited example of this power is the ability of different styles of clothing to change a person's qualities and the ways they move in the social and material world (Keane 2005; Wilson 2008). In his analysis of the relationship between bourbon consumption and manhood, McKeithan (2012) compares the drink to a masculine piece of clothing one can 'don' to gain that quality. The character of a thing's agency and the way it is able to manifest is based also on its inherent material properties (Bauer and Kosiba 2016). For example, stone and water will interact with humans differently, exerting different influences on human practices surrounding them (Bauer and Kosiba 2016). Williams (2008) argues in her study of a 19th century Chinese household in California that the refined, delicate materiality of things involved in Chinese practices of alcohol consumption was important in constructing Chinese masculine identity. Both symbolic and material elements are key structuring factors behind the formation of human practices of consumption of specific material things. Thus, it is by these capacities that material things are able to shape human identity, perception, and behavior in the process of entanglement.

The practices of consumption surrounding alcoholic beverages are constrained by a complex web of symbolic associations and unique materiality. For beverages in a 19th century saloon, these bound-up qualities come from historical cultural attitudes of local and immigrant groups (Remus 2014) and the strategic marketing efforts of rising brand advertisers (Marchand 1985). Symbolic associations surrounding alcohol and drunkenness were multiple and contested at this time, and as Temperance Union influence spread across the American West, the choice to drink or not to drink became a significant moral signal (Gusfield 1991, 407). The genteel Victorian attention to meaningful consumption further made public consumption of alcohol a particularly powerful locus of identity construction. Thus, consumption at the 220 was a "pleasurable act of self-creation" (Mullins 2011, 106) in which humans and things entered into relationships structured by the symbolic and material qualities of the drinks and drinkware as well as the human consumers' desires relative to those qualities. The artifacts recovered from the site of the 220 bear witness to those entanglements and the Victorian concepts of consumption and identity that structured them.

In the following analysis, I consider the entanglements between these artifacts and their consumers in their historical, social, and material contexts. In my analysis of identity, I do not intend to place artifacts or the people associated with them into discreet categories like rich-poor or male-female. While consumption allows people to construct identities related to categories of gender, class, sexuality, etc., individuals approach consumer goods from unique positionalities with specific desires and engage in fluid entanglements that do not allow for such simplistic extrapolation (McKeithan 2012). Rather, I consider the ways subjects manipulated material culture to situate themselves on continua between concepts

like masculine-feminine (Mullins 2011, 157) and the ways in which the material culture, in turn, manipulated them.

**The Vanoli Block**

The building that would come to be known as the 220 was one of the oldest on its block in Ouray's red-light district and was first referred to in the documentary record in 1877 as the newly opened Ouray Hotel (Gregory 1982, 3). This initially respectable establishment experienced two name changes, at least two shooting incidents, and several owners before coming into the possession of John Vanoli in 1885 as the "220" saloon and boarding house. Gambling and prostitution were part of the business before the Vanoli purchase and would continue to be so throughout his time as owner. The 220 gained a reputation as a rough, rowdy, sinful place and was the site of still more shooting incidents in the late 1880s including two involving John Vanoli himself (Gregory 1982, 20). Marked as 'boarding' on Sanborn maps and referred to as a hotel or dance hall in the newspapers, this institution served the function of both brothel and saloon.

Saloons were multifunctional, primary social centers in 19th century Western towns, often serving as the house of government, worship, and other institutions when necessary (Noel 1996, 12). They provided a space for recreational drinking where beverages served to relax tired workers' bodies (Matthews 2010, 139). At combined saloon-brothels like the 220, this included the services of sex workers and dancing girls. Saloons and brothels were primarily marketed toward men, and the 220 would have been no different (Remus 2014). In an 1880 advertisement for the 220 in the Ouray Times, then proprietor John L. Lawler specifically seeks "the boys' patronage" (Gregory 1985, 10). Previous work on the Vanoli Block collection indicates that the population of clients and employees was thoroughly working class (Van Buren et al. 2014). Saloons were significantly segregated by class and ethnicity (Noel 1996, 23), so the patrons of the 220 were almost certainly all white workers. The rise of time regimentation associated with industrialization saw a novel separation of work time and drinking time, and saloons served to furnish the intoxicating material trappings of off-the-clock recreation (Gusfield 1991, 405). They were social spaces for fraternization and fellowship, not necessarily the scenes of constant shootouts (Dixon 2005). Sharing drinks and buying rounds for one another were important parts of fraternization and the construction of common identity among the male patrons (Remus 2014). The unusually high number of shells and bullets recovered by archaeologists, and the numerous contemporary reports of shooting and public indecency indicate that this saloon may be an outlier (Van Buren et al. 2014). Such bawdy places were against the law in Ouray but the town gave its red-light district a pass, perhaps as much for these relaxing effects on the workforce as their financial contributions to the town through fines and fees (Gregory 1982, 8). This homosocial masculine context of recreation and socialization influenced the consumption choices of the patrons.

