

– ARTICLE –

Prey Ranking and Targeting in the Early Colonization of Pacific Islands: A Fijian Case Study

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Abstract

Archaeological research in the western Pacific has documented a range of terrestrial fauna that may have been the target of Lapita-era foraging. How can our knowledge of extinct and extant fauna aid in understanding prey ranking and targeting by foragers in the early years of island colonization? This study employs the Prey Choice model and biological data related to foraging (i.e., ease of mass capture, locomotor skills, hazards, processing requirements, and caloric yield) to identify the ranking of potential foraging targets in Lapita-era Fiji. Using GIS-based analyses of vegetation and topography, the geographic distribution of different prey are predicted for the island of Viti Levu. Tortoises, ground-dwelling forest birds, colonial roosting fruit bats, and colonial nesting seabirds are identified as the highest-ranked prey. Large but hazardous crocodiles and small, highly mobile skinks are identified as low-ranked prey. These organisms would have occupied distinctly different habitats and may have supported distinct and regional hunting/foraging practices in the centuries following Lapita colonization.

Keywords: prey choice; terrestrial foraging; Fiji; Lapita

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1. Modelling Foraging for Pacific Island Archaeological Contexts

Melinda S. Allen's doctoral research of archaeological deposits from the island of Aitutaki, Cook Islands (Allen 1992), was one of the first applications of Human Behavioral Ecology (HBE) to a Pacific Island context. This, and many of Allen's subsequent studies in East Polynesia (Allen 1996, 2002, 2004, 2007, 2012, 2017; Allen and Holdaway 2010; Morrison and Allen 2017; Nims *et al.* 2024), employ an evolutionary framework and mathematical models to explicitly measure the accumulated outputs of foraging in the past, which are further analysed to examine trends and changes to prey targets, modification of technologies used to capture and process animals, and the dynamic responses of animal populations to human foraging pressure. These studies have provided unique and robust insights into the effects of human colonization on East Polynesian islands, and subsequent cultural and ecological change.

The theory and methods exhibited by Allen's applications of HBE, zooarchaeology, and ecological modelling provide a ready-made toolset for the investigation of West Polynesia, in particular the islands that were colonized as part of the expansion of Lapita peoples from the Bismarck archipelago ca. 3300 cal years BP (Kirch 1997, Summerhayes 2010). Archaeological research has determined that Lapita peoples subsisted on diverse fauna, with marine fauna (indicated by the remains of mollusk shells and fish bone) providing the most unequivocal evidence for subsistence strategies that targeted marine organisms (Butler 1988; Groube 1971; Kirch 2021; Nagaoka 1988). However, evidence in the form of microfossils, terrestrial animal bone, and the isotopic analysis of human bone has also indicated a very flexible and ecologically targeted subsistence system that included terrestrial foraging in addition to marine foraging, and low-level food production of carbohydrate-rich plants (e.g., banana [*Musa* spp.] and taro [*Colocasia esculenta*]) within the first centuries of colonization (Horrocks and Bedford 2005, Horrocks *et al.* 2013). The remains of fruit bats, extinct giant tortoises, ground-dwelling forest birds, flighted forest birds, skinks, geckos, crocodiles, and freshwater fish (Bedford 2006; Bouffandeau *et al.* 2019; Field *et al.* 2009; Hawkins 2015; Hawkins *et al.* 2016; Kirch 2021; Worthy and Clark 2009; Valentin *et al.* 2010) have been recovered from archaeological deposits, providing abundant evidence for targeted foraging of large-bodied, or easily collected terrestrial prey. The isotopic analysis of Lapita-era human remains from Palau, Vanuatu, Fiji, and Tonga confirms the varied input of terrestrial and marine foraged foods on human diets, from diverse island environments as well as domesticate production (pig and chicken) (Fenner 2021; Field *et al.* 2009; Herrscher 2018; Kinaston *et al.* 2015; Stone *et al.* 2019).

Most notably with regards to HBE applications, research in Vanuatu (Hawkins 2015) has examined Lapita foraging on Efate Island using both Prey Choice and Patch Choice models. Based upon the frequency and chronology of identified faunal remains from the site of Teouma, Hawkins employs a coarse dichotomous ranking system based on body size (large-bodied prey vs. small-bodied prey) to determine that the earliest Lapita foragers targeted a variety of organisms in both marine and terrestrial patches (2015:64-65). Following an initial focus on fruit bat and sea turtles by the colonizing Lapita community, the most sought taxon was the large-bodied extinct giant tortoise, tentatively identified as *Meiolania damelipi*. During later phases of the Lapita occupation, forest birds (ground-dwelling and flighted) and sea turtles show a marked decline in frequency, while giant tortoises reveal the opposite: their remains increase, suggesting foragers preferentially targeted them, and perhaps even travelled long distances to procure them (Hawkins 2015:163). Hawkins'

analyses suggest that foraging pressure played a role in the targeting of prey. Low-ranked (small-bodied) prey such as fruit bats were continuously targeted in local patches, but the high-ranked (large-bodied) birds and tortoises were sought from increasingly distant patches after they became locally depleted. Cut-marks and the differential presence of tortoise limb bones in the later Lapita deposits suggest that foragers selectively butchered the giant tortoises to retrieve the largest cuts of meat, leaving the less useful portions behind (Hawkins 2015:192-193). Within 300 years of human arrival on Efate, the tortoises had disappeared from the island. Foraging pressure, the introduction of pigs and rats, and other biogeographical changes all likely played a part in their extinction (Hawkins *et al.* 2016).

Hawkins' analyses have implications for other islands in West Polynesia that had similar faunal and cultural sequences, but which lack a similarly rich and well-documented zooarchaeological record for the Lapita period. Paleontological and archaeological research in Fiji has documented the presence of many taxa similar to those recovered on Efate (Anderson *et al.* 2010; Hawkins *et al.* 2016; Steadman 2006; Worthy and Clark 2009). The use of prey ranking, as well as prey and patch choice modelling, is also a useful avenue for further exploration.

This study employs the Prey Choice model (Krebs and Davies 1978) and biological data related to foraging (i.e., ease of capture, processing requirements, and caloric yield) to identify the ranking of potential foraging targets in Lapita-era Fiji. As a second set of analyses, the habitat patches that may have sheltered these organisms are modelled via the analysis of terrain, elevation, temperature, and vegetation using modern data and a geographic information system (ArcGIS Pro). Combining these data with ranked prey data, the landscape of Lapita-era habitats, and the distribution of high-ranked prey at colonization is offered as a reconstruction and model for future research. Commentary on model quality and limitations is included in the discussion section.

2. Foraging Targets in the Lapita Period

The Prey Choice model (Kaplan and Hill 1992) suggests that foragers seek and pursue prey based upon prior knowledge of organism availability and the probability of foraging success. Further, foragers' targeting of prey seeks to maximize caloric returns (especially from protein and fat) and minimize the costs associated with foraging, especially in the form of energy expenditure and time expenditure. Given the antiquity of human presence in Wallacea, Island Southeast Asia, and Island Melanesia, and the similarity of flora and fauna in the islands of Remote Oceania, it is likely that Fiji's Lapita foragers, when seeking terrestrial prey, relied upon transmitted knowledge to inform their decisions on where to forage, and what to seek. Birds, bats, reptiles, amphibians, and insects would have been the most familiar, and required procurement tools (nets, spears, throwing stones) that they would have been proficient in manufacturing and handling. They also may have taken advantage of the naiveté of these particular island animals, that would not have recognized the initial landing of humans as the arrival of a potential predator. These factors suggest that initial foraging trips into the interior of islands would have targeted similar groups of animals known to have been prey elsewhere. They also would have targeted animals that were easily located and captured and offered an opportunity for a greater return relative to the cost expended.