The women present at the 220 were mostly working as prostitutes or dancers, which influenced their drinking practices. Public drinking was considered a male domain, and

Victorian polite society was scandalized by liquor even being within reach of a woman in public spaces (Mullins 2011, 148). While not all women who consumed alcohol in saloons were prostitutes (Dixon 2005, 145), public sentiment equated female public drinking with prostitution (Remus 2014). Working women at the 220 were encouraged to drink with their customers as a sign of sociability and availability (Gregory 1982, 22). While others have noted Victorian prostitutes as having more control over the spaces they worked in (Wilkie 2010, 34), this was not the case here, as most working in the Vanoli block were transitory (Gregory 1982, 9). Despite attempts at genteel presentation, prostitutes were themselves members of the working class like their clients (Mullins 2011, 149).

Saloon owners strove to provide options for their patrons, the various owners of the 220 among them (Noel 1996, 12). In the late 19th century, an increasing portion of drinkers' annual gallonage was provided by larger-scale, industrial beverage producers at the expense of small local operations (Dighe 2017, 26). Before the establishment of the Ouray Brewery in 1884 (Smith 2003, 57), the nearest known local breweries to Ouray were those operated by Charles Fisher in Howardsville and Silverton some twenty miles to the south (Baron 1962, 249). Fisher's operations never produced enough to satisfy demand in their towns and had to import supplementary gallonage, so if these breweries' products were available in Ouray it would have been in small quantities amidst a selection of beers mostly imported from large producers (Baron 1962, 250). The same advertisement quoted above boasted that the "best brands of wines, liquors, and cigars" were "always on hand," (Gregory 1982, 10) indicating that the patrons of the 220 likely had an actual range of beverages from different producers from which to make meaningful consumption choices.

**The 220 Assemblage of Practice**

This project analyzed all alcoholic beverage containers, drinkware, and other drinking accouterments from Operation 3, Suboperations C, D, and E of the Vanoli Block site (5OR30). These suboperations probed into deposits just to the west (rear) of the 220 saloon (Figure 2). Suboperation C is divided into lots C1-8 representing excavation layers, C1 being the surface and C8 being the terminating level. Suboperation E, bordering C directly to the south, is similarly divided into lots E1-6. These suboperations contained midden deposits (C7 and E4) near the saloon wall beneath a layer containing wood flooring and coal, likely representing an outdoor fuel storage area (C4-5 and E3). Refitting glass fragments from lots above and below the fuel storage layer suggest that the coal and wood layer is a permeable barrier, and material above it is mixed with the midden assemblage (Figure 3). Suboperation D investigated a possible privy vault below Suboperation A (not considered in this analysis) to the southwest of C and E and was excavated as one lot: D1. Due to their spatial distance and differing stratigraphic contexts, I consider the C-E and D assemblages separately in the following analysis. Vessels and drinkware were typed by contents based on color and body and finish morphology with reference to previous identifications made by Van Buren et al. (2014). I further made minimum number of vessel (MNV) estimates within these types using diagnostic fragments (bases and finishes) after

separating by color. Non-diagnostic glass artifacts had already been removed from the collection, so analysis focused on the remaining diagnostic elements.

The C-E deposits contained beverage bottles and variety of drinkware associated with pre-prohibition saloon activity. The assemblage included an MNV of 25 bottles comprising mostly beer bottles with some wine and liquor bottles (Figure 4) and an MNV of 15 drinkware vessels, including stemware and whiskey glasses. Table 1 shows the makers' marks represented on suboperation C and E beer bottles and their date ranges, which indicate a manufacturing time range from the late 1860s to the 1890s. The one complete green glass wine bottle is consistent with turn molding, a manufacturing technique used 1880-1920. Practices of reuse prevent assigning this exact date range to the deposit (discussed further below), but the general agreement among the date ranges and the relatively short life of a recycled bottle indicate that this assemblage is likely associated with saloon activity between 1877 and the early 1900s.

The collection from C-E contained an MNV of 16 beer or ale bottles. Beer's dominance in this assemblage is unsurprising, as late 19th century Americans drank more absolute alcohol in beer than in liquor and wine combined—with an average ABV of 3-4% in draft and bottled beer, that's a lot of gallonage (Dighe 2017, 25). The assemblage seems to lack any indication of the mugs and steins that were commonly used at the time and described in accounts of the saloon. This could be the result of the common practice of customers bringing their own drinking vessels for beer to Ouray saloons (Smith 2003, 57).

The bottles' role in this assemblage of practice was not momentary, but continual. The extreme bottle shortage in the West at this time meant that beer producers could not turn a profit unless most empty bottles were returned (Lockhart 2006). The thick-walled bottles necessary for containing carbonated beer were expensive to produce and almost always had to travel from east of the Mississippi, incentivizing reuse (Lockhart 2006). The beer bottles here are all examples of this standardized type intended for shipping, known as "Export" bottles (Lockhart 2006). In actual practice there was little attention paid to returning bottles to their original manufacturer, and sellers did not discriminate about whose mark was on the bottles they refilled (Lockhart 2006). Thus, the bottles went out from their producer, entangled with humans in diverse settings, and carried on doing so, embodying what Antczak and Beaudry (2019) call the "itinerancy" of things. While this creates a point of difficulty for dating assemblages, it is a remarkable instance of dynamic social relationships between people and things structured by the things' innate material properties.

Beer had strong familial connotations at this time. It was seen as a healthful beverage, and families of all stations drank it together at meals (Wilkie 2010, 76). Beer was also the working class's alcohol of choice in the late 19th century and was becoming an increasingly masculine beverage (Dighe 2017, 26). Workers consumed it together during breaks from work for refreshment and relaxation (Dighe 2017, 24). Export bottles contain large servings, lending themselves to the practice of drink-sharing and round-buying described above. Given how much beer is present, its absence from the advertisement quoted above listing the available luxuries of this establishment is further testament to its

humble, homely place among the available beverages. With these qualities bound up within it, entanglements with beer brought to its consumers a familial and fraternal atmosphere.