Paleontological, archaeological, and biological surveys of the Southwest Pacific region (excluding New Zealand) provide a list of potential Lapita-era prey for Viti Levu, Fiji, that would have been accessible to foragers on foot (**Table 1**). The generated list includes taxa that are extant in the

Fiji Islands today, as well as those that are extinct and known only from the fossil record but were present at the time of human colonization (i.e., giant land tortoises, ground-dwelling birds, and some species of iguana). This list *excludes* birds that can fly to escape predation and generally nest in solitary arrangements in high tree canopies or cliffs (i.e., perching birds, owls, herons, and falcons) and flighted seabirds that breed on offshore atolls and pinnacles (i.e., boobies, albatrosses). The list *includes* ground-dwelling birds, insects, or bats that were flightless or poor fliers (i.e., megapodes and rails) or nest in burrow colonies at high elevation in the interior (seabirds such as petrels and shearwaters). The list also *includes* bats that roost in tree canopy colonies (fruit bats) or cave vault colonies (insect bats), but it *excludes* introduced rats (*Rattus exulans*, *Rattus praetor*), under the premise that these populations would have required several years to increase in number following initial colonization of Viti Levu.

The Prey Choice model has been developed via the study of hunters and gatherers' ability to evaluate foraging choices within an evolutionary framework. Described in detail elsewhere (Broughton 1997; Kennett and Winterhalder 2006; Smith 1983; Smith and Winterhalder 1999; Stephens and Krebs 1986) and also developed for cases in the Pacific Islands (Allen 1992; Field and Graves 2015; Field *et al.* 2016; Hawkins 2015; Moniz Nakamura 1999), these models require three components to be identified: the decisions related to foraging, currencies used to measure the costs and benefits of foraging options, and constraints on both the decisions and currencies. The Prey Choice model assumes that foragers will seek options that will maximize their energy capture (calories, which can be estimated by proxy using body weight), taking into account the cost expended on pursuing, capturing, and processing prey (Kaplan and Hill 1992). These models use a ranking system to order prey targets into a hierarchy of choices. Organisms that would yield a high energy return relative to the cost of acquisition and processing would be deemed "high rank" and are expected to have been the focus of foraging bouts. In contrast, low-return, high-processing cost organisms would be "low rank" and be selected by foragers only when other options were not available. The model is used to make predictions about which prey foragers will seek under varying social or environmental conditions, where foragers will only add low-ranked prey when the availability of the highest-ranked prey is low. In this way, subsistence choices could change over time as a flexible response to changing conditions, with lower-ranked prey being taken more often in cases where preferred prey decline as a result of intensive foraging (Broughton 1997; Nagaoka 2001, 2002). Processing and capture techniques can also alter the position of prey in the rank by reducing processing and capture costs. For example, smaller-bodied prey that are collected *en masse* using nets or traps can be higher ranked than larger prey when the net resource return rate of the group exceeds the returns of a single large prey item.

In order to operationalize the Prey Choice model in a case study, anthropologists have the burden of determining the factors that influence foraging efficiency. Typically, taxa are placed in an ordered ranking, which indicates the profitability of prey (net energy return) relative to the cost of pursuit, capture, and processing. This has historically been measured using scaled proxy measures, including individual body size (roughly equivalent to energetic return of harvested meat), and locomotor skills (flight-capable, flightless, terrestrial, or arboreal) that would affect capture (Broughton 1997). These data can be extracted from modern biological studies of Pacific fauna. The scaling of these costs is ordinarily ranked according to a rough estimate of energetic investment (search and capture costs) and return (net energy yield). Organisms with smaller body sizes, but

which may be susceptible to mass capture, can be included in ordinal rankings. In these cases, the total body mass of captured individuals is used to determine prey rank. These *en masse* calculations can be estimated from biological surveys of nesting sites, or ethnographic studies of collected organisms from a net or trap.

In this model for Viti Levu, all the prey are assumed to have been naïve to the threat posed by humans during the initial phases of island colonization. Strategies to evade capture, such as fleeing, hiding, and silencing, are assumed to have been minimal; breeding calls, nestling sounds, and scat would have all been used to detect and locate solitary organisms and colonies. It is assumed here that Lapita foragers would have had a working knowledge of nets, clubs, and spears, and could have used these tools to capture terrestrial prey, including birds, reptiles, mammals, and amphibians. Processing would have included butchery, skinning, and discard of inedible parts. Cooking in the Lapita period likely included simple open-fire roasting and more complex earth-oven roasting. Some organisms would have required more post-capture processing. Based upon Hawkins' (2015) analyses of giant-turtle remains, the reptiles were subject to butchery and may have required more intensive physical processing after capture (e.g., moderate butchery and skinning to remove tough, inedible skin). These prey are ranked as having higher handling and processing costs, as opposed to prey that could have been minimally gutted and roasted whole (such as birds or fruit bats), which require less effort and thus lower cost. Prey that pose a hazard to the forager, such as dangerous bites from crocodiles or toxins from some snakes, are ranked as having a higher handling cost than prey without such defences. Foragers may have seen these prey as potentially costly despite their larger body size.

Calculation of the energetic cost of searching, capturing, and processing prey is beyond the scope of this study. Because of this, the Prey Choice ranking for each prey item is estimated based upon ordinal scoring within five proxy measures: prey body mass, susceptibility to mass capture, locomotor skills of the prey, processing requirements after capture, and possible hazards during capture (**Table 2**). Each proxy measure is unweighted relative to each other, but the ranks within span the same range of 1-5; this range was selected arbitrarily but is meant to allow for differentiation between diverse prey, which range from insects to birds to large reptiles. For example, a frequency distribution was calculated to create four weight classes to span prey body mass (less than 1 gram to 99 kilograms), and a fifth class was added for organisms with extreme weights, primarily the giant tortoise *Meiolania* spp., which could have exceeded 300 kilograms. Similarly, the susceptibility to mass capture was ranked 1-5; organisms that roost or nest in colonies were ranked higher, with the highest ranks for daily roosters (such as fruit bats), and the lowest for organisms that nest or roost singly. This ranking seeks to estimate the mass-capture effect (i.e., capturing 20+ burrow-nesting seabirds from a large colony, which would be equivalent in body weight to a large ground-dwelling but single-nesting forest bird). The combined summation of ordinally scaled attributes determines a prey's rank in the Prey Choice model. Using this scale and data from modern, historic, and extinct Fijian taxa, Table 3 presents all the taxa in a ranked order (10-18). Supporting data are appended in the Online Supplement.

Table 1: List of terrestrial prey types known from archaeological, paleontological, and biological surveys.