Brand is difficult to determine in most cases because of the Western preference for paper labels rather than embossing on bottles (Lockhart 2007), but some of the bottles profess their affiliation with the Anheuser-Busch corporation. Among the assemblage of suboperation C are multiple aqua glass Budweiser bottles bearing the Carl Conrad & Co. maker's mark with the word "Budweiser" embossed on the body (MNV = 3). Anheuser-Busch produced Budweiser beer in these bottles in partnership with Conrad from 1876 to 1882 (Lockhart 2006). Large brewers made beers like Budweiser to be lighter and blander to both appeal to workers wanting a refreshing drink and to assuage the temperance movement (Dighe 2017, 25). Brewing industry trade journals from the time emphasize beer as a temperance-friendly beverage meant for refreshment rather than intoxication as a defense against looming prohibition (Dighe 2017, 25). It was not seen as a dangerous intoxicant like whiskey, and the temperance movement generally excused its consumption until the end of the 19th century when popular opinion began to lump it in with hard liquors (Wilkie 2010, 76). Lighter did not mean cheap, however, as the rice additives used to lighten Budweiser beer made it more expensive (Dighe 2017, 24). National beer brands like Budweiser therefore contained symbolic and material qualities acceptable (or at least less objectionable) for believers in temperance who did not want to be left out of important socializing. The presence of multiple Budweiser bottles represents the consumers' willingness to pay extra for a lighter beverage that was more oriented to refreshment and temperance but still allowed participation in public social alcohol consumption and identity construction.

Liquor and its attendant vessels were also part of this assemblage of practice. The liquor tumblers are mostly of a type characterized by a narrow base decorated with vertical flat facets and a decorative pattern of 3 textured rings circling just below the rim (Figure 3). These glasses produce an MNV of 5 from a total of 12 specimens. The midden assemblage also contained one corner fragment of a decorated glass vessel, likely a shoulder or body fragment of a fine liquor decanter. Four liquor bottles were also present, all with different base and body styles. While these may seem like low numbers, it is important to remember that whiskey goes a lot further than beer gallon-for-gallon, and glasses and decanters are not disposable. This assemblage also does not contain any of the barrels that whiskey was transported in, which may be deflating the amount of liquor apparent in the assemblage. Whiskey consumption was on the decline in the late 19$^{th}$ century as beer consumption rose (Dighe 2017, 26), but it still remained the most ubiquitous hard liquor in Western saloons (Noel 1996, 25). Common liquor consumption practice in saloons involved mixing it with water, and customers were often given a whiskey bottle and a cup of water to mix for themselves and their companions (Noel 1996, 25). This is another example of the social drinking practices in saloons in which simultaneous entanglement with beverages promoted sociality and formed common identity. Liquor drinking, especially whiskey, was associated with masculinity, but unlike beer it implied a preference for greater intoxication and thus received the most villainization from temperance groups (Dighe 2017, 26). Hard liquors, by

their material properties, are also associated with toughness, as consuming them can be more of a challenge. It could imbue its consumer with a kind of masculinity that could be seen as rough or dangerous to some. This may have been desirable to frontier miners wishing to earn the respect of their peers and a place in the ranks of the manly. These qualities also make it an appropriate participant in a space like a brothel saloon in which Victorian ideals of domesticity were flaunted (Wilkie 2010).

The presence of one glass swizzle stick (a utensil for stirring one's cocktail) in Suboperation C indicates that some of the liquor was consumed through cocktails at the 220. Women generally avoided consuming straight hard liquor, but cocktail consumption was on the rise among American women in the late 19th century as some were beginning to assert autonomy through public drinking at this time (Remus 2014). Thus, cocktail consumption an important locus of strategic manipulation of materials (Remus 2014). While their opportunities to drink were mostly mediated by interactions with men, the women of the 220 may have entangled with cocktails with this in mind. Whether consumed straight or in a cocktail, liquor presented a useful tool for gendered subjects wishing to place themselves in their desired niche among masculine and feminine identities.

Wine and champagne also played a role at this site of consumption. Fragments of wine or champagne bottles representing an MNV of 5 were among the midden artifacts, including one nearly complete vessel. The stemware collection is comprised of 18 specimens representing an MNV of 10. The assemblage shows tremendous variation, with no two goblet styles repeated and bases ranging from 4-7cm in diameter. While the sample size is small, this pattern is likely the result of the stemware's fragility leading to breakage and regular replacement without prioritizing maintaining a matched set. The varying sizes of base likely indicate multiple types of stemware other than wine or champagne glasses, like cognac or sherry snifters (Dixon 2005, 104). The lower number of wine bottles paired with the range of broken stemwares indicates that wine consumption occurred regularly if in lesser quantities than beer.