Prey Type	Regional Archaeological Evidence	References
Tortoise		
<i>*Meiolania</i> spp.	New Caledonia (Tiga, Pindai Caves)	Daza <i>et al.</i> 2015
		Anderson <i>et al.</i> 2010
	Vanuatu (Teouma, Vao, Urupiv, Port Olry, Arapus)	White <i>et al.</i> 2010
		Hawkins 2015 Hawkins <i>et al.</i> 2016 Pike <i>et al.</i> 2022
	Fiji (Yanuca, Naigani)	Irwin <i>et al.</i> 2011 Worthy and Clark 2009
Iguana		
<i>*Lapitiguana impensa</i> <i>Brachylophus fasciatus</i> <i>Brachylophus vitiensis</i> <i>Brachylophus bulabula</i> <i>*Brachylophus</i> undescribed	Fiji (Qaranioso II, Qaranipuqa)	Pregill and Worthy 2003 Worthy and Clark 2009 Irwin <i>et al.</i> 2011 Morrison 2003 Worthy and Anderson 2009 Irwin <i>et al.</i> 2011 Harlow and Biciloa 2001
	Tonga (Tongoleleka)	Pregill and Steadman 2004 Steadman <i>et al.</i> 2002
Boa Snake		
<i>Candoia bibroni</i>	New Caledonia (Tiga)	Daza <i>et al.</i> 2015
<i>Ogmodon vitianus</i>	Fiji (Lakeba, Malaqereqere, Qaranioso II)	Best 1984 Worthy and Clark 2009 Steadman <i>et al.</i> 2002b Harlow and Shine 1992 Morrison 2003 Carille 2012
	American Samoa (Ana Pe’a Pe’a)	Steadman and Pregill 2004
Ground Frog		
<i>*Platymantis megabotoniviti</i> <i>Platymantis vitiensis</i> <i>Platymantis vitianus</i>	Fiji (Malaqereqere)	Worthy and Anderson 2009 Worthy and Clark 2009 Osborne <i>et al.</i> 2013 Narayan <i>et al.</i> 2008 Worthy 2001a Morrison 2003
Geckos and Skinks		
<i>Cryptoblepharus eximius</i>	New Caledonia (Tiga)	Daza <i>et al.</i> 2015
<i>Emoia caeruleocauda</i> <i>Emoia campbelli</i> <i>Emoia concolor</i> <i>Emoia cyanura</i>	Fiji (Malaqereqere)	Morrison 2003 Worthy and Clark 2009 Morrison 2003 Worthy and Anderson 2009
<i>Emoia impar</i>	American Samoa (Ana Pe’a Pe’a)	Steadman and Pregill 2004
<i>Emoia mokosariniveikau</i> <i>Emoia nigra</i> <i>Emoia parkeri</i> <i>Emoia trossula</i> <i>Gehyra mutilata</i> <i>Gehyra oceanica</i> <i>Gehyra vorax</i> <i>Hemidactylus garnotti</i> <i>Hemiphyllodactylus typus</i> <i>Lepidodactylus lugubris</i> <i>Lepidodactylus manni</i> <i>Lipinia noctua</i> <i>Nactus pelagicus</i>		

Crocodile		
<i>*Volia athollandersoni</i>	Vanuatu (Arapus)	Mead <i>et al.</i> 2002
<i>*Mekosuchus kalpokasi</i>	Fiji (Volivoli, Wainibuka, Naigani)	Worthy and Clark 2009 Irwin <i>et al.</i> 2011 Worthy and Anderson 2009 Molnar <i>et al.</i> 2002
	New Caledonia (Pindai Caves)	Anderson <i>et al.</i> 2010
Ground-dwelling birds		
<i>*Megapodius freycinet</i>	Fiji (Qaranipuqa, Wakea, Navatu 17a, Qaranioso II)	Baptista <i>et al.</i> 1997
<i>Megapodius amissus</i>		Worthy et al 1999
<i>Megapodius alimentum</i>		Worthy 2000
<i>Megapodius molistructor</i>		Worthy 2001b
<i>Megavitiornis altirostris</i>		Worthy 2004
<i>Gallicolumba stairi</i>		Worthy and Clark 2009
<i>Natunaornis gigoura</i>		Steadman 2006
<i>Nesoclopeus poecilopterus</i>		Irwin <i>et al.</i> 2011
<i>Gallirallus philippensis</i>		Best 1984
<i>Porzana tabuensis</i>		Tonga (Tongoleleka)
<i>Porphyrio porphyrio</i>		Steadman <i>et al.</i> 2002a
<i>*Gallirallus</i> sp.	American Samoa (To’aga)	Steadman 2006
Beetle larvae		
<i>Xixuthrus</i> sp.	Fiji †	Ryan <i>et al.</i> 1989
<i>Olethrius</i> sp.		Duffels and Ewart 1988 Dillon and Dillon 1952 Watling 1986
Cicada		Ryan <i>et al.</i> 1989
<i>Raiateana knowlesi</i>	Fiji †	Duffels and Ewart 1988 Watling 1986
Colonial, burrow-nesting seabird		
<i>Pterodroma brevipes</i>	Fiji (Volivoli II, Korobasabasaga†)	Watling 2004
<i>Pterodroma</i> sp.		Worthy and Clark 2009
<i>Pseudobulweria macgillivrayi</i>		Worthy and Anderson 2009
<i>Pseudobulweria rostrata</i>		Roth and Hooper 1990
<i>Puffinus pacificus</i>		
Colonial, tree-roosting bats		
<i>Mirimiri acrodonta</i>	Fiji, Tonga, Samoa† Fiji (Volivoli II, III)	Pernetta and Watling 1978
<i>Pteropus samoensis</i>		Worthy and Clark 2009
<i>Pteropus tonganus</i>		Worthy and Anderson 2009 Wilson and Mittermeier 2019 Miller and Wilson 1997
Colonial, cave-roosting bats		
<i>Notopteris macdonaldi</i>	Fiji† Fiji (Qaranioso II)	Pernetta and Watling 1978
<i>Emballonura semicaudata</i>		Worthy and Clark 2009
<i>Tadarida bregullae</i>		Worthy and Anderson 2009 Waldien and Scanlon 2021 Wilson and Mittermeier 2019
* extinct		
†19 th century observation		
‡modern data		

Table 2. Attributes and ordinal scaling (with an ordinal value for each) for body mass, susceptibility of mass capture, locomotor skills, processing requirements, and hazards.

Attributes	Rank
<i>Body mass (kg)</i>	
> 100 kg	5
15-99 kg	4
1-15 kg	3
400-999 g	2
1 - 399 g	1
<i>Susceptibility to Mass Capture</i>	
High (daily colonial roost)	5
Moderate-high (nocturnal colonial roost)	4
Moderate (annual colonial nest)	3
Low (singular nest/roost)	1
<i>Locomotor skills</i>	
slow, terrestrial	5
slow, semi-terrestrial	5
slow, arboreal	4
moderate, terrestrial	4
moderate, semi-terrestrial	4
moderate, terrestrial (inside burrow)	4
moderate, arboreal	3
moderate, semi-arboreal	3
moderate, semi-arboreal	3
moderate, arboreal (while roosting)	2
moderate (while roosting)	2
fast, terrestrial	1
fast, arboreal	1
<i>Processing requirement</i>	
none	5
low, skinning and butchery	4
moderate, skinning and butchery	3
<i>Possible hazard</i>	
none	5
minor bite/tail swipe	3
moderate tail swipe	2
major bite, tail swipe	1

Table 3. Ranked Order for modern, historic, and extinct Fijian taxa.

Taxa	Prey Type	Rank
<i>Pteropus samoensis</i>	Colonial, tree-roosting bat	18
<i>Pteropus tonganus</i>	Colonial, tree-roosting bat	18
<i>Raiateana knowlesi</i>	Cicada	18
<i>Megapodius amissus</i>	Ground dwelling bird	17
<i>Megapodius molistructor</i>	Ground dwelling bird	17
<i>Megavitiornis altirostris</i>	Ground dwelling bird	17
<i>Natunaornis gigoura</i>	Ground dwelling bird	17
<i>Puffinus pacificus</i>	Colonial, burrow nesting seabird	17
* <i>Meiolania</i> spp.	Tortoise	17
<i>Megapodius alimentum</i>	Ground dwelling bird	16
* <i>Megapodius</i> sp.	Ground dwelling bird	16
<i>Pseudobulweria rostrata</i>	Colonial, burrow nesting seabird	16
<i>Pterodroma brevipes</i>	Colonial, burrow nesting seabird	16
<i>Pterodroma</i> sp.	Colonial, burrow nesting seabird	16
<i>Pseudobulweria macgillivrayi</i>	Colonial, burrow nesting seabird	16
<i>Candoia bibroni</i>	Boa snake	16
<i>Notopteris macdonaldi</i>	Colonial, cave-roosting bat	16
<i>Emballonura semicaudata</i>	Colonial, cave-roosting bat	16
<i>Tadarida bregullae</i>	Colonial, cave-roosting bat	16
<i>Xixuthrus</i> sp.	Beetle larva	16
<i>Olethrius</i> sp.	Beetle larva	16
<i>Mirimiri acrodonta</i>	Non-colonial tree-roosting bat	15
<i>Nesoclopeus poecilopterus</i>	Ground dwelling bird	15
<i>Porphyrio porphyrio</i>	Ground dwelling bird	15
<i>Gehyra oceanica</i>	Skinks and geckos	15
<i>Nactus pelagicus</i>	Skinks and geckos	15
* <i>Platymantis megabotoniviti</i>	Ground frog	15
<i>Gallicolumba stairi</i>	Ground dwelling bird	14
<i>Gallirallus philippensis</i>	Ground dwelling bird	14
<i>Porzana tabuensis</i>	Ground dwelling bird	14
* <i>Gallirallus</i> sp.	Ground dwelling bird	14
<i>Platymantis vitiensis</i>	Ground frog	14
<i>Platymantis vitianus</i>	Ground frog	14
<i>Gehyra mutilata</i>	Skinks and geckos	14
<i>Gehyra vorax</i>	Skinks and geckos	14
<i>Lepidodactylus lugubris</i>	Skinks and geckos	14
<i>Lepidodactylus manni</i>	Skinks and geckos	14
<i>Lipinia noctua</i>	Skinks and geckos	14
<i>Ogmodon vitianus</i>	Boa snake	14
* <i>Lapitiguana impensa</i>	Iguana	13
<i>Brachylophus fasciatus</i>	Iguana	13
<i>Brachylophus vitiensis</i>	Iguana	13
* <i>Brachylophus undescribed</i>	Iguana	13
* <i>Volia athollandersoni</i>	Crocodile	13
* <i>Mekosuchus kalpokasi</i>	Crocodile	13
<i>Cryptoblepharus eximius</i>	Skinks and geckos	12
<i>Emoia caeruleocauda</i>	Skinks and geckos	12
<i>Emoia campbelli</i>	Skinks and geckos	12
<i>Emoia concolor</i>	Skinks and geckos	12
<i>Emoia cyanura</i>	Skinks and geckos	12
<i>Emoia impar</i>	Skinks and geckos	12
<i>Emoia mokosariniveikau</i>	Skinks and geckos	12
<i>Emoia nigra</i>	Skinks and geckos	12
<i>Emoia parkeri</i>	Skinks and geckos	12
<i>Emoia trossula</i>	Skinks and geckos	12
<i>Hemidactylus garnotti</i>	Skinks and geckos	12
<i>Hemiphyllodactylus typus</i>	Skinks and geckos	12
* extinct		

3. Highest Ranked Prey: Tortoises, Ground Dwelling Birds and Burrow-nesting Seabirds, Bats, Insects, and Insect Larvae (rank 18-16)

The largest highly-ranked taxon was the extinct giant horned tortoise, *Meiolania* spp., that would have weighed several hundred kilograms and been armoured with a heavy carapace and a clubbed tail. Known from two archaeological contexts and a single fossil in Fiji, this tortoise would have been slow moving and limited to defending itself by retracting its head and limbs and laying undetected in vegetation. Whether its tail would have been hazardous is unknown. Demographic reconstruction for other giant land tortoises suggests that *Meiolania* spp. may have been relatively abundant in more open regions, especially the leeward sides of islands, which contain sparser and more low-lying vegetation, as opposed to dense forest. Hunting these animals would have required skilled detection, as they move quietly and do not attract predators with noise or calls. Once captured, their size and carapace would have required a greater investment of energy and time for butchery and transport (Hawkins 2015).

Also highly ranked were the ground-dwelling birds, especially megapodes, which have a large body size, are predominantly terrestrial and reside in interior forests, and which utilize earth and leaf-litter to incubate their eggs in semi-permanent mounds (*Megapodius amissus*, *M. molistructor*, *M. alimentum*, and *Megavitiornis altirostris*). These species are known from the archaeological and paleontological record in Fiji, and others are likely to have been extant, but are not yet identified. Foragers encountering these birds would have been able to identify their annual nesting sites for future harvesting and also enjoyed few procurement hazards and low processing costs. Adults, chicks, and eggs would have been easily collected, and their large body and egg size provided a rich caloric yield. Processing would have been limited to gutting and roasting whole.

Colonial, burrow-nesting seabirds such as petrels and shearwaters (*Pterodroma brevipes*, *Pseudobulweria macgillivrayi*, *P. rostrata*, and *Puffinus pacificus*) are similarly high ranked due to their large body size and ease of mass capture. Modern breeding colonies and burrows exist at the higher elevations of remote islands in Fiji (Watling 2004), but 19th century observations identified similar colonies in the highlands of Viti Levu (Von Hugel 1875, in Roth and Hooper 1990:76-77) at elevations above 400 meters and distances of 70 km from the coast. Their bones have also been found in coastal caves in Western Viti Levu, indicating the possible presence of colonies in that region in antiquity (Worthy and Clark 2009). Although they visit their burrows under the cover of darkness, their calls would have alerted foragers to their presence. Foragers would have easily collected adults, chicks, and eggs, which could have been minimally processed and consumed with no hazard to the forager.

The large-bodied (15 kg) and giant flightless pigeon (*Natunaornis gigoura*) is known only from the fossil record on Viti Levu (Worthy 2001b). Its breeding and nesting habits are unknown, but it likely subsisted on palm fruits and seeds of the forest floor. Like the extinct Columbids of the Indian Ocean (including the famous Dodo bird), these birds may have been identified via their calls and captured by hand with minimal hazard. They could also have been roasted whole, and nesting pairs collected along with chicks and eggs.

Other highly ranked taxa included colonial-tree roosting fruit bats (*Pteropus samoensis* and *Pteropus tonganus*). These animals have a larger body size and are found in gregarious and noisy colonies during the daylight hours, but can be difficult to procure as these are positioned high in the canopies of tall trees. Once a colony is discovered, bats can be pelted with stones or mass captured

using nets. The Lapita deposits of Teouma, Efate have abundant remains of fruit bat, indicating that these animals were targeted *en masse*. Their moderate body size, lack of mobility when knocked to the ground, and minimal hazard from bites or wing swipes would have made them easy targets for foragers. Their skin and hair would have required no processing and could have been scorched off as part of the roasting process.

Smaller, colonial-cave roosting insect bats (*Notopteris macdonaldi*, *Emballonura semicaudata*, and *Tadarida bregullae*) may have been similarly procured from the vaulted ceilings of caves. Nets, burning torches, and branches could be used to simply sweep colonies off of rocks and capture them *en masse*.

Another colonial nester, the Fijian cicada (*Raiateana knowlesi*), emerges every eight years in immense numbers on the forest floor of Fiji's interior. With large bodies and relatively slow locomotor skills, these insects can be collected *en masse*, providing a rich harvest and requiring the most minimal processing prior to consumption. Once a hatching cycle began, the calls and vibrations of these insects would have been detectable over several weeks during the day and night, attracting foragers to their location.