Wine consumption from stemware is associated with higher-end establishments in the West, as it is connected with high-class refinement of taste and high-class spending (Dixon 2005, 105). It represents a level of luxury above beer and whiskey, as it was almost always imported and significantly more expensive (Remus 2014). Wine and champagne were forms of alcohol acceptable for respectable women to consume at home, but public consumption in a place like this was the domain of the sex worker (Remus 2014). Entanglements with stemware would have lent the consumer of its contents an air of gentility and its specific material is an important part of this. While one can grasp stemware with a fist, the delicate materiality of a wine glass encourages a gentle grip with the fingers. This is in stark contrast to the utilitarian simplicity of bottles, mugs, steins, and glasses for beer which encourages grasping with the whole hand. Those wishing to take on genteel qualities, whether prostitute or patron, would have felt the wine glass' draw.

Suboperation D yielded a very different assemblage from the one in C-E. Wine and champagne bottles dominate this assemblage with a MNV of 10, at least 1 beer bottle, and

no drinkware (Figure 5). The wine bottle collection shows little variation in form. There is variation in base markings (all non-diagnostic), however all possess the same shallow kick and diameter is consistent across nearly all at 5.5cm. The base portions of these bottles show the vertical internal bubbles, lack of embossing, and slight widening up from the base that are characteristic of hand-blowing with a dip mold. The finishes associated with the bases are hand-applied, supporting this conclusion. Dip molding fell out of practice in the US and Europe in the late 1870s, when it was overtaken by full-body molding methods. This means that this deposit represents consumption of wine from bottles older than the 220 building, and possibly older than Ouray itself. The one outlier of this pattern is the 2.5cm diameter base of a champagne bottle. This style of champagne bottle was eccentric, with the tiny base that flared out into a decorated globe before narrowing back into the finish, and likely would have held one of the finer champagnes in the saloon's cabinet. The discreet boundaries of this deposit and almost uniform nature of the assemblage raise the possibility of a single deposition event. Consumption of old wine, fine champagne, and other beverages in a short time span likely indicates some kind of celebration, or perhaps just a particularly conspicuous moment of consumption. Saloons in Ouray were open on all the high holidays and would certainly have witnessed heightened celebration on those days (Gregory 1982). This deposition pattern could also indicate changes in practice among different owners of the saloon—these could be remains of the fine wines advertised by John L. Lawler. Whatever the reason for this distribution, it certainly represents an expensive round of drinks. This indicates that part of this assemblage of practice were punctuated events of celebration in which drinking practices and human selection values relative to beverages changed.

Taken together, these artifacts form a full picture of the 220's assemblage of drinking practice. Here humans, beverages, and their material trappings entangled as Ouray's saloon community pleasurably formed and expressed their identities. As they drank, they took in both the symbolic and the material qualities of their chosen beverages, experiencing entanglement "sensuously and aesthetically" (McKeithan 2012). Humans drank beer from bottles on their own journeys, taking in its familial, refreshing qualities. They drank liquor, selectively associating themselves with its complex amalgam of masculinity and danger. Similarly, wine and champagne lent their qualities to those desiring associations with refinement or engaging in celebration. These entanglements were structured by and facilitated social practices promoting sociality and common identity. Humans' desires relative to these material agents are contextually fluid and thus so are their strategies of entanglement with them. These choices were public and visible, making this a particularly powerful site of consumptive identity construction.

**Conclusion**

New Materialist frameworks like "assemblages of practice" acknowledge the vibrancy and agency of things alongside humans (Antczak and Beaudry 2019). This study of the assemblage of drinking practice at Ouray's 220 saloon demonstrates the potential of these

frameworks to illuminate the relationship between commodity consumption and identity in a new and meaningful way. While identity arises from several coalescing factors, this project has described a significant part of that process for the patrons of the 220. Concepts of the self and society are linked to relations and structures of power, making consumption choices and practices inherently political (Mullins 2011, 115). These behaviors for the working-class patrons and employees of the 220 are therefore of special interest to researchers studying this significant moment in labor history. Collective action among Colorado miners was in motion and gaining momentum at the time of the 220's heyday, as seen in the 1913 Ludlow massacre (Shackel 2009, 59). Gusfield notes that "any point of gathering that is exclusive…for a specific group becomes a potential and actual source of political motivation for a class" (1991, 412). Ouray's 220 was certainly one such gathering place, Studies like this one which seek to describe identity construction processes among working class people and the active role of material components in those processes lay the groundwork for explorations of class consciousness and collective action in relation to dynamic material conditions.

## Figures and Tables

| Base Mark | Level | Manufacture Date |
|---|---|---|
| DSG Co. | C1, C7 | 1878-1893 |
| McKee & Co | C3 | 1872-1899 |
| A | C5 | 1865-1893 |
| CC & Co. | C6 | 1876-1882 |
| MG Co | C7 | 1878-1884 |
| F.H.G.W. | C7 | 1882-1896 |

*Table 1: Suboperation C maker's mark date ranges (from sha.org)*

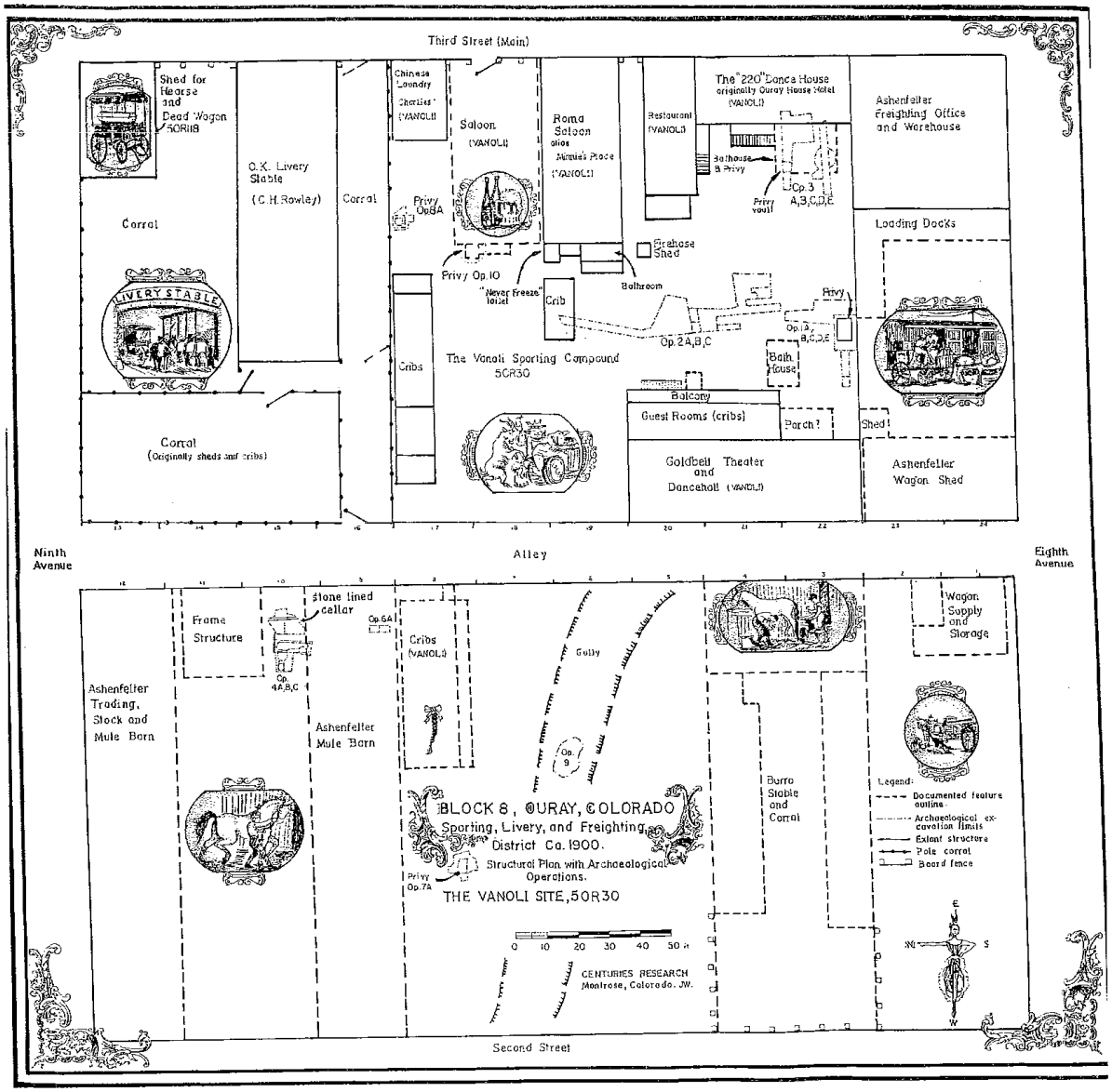


*Figure 1: Map of Ouray's Block 8 showing the 220 and associated excavation units in the top right. Map by Steven Baker in Van Buren et al. 2014.*