Other prey items that are highly ranked are non-hazardous organisms that are widely found in forested environments, but in singular numbers. The large bodied non-colonial Monkey faced bat (*Mirimiri acrodonta*) is also included as high-ranked due to its size, but its procurement would have targeted single individuals or females with young from clumps of tall ferns. The larvae of the Fiji long-horn beetle (*Xixuthrus* sp.) and coconut beetle (*Olethrius* sp.) are of immense size compared to most insects and remain a local delicacy in Fiji. These can be manually extracted from rotting logs with simple tools. The Fijian boa snake (*Candoia bibroni*) is also of larger body size and non-venomous, but arboreal and not easily detected or procured from the ground. Securing this prey would have required some climbing and grappling once the snake was targeted.

4. Middle-Ranked Prey: Small ground dwelling birds, large geckos, and frogs (rank 15-14)

The middle-ranked prey items include animals with a range of body sizes, but which have qualities that would have made them difficult (or dangerous) to procure and process, and with no opportunities for mass capture. For example, the purple swamp hen (*Porphyrio porphyrio*), extinct bar-winged rail (*Nesoclopeus poecilopterus*) and the diminutive rails and crake (*Galicolumba stairi*, *Gallirallus philippensis*, *Gallirallus* sp., *Porzana tambuensis*) are/were larger ground-dwelling birds, and may have been more volant than megapodes, but have/had more dispersed (and hidden) nesting behaviors. Obtaining these prey would have required speed and/or nets for detecting and catching them in marshy environments and underbrush.

Middle-ranked prey also included the large-bodied geckos and skinks (*Gehyra oceanica*, *Nactus pelagicus*, *Cryptoblepharus eximius*, *Gehyra mutilata*, *G. vorax*, *Lepidodactylus lugubris*, *L. manni*, and *Lipinia noctua*) which can be caught by hand on tree trunks and outcrops. Similarly, the annual breeding period of the large-bodied extinct Fijian ground frog (*Platymantis megabotoniviti*) may have attracted foragers to leaf litter and tree trunks in the deep forest. These organisms also would have required minimal tools for capture and processing. The small-bodied ground frogs (*Platymantis vitiensis* and *P. vitianus*), ground-dwelling boa snake (*Ogmodon vitianus*) may have similarly been collected with little effort, but with low caloric returns.

5. Low-Ranked Prey: Smaller Ground Birds, Smaller Skinks and Geckos, Iguanas, and Crocodiles (rank 13-12)

The lowest ranked prey include taxa that are either hazardous, of small-body size, elusive, or require intensive processing. These prey include the extinct crocodiles (*Volia athollandersoni* and perhaps *Mekosuchus kalpokasi*) which were of considerable size (60-90 kg) and may have been semi-terrestrial. Based upon the behaviour of other crocodilians, these animals would have posed a considerable hazard to hunters, resulting in extensive and life-threatening injuries if capture techniques were unrefined. They were also likely to have moved quickly into streams or rivers to evade hunters. If they were captured, both species of crocodile would have required extensive processing, including the removal of thick skin and scaly armour, and butchery of the body.

The Fijian iguanas (*Brachylophus fasciatus*, *B. vitiensis*) and perhaps two extinct species (*Lapitiguana impensa* and another species of *Brachylophus*) are larger bodied but also in the low-ranked category due to their restriction to tree branches in the high canopy, and leaf-colored camouflaging, which would have made them difficult to detect and access. If they could have been knocked down from branches or captured with nets or snares, they also may have posed a minor hazard due to bites and tail slaps. If procured, they would have required more advanced processing to remove tough and inedible skin, scales, and claws.

Several species of small-bodied gecko and skink (*Emoia caeruleocauda*, *E. campbelli*, *E. concolor*, *E. cyanura*, *E. impar*, *E. mokosariniveikau*, *E. nigra*, *E. parkeri*, *E. trossula*, *Hemidactylus garnotti*, *Hemiphyllodactylus typus*) may have been diminutive enough to not merit the effort to procure, when encountered. They also tend to lead solitary lives in leaf-litter and on tree-trunks, making little noise or movement to attract foragers. Encounter and capture of these animals may have been episodic or restricted to children and foraging practice.

6. GIS-based Model of Prey Habitats for Viti Levu, Fiji

The ranking of prey indicates that certain taxa would have been identified (and perhaps already known, given pre-existing knowledge of Pacific Island biodiversity) and sought as the target of foraging during the Lapita period. As this study seeks to model prey choice within the context of island exploration and early exploitation, a GIS-based model of Viti Levu was created using ArcGIS Pro to simulate the distribution of target taxa. This model used modern biological survey data for each taxon (**Table 1**), as well as historic and archaeological records of known colony and cave locations, to build a set of criteria for the physical distribution of each taxon (**Table 4**). GIS data in the form of modern topographic, elevation and slope data were rendered as a raster-based digital elevation model derived from the SRTM30+ Global 1-km Digital Elevation Model (**Figure 1**). The modern coastline was employed in this study, but the Lapita-era coastline would have been approximately 1.5 meters higher (Clark and Anderson 2009).

Table 4. Variables used in GIS analyses to determine potential taxa habitat during Lapita period, Viti Levu, Fiji.

	Elevation and Temperature	Terrain	Vegetation	Known colonies
Tortoise				
* <i>Meiolania</i> spp.	<500 m and >25° C	<30°	Open space	no
Iguana				
* <i>Lapitiguana impensa</i>	<500 m and >25° C	All	Wet/dry forest	no
<i>Brachylophus fasciatus</i>	<500 m and >25° C	All	Wet/dry forest	no
<i>Brachylophus vitiensis</i>	<500 m and >25° C	All	Wet/dry forest	no
* <i>Brachylophus</i> undescribed	<500 m and >25° C	All	Wet/dry forest	no
Boa Snake				
<i>Candoia bibroni</i>	<500 m and >25° C	All	Wet/dry forest	no
<i>Ogmodon vitianus</i>	<500 m and >25° C	<30°	Wet/dry forest	no
Ground Frog				
* <i>Platymantis megabotoniviti</i>	<300 m and >27° C	<30°	Wet forest	no
<i>Platymantis vitiensis</i>	<300 m and >27° C	<30°	Wet forest	no
<i>Platymantis vitianus</i>	<300 m and >27° C	<30°	Wet forest	no
Geckos and Skinks				
<i>Cryptoblepharus eximius</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Emoia caeruleocauda</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Emoia campbelli</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Emoia concolor</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Emoia cyanura</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Emoia impar</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Emoia mokosariniveikau</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Emoia nigra</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Emoia parkeri</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Emoia trossula</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Gehyra mutilata</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Gehyra oceanica</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Gehyra vorax</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Hemidactylus garnotti</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Hemiphyllodacylus typus</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Lepidodactylus lugubris</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Lepidodactylus manni</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Lipinia noctua</i>	<300 m and >27° C	<30°	Wet/dry forest	no
<i>Nactus pelagicus</i>	<300 m and >27° C	<30°	Wet/dry forest	no
Crocodile				
* <i>Volia athollandersoni</i>	<200 meters and >28°C	<30°	Lowlands, riparian areas	no
* <i>Mekosuchus kalpokasi</i>	<200 meters and >28°C	<30°	Lowlands, riparian areas	no
Ground-dwelling birds				
* <i>Megapodius</i> sp.	<200 meters and >28°C	<30°	Wet/dry forest	no
<i>Megapodius amissus</i>	<200 meters and >28°C	<30°	Wet/dry forest	no
<i>Megapodius alimentum</i>	<200 meters and >28°C	<30°	Wet/dry forest	no
<i>Megapodius molistructor</i>	<200 meters and >28°C	<30°	Wet/dry forest	no
<i>Megavitiornis altirostris</i>	<200 meters and >28°C	<30°	Wet/dry forest	no
<i>Gallicolumba stairi</i>	<500 m and >25° C	<30°	Wet/dry forest	no
<i>Natunaornis gigoura</i>	<500 m and >25° C	<30°	Wet/dry forest	no
<i>Nesoclopeus poecilopterus</i>	<200 meters and >28°C	<30°	Wet/dry forest	no
<i>Gallirallus philippensis</i>	<200 meters and >28°C	<30°	Wet/dry forest	no
<i>Porzana tabuensis</i>	<200 meters and >28°C	<30°	Wet/dry forest	no
<i>Porphyrio porphyrio</i>	<200 meters and >28°C	<30°	Wet/dry forest	no
* <i>Gallirallus</i> sp.	<200 meters and >28°C	<30°	Wet/dry forest	no
Beetle larvae				
<i>Xixuthrus</i> sp.	<300 m and >27° C	<30°	Wet forest	no
<i>Olethrius</i> sp.	<300 m and >27° C	<30°	Wet forest	no
Cicada				
<i>Raiateana knowlesi</i>	200-500 meters and >25° C	<30°	Dry forest	no
Colonial, burrow-nesting seabird				
<i>Pterodroma brevipes</i>	>900 meters and >18° C	All	Wet/dry forest	yes
<i>Pterodroma</i> sp.	>900 meters and >18° C	All	Wet/dry forest	yes
<i>Pseudobulweria macgillivrayi</i>	>900 meters and >18° C	All	Wet/dry forest	yes
<i>Pseudobulweria rostrata</i>	>900 meters and >18° C	All	Wet/dry forest	yes
<i>Puffinus pacificus</i>	>900 meters and >18° C	All	Wet/dry forest	yes
Colonial, tree-roosting bats				
<i>Pteropus samoensis</i>	<500 m and >25° C	All	Wet/dry forest	no
<i>Pteropus tonganus</i>	<500 m and >25° C	All	Wet/dry forest	no
Colonial, cave-roosting bats				
<i>Notopteris macdonaldi</i>	<500 m and >25° C	Cave	Wet/dry forest	yes
<i>Emballonura semicaudata</i>	<500 m and >25° C	Cave	Wet/dry forest	yes
<i>Tadarida bregullae</i>	<500 m and >25° C	Cave	Wet/dry forest	yes
Non-colonial, tree-roosting bat				
<i>Mirimiri acrodonta</i>	<500 m and >25° C	All	Wet/dry forest	no
* extinct				