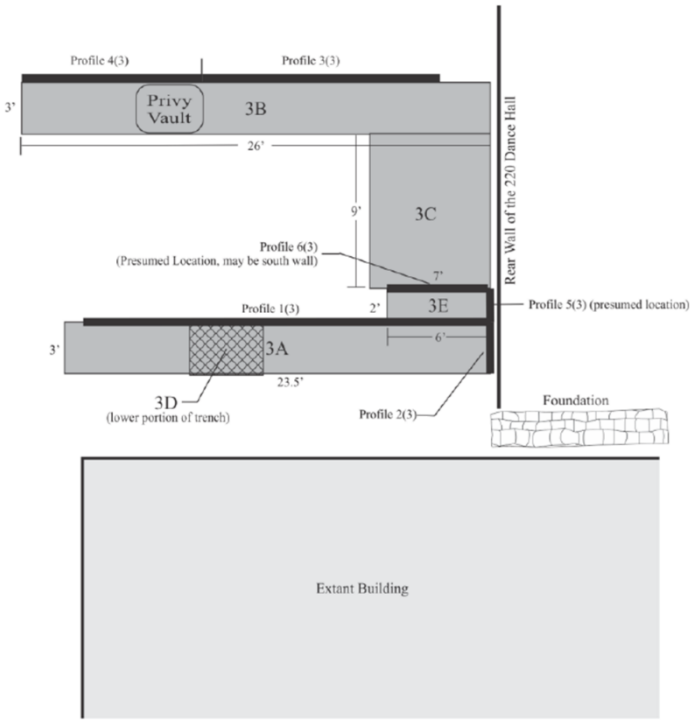


*Figure 2: Operation 3 suboperation map from Van Buren et al. 2014*

*Figure 3: refitting shards of a whiskey glass: rim from C7, base from C3*

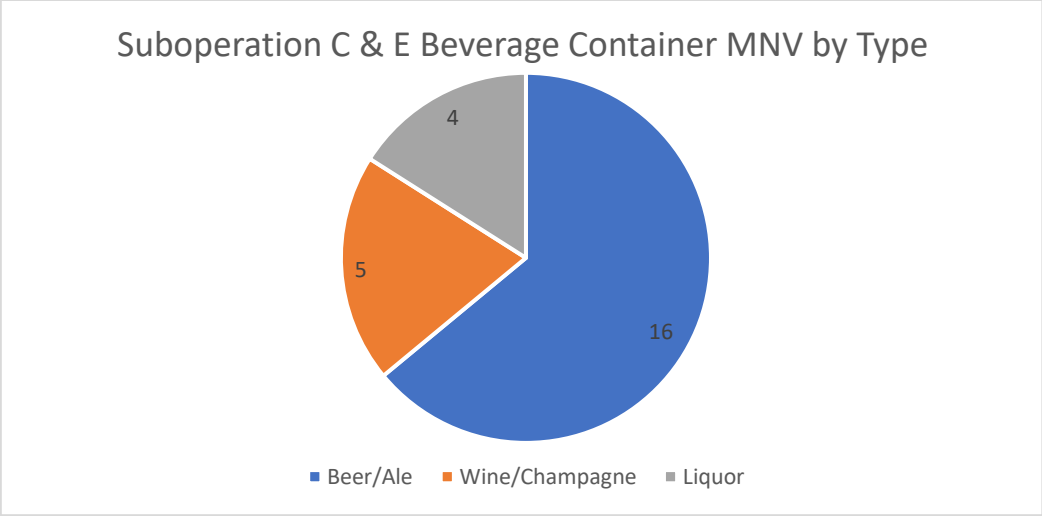


*Figure 4: Beverage container MNV counts by contents type.*

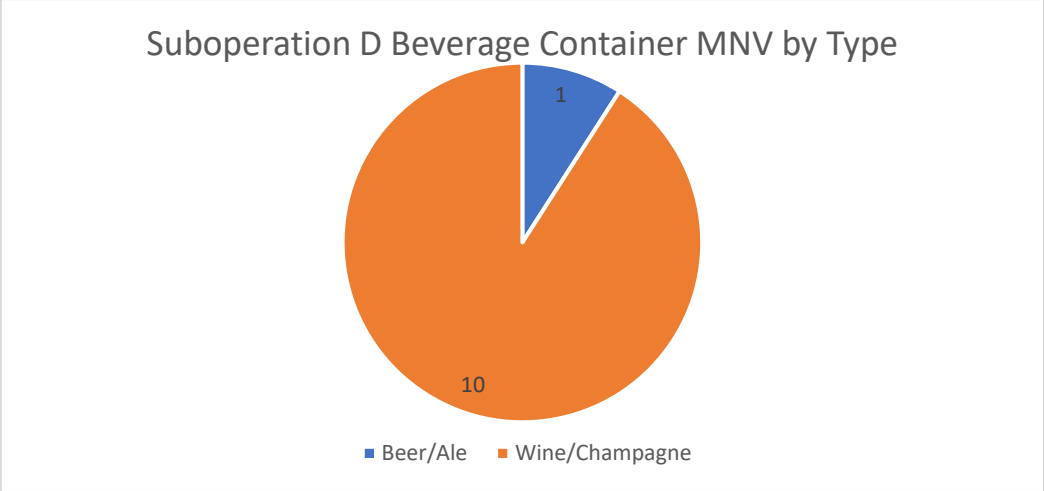


*Figure 5: Beverage container MNV counts by contents type.*

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**Haplorhine Nocturnality: Comparative Selection in Two Exceptional Primates**

Rachel Winter

## Abstract

Tarsiers have historically been categorized alongside the earliest confirmed primates - Omomyoidea - in the Suborder Haplorhini. Due to their shared adaptive characteristics, this proposed lineage is collectively referred to as Tarsiiformes. One similarity between Tarsiiformes has provoked particular intrigue in their origins – nocturnality. While nocturnality is standard within the Suborder Strepsirrhini (lemurs, lorises, and galagos), it is only observed in two species of haplorhines: tarsiers and owl monkeys. The comparison of similarities and differences between these two species may provide context for the evolutionary processes that they have undergone. Tarsiers are the only known nocturnal mammal equipped with full color vision (trichromatic). Alternatively, the owl monkey is the only known primate lacking color perception (monochromatic). Although some of their adaptive strategies are similar, both species have also developed opposing strategies despite their shared evolutionary histories. My comparative examination of the two nocturnal haplorhines is concentrated on a central component of modern evolutionary theory –why would natural selection favor the development of seemingly contradictory adaptations in two species that are both addressing nocturnality? This project draws from theoretical perspectives from biological anthropology, primate paleontology, vertebrate paleontology, primatology, and evolutionary biology. The results place adaptations within the context of the emergence of conditions associated with nocturnality. This project will explore several hypotheses to form a clearer understanding of the evolutionary history of haplorhines.

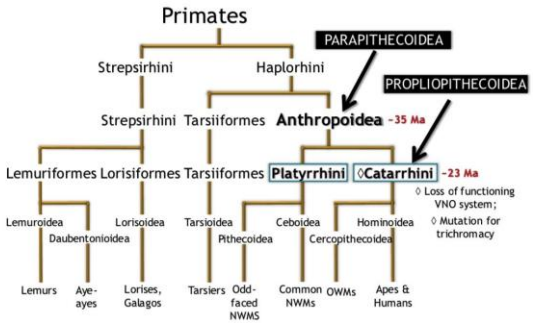


*Figure 1: Primate Classification & Origin Estimations (after Fleagle 2013)*

## Hypotheses:

This project will investigate multiple hypotheses that may explain the relationship between these species and their adaptive development. First, Eocene Tarsiiformes (Omomyoids) may have evolved a retinal fovea and trichromacy for crepuscular (dusk-dawn) activity. Since primates are visually oriented, perhaps there was greater selective pressure for this adaptation to low-light conditions. However, if this is not the case, there may be another benefit to trichromacy not currently recognized.

Secondly, tarsiers may have independently developed trichromacy after diverging from the lineage that led to Anthropoids about 35 million years ago.
If not, tarsier trichromacy must be ancestral & retained from an ancestral form of Tarsiiforme.

Finally, ancestral owl monkeys, after the divergence of platyrrhines about 34 million years ago, were probably diurnal. The loss of all color cone cells and monochromatic state of owl monkey color perception today may have been due to selection for eye enlargement. This would compensate for nocturnality in a haplorhine who, like all haplorhines, lacks a tapetum lucidum but filled an empty nocturnal niche in New World tropical America. It is also possible that there are other variables that could certainly have caused owl monkeys to lose color cone cells.

**Methods**

This project is based on research data obtained from published literature on extinct and extant primate taxa. This enabled a census of the data to establish the timing and appearance of traits.

**Color Perception Biology: Haplorhine Retinal Fovea**

Unlike strepsirhine primates who retain a mammalian tapetum lucidum, haplorhine primates (tarsiers, monkeys, apes, humans) exhibit a derived visual adaptation known as the retinal fovea (Jones et al. 1992).

The retinal fovea is an anatomical feature in the eye that improves the resolution of images by picking up more light. Alternatively, the tapetum lucidum is an ancient mammalian feature that reflects movement in low-light conditions (Ross 1996).

Whereas the tapetum lucidum is beneficial to nocturnal primates, the retinal fovea is more advantageous for the largely diurnal haplorhines. Therefore, it seems counter-intuitive that two haplorhines (tarsiers and owl monkeys) have adopted nocturnal niches. The development of the retinal fovea may point to a novel adaptive strategy in primates.

**Haplorhine Color Perceptivity**

Whereas numerous vertebrates (fish, reptiles, birds) have full trichromatic color perception (sensitive to red-yellow-blue hues), most mammals are dichromatic (blue-yellow perceptive) (Fleagle 2013; Jones et al. 1992). Among primates, trichromacy is restricted to most, but not all, haplorhine primates (Fleagle 2013; Jones et al. 1992).

The Eocene (56 Ma) common ancestor of haplorhines likely had a retinal fovea. This suggests trichromacy but cannot be confirmed (Rose et al. 2012). It is in the lineage that gave rise to the trichromatic nocturnal tarsiers, who may be only moderately distinct from the Eocene common ancestor. It also gave rise to both the dichromatic Platyrrhines and trichromatic Catarrhines.

One of the benefits of the retinal fovea involves color perception via photoreceptors (cone cells). The foveal pit at the back of the haplorhine eye is packed with two types of

cells; rod cells associated with light perception and cone cells associated with color perception.

Strepsirrhines, like most mammals, are dichromatic. In contrast, trichromacy is present in all catarrhines (Old World monkey, apes, humans), tarsiers and one platyrrhine New World monkey (the howler monkey).

**Nocturnal Haplorhines?**

What about color perception in the two nocturnal haplorhines - - the tarsier and platyrrhine owl monkey? The nocturnal tarsiers have trichromatic vision (*they can see in the full color range*). Conversely, the nocturnal owl monkeys have monochromatic vision (*they lack all color perception)*. This incongruity presents an opportunity to investigate the underlying evolutionary and phylogenetic factors contributing to such contrasting visual adaptations between owl monkeys and tarsiers.

Tarsiiformes are thought to have retained nocturnal traits from the ancestral omomyoids, yet they have the trichromatic vision of the more recently diverged diurnal haplorhines (Rose et al., 2012). The platyrrhines, which have dichromatic vision, are descended from Parapithecoids (~35 mya) (Rose et al. 2012). Catarrhines diverged from Parapithecoidea around 23 mya, developing trichromacy at around the same time they diverged (Zhang and Webb 2003).

Trichromacy has arisen in haplorhines on three separate occasions. While the exact dates cannot be confirmed, it would appear to have risen in the tarsier lineage, the Catarrhine lineage (Propliopithecoidea, about 23 million years ago), and once again in the howler monkey lineage (Fleagle 2013; Zhang and Webb 2003; Liman and Innan 2003; Webb et al. 2004).

The multiplicity of this development begs the question: What are the uses of trichromacy? How do various primates use trichromacy to address different adaptive challenges?

**Pheromones and Visual Dependency**

It is the shift from pheromone dependent reproduction to visual dependent reproduction that may indicate an increasing reliance upon visual adaptations. Where as most reptiles and mammals are dependent upon pheromone communication to find reproductive opportunities, primates exhibit more variation. Strepsirhine primates are less dependent on sense of smell, and haplorhine primates are strongly dependent on visual perceptivity (e.g., colorful faces, colorful pelage, secondary sexual characteristics not associated with reproductive anatomy).