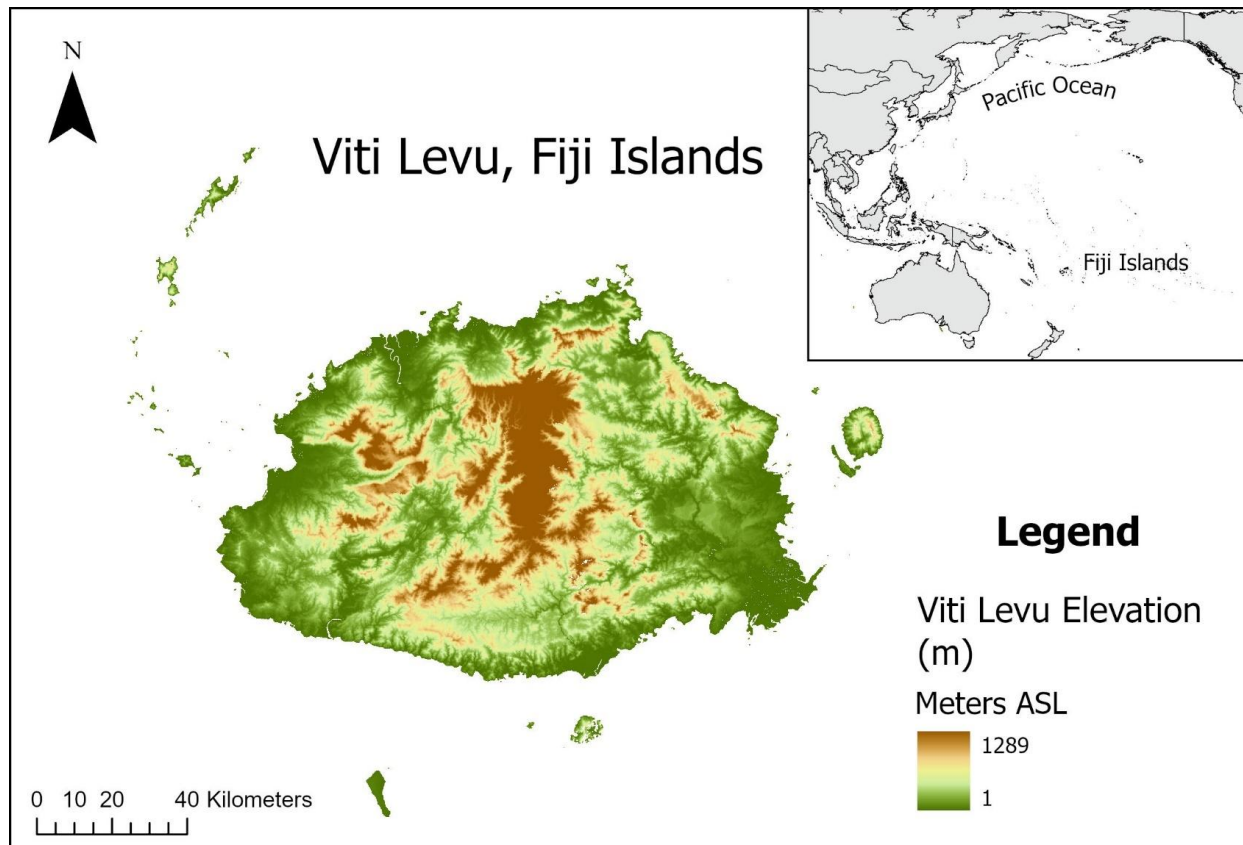


Figure 1. Digital elevation model of Viti Levu, Fiji Islands, showing elevation and topography with graduated color. Data source: SRTM30+ Global 1-km Digital Elevation Model.

Modern vegetation data in a raster-format was obtained from the European Space Agency CCI Climate Change Initiative land cover maps of the world, 1992-2020 series. Temperature data for Viti Levu was reconstructed from a database housed at Oregon State University (OSUGISci 2025). Classificatory tools in ArcGIS Pro were used to isolate layers representing the extent of modern wet and dry forests, and modern savannah and open parkland, which are remnants of vegetation regimes that formed in the mid-Holocene (Hope *et al.* 2009) (**Figure 2**). Using these main datasets as well as tabular data for annual temperature and rainfall, the analytical tools within ArcGIS Pro (primarily Reclassify and Raster Calculator) were used to generate digital outputs of “habitat patches” that included or excluded critical variables for each taxon, such as gentle terrain, high elevations with cooler temperatures, and expanses of wet or dry forests, and open grassland/parkland. The modelled patches for Viti Levu are displayed in Figure 3. In each case, the modelled distribution of each prey is indicated by color shading against a plain grey background.

A complicating factor in this study is the use of modern data to model the extent and type of vegetation in Lapita-era Fiji. Paleoenvironmental studies using microfossils and charcoal have documented the character and diversity of Fiji’s mid-Holocene vegetation and fire history (Hazard 2017; Hope *et al.* 2009; Mueller-Dombois and Fosberg 1998; Roos *et al.* 2016, 2023; Watling 2005). These studies have revealed the mid-Holocene extent of palms and hardwoods in Fiji, as well as their decline ca. 3000 BP. Following human colonization and settlement, forests were variably and

gradually replaced with shrubs and grasses, producing a mosaic of economic and native plants, and a more open parkland environment on the leeward side of the island (Hope *et al.* 2009). Although different plants are present in the modern vegetation dataset, the overall pattern of windward/leeward tree canopy vs. open parkland is likely to be broadly equivalent to what existed in prehistory.

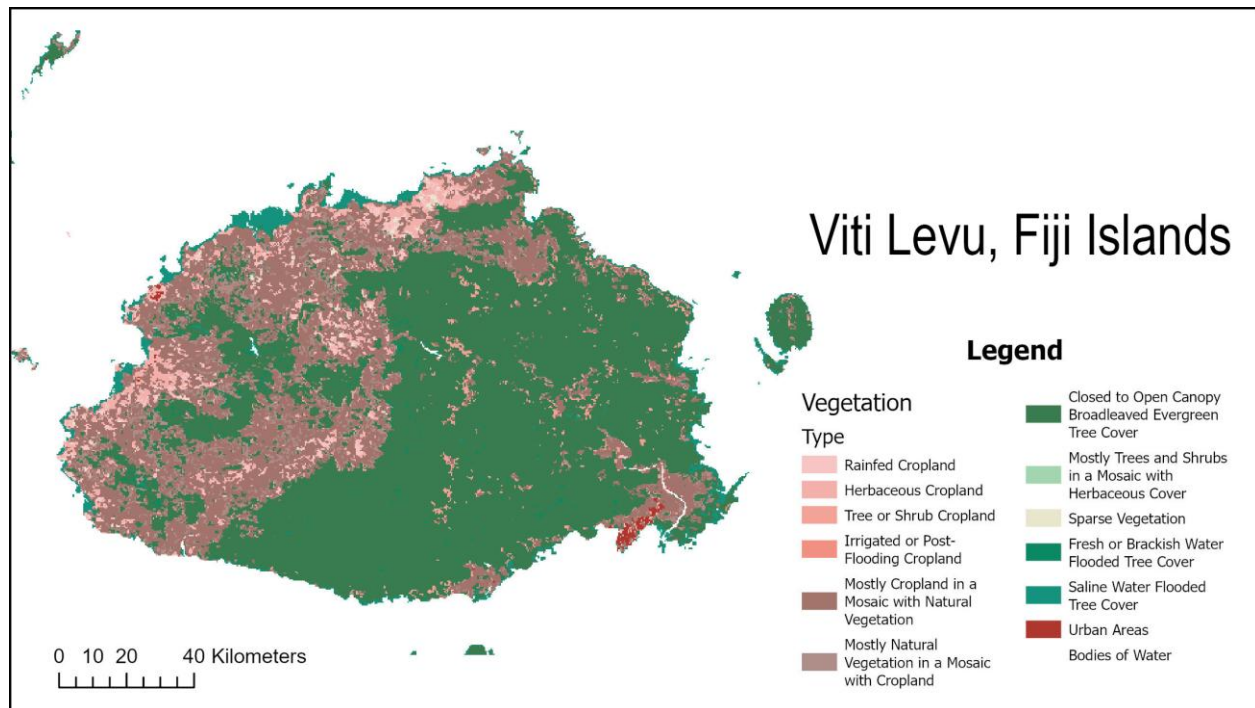


Figure 2. Raster formatted vegetation data for Viti Levu, ca. 1992. Source: European Space Agency CCI Climate Change Initiative.

7. Geographic Distribution of High Ranked Prey

Figure 4 reveals the predicted geographic distribution of the largest-bodied and highest-ranked prey during the Lapita colonization period: the giant land-tortoises, the megapodes, the ground-dwelling giant pigeon, and colonial burrowing seabirds. This image excludes colonial tree-roosting bats as they are found throughout Viti Levu at elevations below 500 meters, and cicada, which have eight-year brood cycles. The megapodes and the extinct giant Columbids would have inhabited the lower elevations of the wet and dry forests of Viti Levu, preferring the gently sloping terrain for feeding and nesting. The Southern coast of Viti Levu, as well as the extensive basins of the Rewa and Wainibuka River in Eastern Viti Levu, would have offered the greatest expanses of this forest habitat. These are also areas that are wetter and warmer, and riparian areas would have contained abundant habitat for rails and other ground-dwelling birds. It is also in these areas that populations of forest birds may have persisted for some time, withstanding the pressure of human predation and the introduction of rats, which would have consumed chicks and eggs.

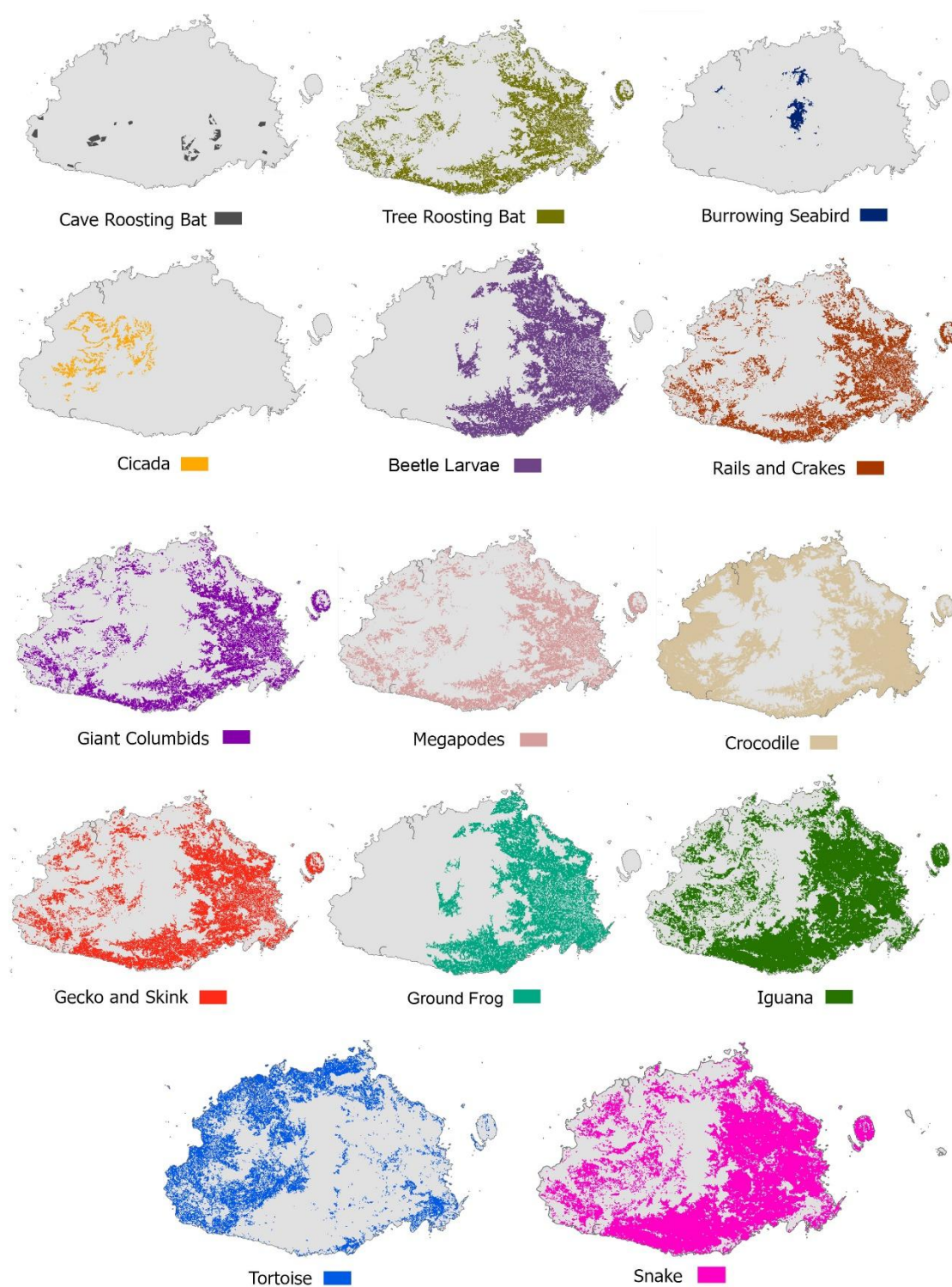


Figure 3. Modeled habitat patches for Lapita-era foraging targets. Distributions based upon modern ecological variables and habitat preferences of modern taxa.