Pheromones play a large role in the reproductive selection process for most mammals, which heavily impacts the selective pressure on primate visual system. Some evidence has shown a correlation between primate pheromone usage and visual adaptations. The use of pheromones involves the vomeronasal organ (VNO), an integral organ positioned in the nasal cavity, that is responsible for detecting pheromone signaling that is active during social expressions, such as sexual receptivity (Liman & Innan 2003).

Tarsiers have a fully functional VNO system, indicating that they use pheromones for sexual selection (Evans 2006; Liman and Innan 2003). Owl monkeys have a partially functioning VNO system, as do all platyrrhines, suggesting that they rely in part upon pheromones for sexual selection (Evans 2006; Liman and Innan 2003).

Old World Monkeys (and catarrhines) lost VNO function at roughly the same time as they developed trichromacy, suggesting that a decrease in pheromone reliance may have led to an increase in visual dependency. This coincided with an increased reliance on visual cues for sexual selection (Zhang and Webb 2003). Drill monkey males have red markings on their face to signal that they are of reproductive age (Figure 1). Female drills do not have these same markings. Without trichromatic vision, females would be unable to perceive these markings. Trichromatic vision has played a significant role across many primate taxa for a variety of adaptive strategies. However, where tarsiers and owl monkeys fit within those strategies is uncertain.

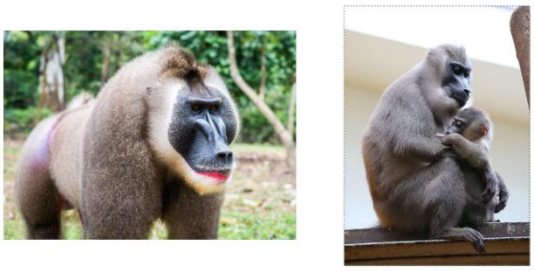

*Figure 2: Male drill monkey on the left, female drill monkey on the right. (Wikipedia 2024)*

**Discussion:**

Why would natural selection favor the retention of nocturnal adaptations in one species and the secondary adoption of nocturnality in another? If natural selection favored trichromacy in tarsiers, then it is more than likely that their ancestral forms had a discrete need for the perception of the color red. There are a handful of proposed benefits associated with trichromatic vision, but none of them seem to apply to tarsiers.

The first of these benefits is that trichromacy aids in diurnal vision, cooperating with a retinal fovea to enhance resolution in well-lit settings (Kawamura 2016).

Trichromatic vision also allows primates to perceive sexual swellings and brightly colored genitals (*e.g.*, baboons, vervets, chimps).

Toxic plants are a threat for folivorous primates, and trichromatic vision may also help to determine which plants are safe to eat. Dangerous plants like poison ivy indicate their toxicity through red, a color that can only be perceived by trichromatic animals. Trichromacy also appears to play a role in the visual detection of ripe fruit as opposed to unripe (Lucas et al. 2003; Sánchez-Solano et al. 2020).

Owl monkeys do not perceive color at all, suggesting that trichromacy does not provide a benefit to nocturnal vision (Fleagle 2013).

**Conclusion:**

Based on known benefits associated with trichromacy, tarsiers have no need for full-color vision. However, there may be unknown advantages to nocturnal trichromacy.

What about the nocturnal, but singularly monochromatic, owl monkey? Unlike tarsiers who descended from large-eyed nocturnal omomyoid ancestors, owl monkeys descended from a small-eyed diurnal ancestor. Selection appears to have operated on eye enlargement but at the expense of color cone cells. As a result, the owl monkey is the only nocturnal anthropoid.

Whether trichromacy was a retained or derived adaptation, tarsiers appear to have a use for color perception that owl monkeys do not, and this could provide insights on the importance of color perception not only in primates, but also in vertebrates.

Did the Eocene Tarsiiformes (Omomyoidea) have trichromacy? It is possible that genetic testing of tarsiers or other haplorhines could provide this information. Whether or not they had this adaptation would allow for a clearer picture of the development of primate visual adaptations and their ancestral history.

Did tarsiers inherit trichromacy from ancestral Omomyoidea or did it occur independently? If tarsiers did independently develop trichromacy, the reasons why it was selected for could provide insight on the adaptive benefits of trichromacy as well as their evolutionary past.

What is the relationship between degree of VNO reproductive reliance and visual dependency? Based on the timing of the development of trichromacy in catarrhines and the corresponding loss of VNO function, it seems like primates have an evolutionary history of becoming increasingly visually reliant.

Owl monkeys, however, lost the ability to see any color. Does this indicate a loss of visual dependence? It may be that owl monkey visual adaptations took another direction, one that enlarged the size of their eyes at the expense of color cone cells. More genetic studies are needed to explore this, but it could be possible that there is a genetic relationship between color cones and eye enlargement that might be observable in owl monkeys.

In order to better understand the emergence of trichromacy (or loss thereof), a broader understanding may need to be synthesized. What do other vertebrates gain from trichromacy and what types of niches favor this adaptation? Comparing trichromacy in primates to that of other vertebrates could offer perspective on its application across a variety of niches. If there is a benefit to trichromacy that is not currently known, this data could illuminate factors that contribute to its adaptive success.

**Acknowledgements**

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