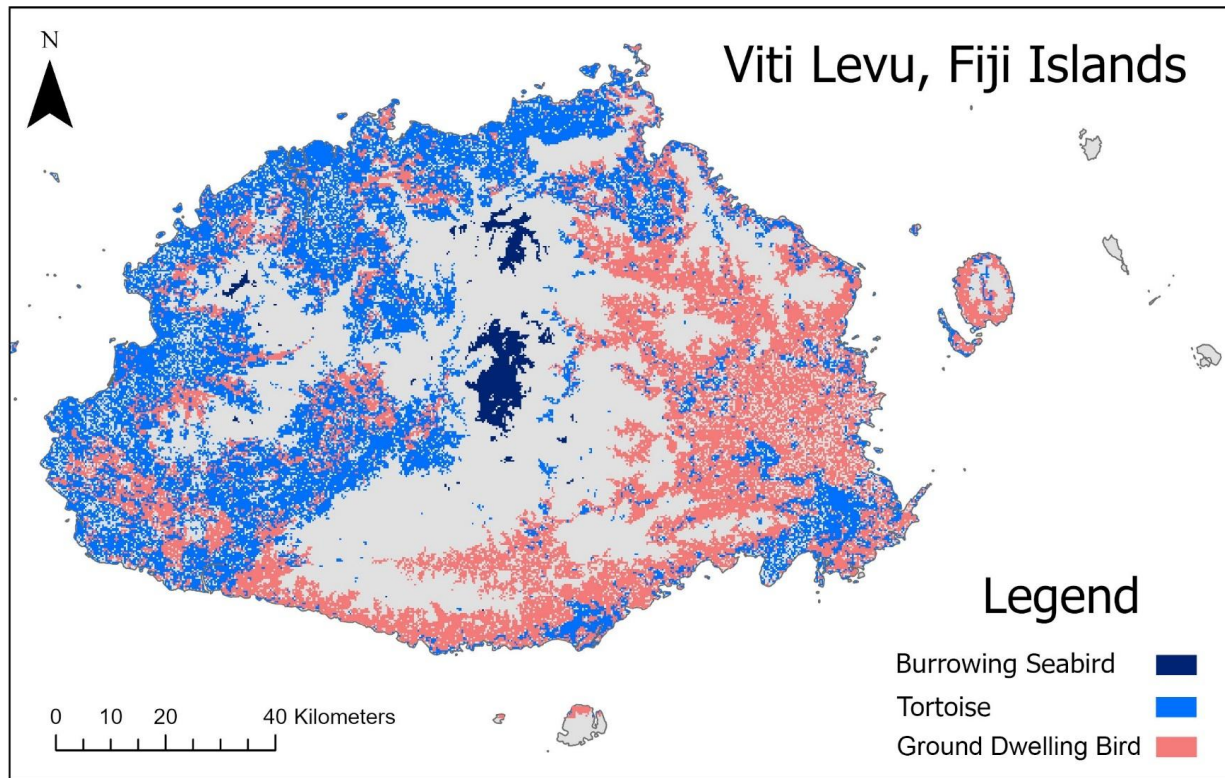


Figure 4. Combined map of high ranked taxa: burrowing seabird, tortoise, and ground-dwelling birds.

This reconstruction suggests that western Viti Levu, which is the leeward side of the island, would have provided more suitable habitat for giant land-tortoise. The dry hardwood forest in the Sigatoka Valley, as well as more gently sloped, open parkland landscape around Nadi Bay and the Ba River Valley, would have provided abundant forage and fewer mobility obstacles for tortoises than the dense forests of eastern Fiji. Following the pattern of foraging seen in Lapita-era Vanuatu, land-tortoise populations may have been targeted exclusively in this region. Their size, lack of mobility, and relative ease of encounter in more open habitats would have made them preferential targets compared to forest-dwelling megapodes and giant pigeons.

Burrowing colonies of seabirds such as petrels and shearwaters may have also been a target of early foragers, but their distributions would have been limited to the higher elevations of Viti Levu (at least above 500 meters, and more likely in the range of 900 meters asl), which are considerably wetter and cooler than the lowlands. The modelled locations for these prey include portions of the Nadrau Plateau in central Viti Levu, and high elevation mountains in the south (Korobasabasanga), west (Koroyanitu), and north (Tomanivi). Foragers would have had to search for bird colonies across high and difficult terrain, or perhaps detect them at night following mating calls, but once they were located they would have been regularly exploited *en masse*. It is possible that burrowing seabird colonies existed at lower elevations in antiquity, prior to eradication by humans and rats.

8. Discussion and Implications

The results of prey ranking in this study identified a range of potential foraging targets for humans arriving on Viti Levu, but specifically identified large-bodied tortoise, megapodes and other ground-dwelling birds, and colonial seabirds as the most likely to be sought on foraging bouts. These taxa also require lower processing and search costs, due to their body qualities and susceptibility to mass capture. Importantly, these modelled outcomes match what is known for the Lapita-aged faunal assemblages of Teouma (Hawkins 2015) and Tongoleleka, in Tonga (Steadman *et al.* 2002), although Tonga did not have a population of giant tortoises, but rather sizeable iguanas. The similarity of the assemblages to the modelled outcome for Fiji can be attributed to the weighting of additional attributes in addition to body size (e.g., susceptibility to mass capture, processing requirements, locomotor skills, and hazards). If all the variables *but* body size are removed, the rankings shift to include other taxa, namely crocodile and boa snake, with the possible inclusion of giant iguanas. The paucity of crocodiles in Lapita assemblages across Western Polynesia and Island Melanesia, and the abundance of lower-ranked prey such as fruit bat, suggest that the costs associated with targeting larger, but more hazardous species, are critical considerations.

If these modelled prey ranks are assumed to be correct, what does this suggest for the trajectory of Lapita foraging on Viti Levu? One important difference is the size of Viti Levu, which spans approximately 10,388 km². Efate Island encompasses 899 km², and Lifuku Island, where the site of Togoleleka is located, is a mere 11.4 km². These vast differences in size suggest that the rapid extinction (within 300 years) of tortoises and ground-dwelling birds that are known for Lifuka and Efate may not have occurred on Viti Levu. The sheer size of the island would have provided an extensive habitat for animal populations, and space for them to escape foraging pressure. Although the megafauna of Viti Levu did ultimately go extinct, the rates of extinction may have been slower than what is documented for Efate, extending past the Lapita era, and with the potential for refuge populations of animals existing in remote valleys. Future research in Western Viti Levu may yet reveal a longer sequence of Lapita-era tortoise hunting, extending past that seen in Vanuatu. Eastern Viti Levu may similarly contain a longer sequence of forest-bird hunting. The prey-ranks and habitat reconstructions described here suggest a need for additional archaeological research in Fiji, especially beyond the well-surveyed coastlines and offshore islands.

Supplementary Materials

The supporting information can be downloaded at <https://doi.org/10.70460/jpa.v16i2.402> S1: Taxa ranking data.

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Data Availability Statement.

Data can be found in the text or in the supplementary materials.

Partnerships

This research did not use any primary data from Indigenous contexts.

Conflicts of Interest

The authors declare no conflicts of interest.

AI Disclosure Statement

No GenAI was used for any part of this research or manuscript preparation.

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