Late Pleistocene/Early Holocene sites in the montane forests of New Guinea yield early record of cassowary hunting and egg harvesting

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How early human foragers impacted insular forests is a topic with implications across multiple disciplines, including resource management. Paradoxically, terminal Pleistocene and Early Holocene impacts of foraging communities have been characterized as both extreme—as in debates over human-driven faunal extinctions—and minimal compared to later landscape transformations by farmers and herders. We investigated how rainforest hunter-gatherers managed resources in montane New Guinea and present some of the earliest documentation of Late Pleistocene through mid-Holocene exploitation of cassowaries (Aves: Casuariidae). Worldwide, most insular ratites were extirpated by the Late Holocene, following human arrivals, including elephant birds of Madagascar (Aepyornithidae) and moa of Aotearoa/New Zealand (Dinornithiformes)—icons of anthropogenic island devastation. Cassowaries are exceptional, however, with populations persisting in New Guinea and Australia. Little is known of past human exploitation and what factors contributed to their survival. We present a method for inferring past human interaction with mega-avifauna via analysis of microstructural features of archaeological eggshell. We then contextualize cassowary hunting and egg harvesting by montane foragers and discuss the implications of human exploitation. Our data suggest cassowary egg harvesting may have been more common than the harvesting of adults. Furthermore, our analysis of cassowary eggshell microstructural variation reveals a distinct pattern of harvesting eggs in late ontogenetic stages. Harvesting eggs in later stages of embryonic growth may reflect human dietary preferences and foraging seasonality, but the observed pattern also supports the possibility that—as early as the Late Pleistocene—people were collecting eggs in order to hatch and rear cassowary chicks.

montane rainforests | Sahul | megafauna | cassowary | ratites

Once considered marginal environments ill-suited to human colonization, tropical rainforests have yielded substantial evidence of diverse adaptive strategies from the Late Pleistocene (LP) through the Holocene (1). Montane rainforests present additional challenges to human occupation in terms of resource acquisition, locomotion, and thermoregulation. Recent research has further demonstrated the adaptive flexibility of *Homo sapiens* and reinforced the need to rethink the range of dynamic interactions between humans and rainforest environments (2). In this paper, we present an intensive study of premodern cassowary (*Casuarius* spp.) hunting and egg collecting to shed light on human-cassowary interactions in Sahul/Asia-Pacific during the LP and Holocene. Native to the rainforests of northeastern Australia and New Guinea, and the largest extant native vertebrate on New Guinea, this keystone taxon presents a unique opportunity to gain insights into the complex interactions between human communities and rainforests (Fig. 1). We ask whether archaeological remains of cassowary—bone and especially eggshell—reflect intentional human management of cassowaries by mobile foragers and discuss the far-ranging implications of human–cassowary interactions in terms of the composition and persistence of rainforest communities. Specifically, we present a multianalytical approach for evaluating eggshell microstructures associated with embryonic development. Using three-dimensional (3D) laser microscopy to scan eggshell surfaces, we combine statistical modeling of surface texture with visual assessments of microstructural morphology, in order to assign archaeological eggshells to stages of ontogeny (Fig. 2). In particular, the appearance of pitting at the tips of the eggshell mammillary cones is an indication of more developed stages of embryonic growth (reference *SI Appendix*, S1.10). We then use these ontogenetic assignments to characterize patterns of human exploitation (3). We focus on archaeological assemblages spanning the Last Glacial Maximum (LGM) through the Late Holocene (LH) from two rock shelters—Yuku and Kiowa—in the montane rainforests of eastern New Guinea (Fig. 3) and report a series of ^{14}C dates to further resolve the chronology of eggshell collecting at these sites (*SI Appendix*, Fig. S10).

Significance

Eggshell is an understudied archaeological material with potential to clarify past interactions between humans and birds. We apply an analytical method to legacy collections of Late Pleistocene to mid-Holocene cassowary eggshell and demonstrate that early foragers in the montane rainforests of New Guinea preferentially collected eggs in late stages of embryonic growth. This finding suggests that foragers regulated the exploitation of cassowaries and may have hatched eggs to rear chicks. The montane rainforests of New Guinea may thus present the earliest known evidence of human management of avian breeding.

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Fig. 1. Human–cassowary interactions in highland Papua New Guinea (PNG): (*A*) Endemic fruit forming key components of cassowary diet; (*B*) hunters butchering a carcass of a Dwarf Cassowary (*C. bennetti*); (*C*) man wearing headdress including cassowary feathers; (*D*) juvenile cassowary (*C. bennetti*) being reared in a village in highland PNG; (*E*) adult male cassowary (*C. bennetti*) in captivity in a village in highland PNG; and (*F*) man wearing a cassowary quill nose ornament and an armband with a cassowary bone dagger. Photo credits: A. Mack.

The analytical method we present has great potential to elucidate human interactions with avian species globally and may greatly expand our understanding of the decline and extinction of many large flightless birds following human colonization of new regions.

The extent to which foraging societies transform landscapes through resource use and management is an enduring question in anthropology and historical ecology (4, 5). Despite widespread evidence of ecological shifts correlated with land use by foraging communities and compelling examples of forager niche construction (6–8), the view that agriculture results in more intentional and intensive landscape-level changes persists—particularly in periods preceding LH global land use (9). However, these assumptions about the minor influence of foraging communities on landscapes are inconsistent with behavioral ecology models of predator–prey dynamics that have been applied to investigations of the impacts of hunter-forager societies on populations of prey species (10). These models predict that broad-spectrum predator species likely have more significant impacts on the population dynamics of individual prey species, as predators with flexible resource use are less sensitive to changes in the population dynamics of individual prey than specialized predators (10). These models, when applied to study the differential impacts of *H. sapiens* versus

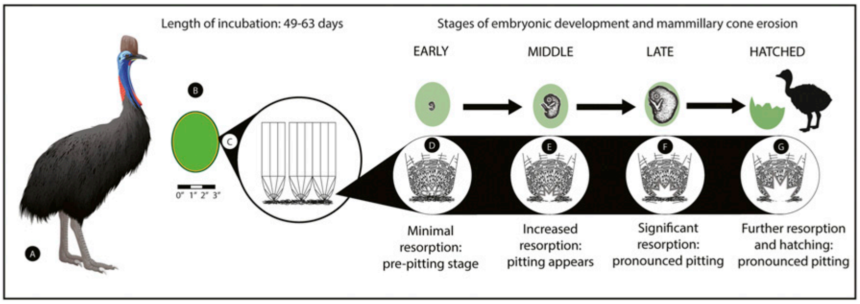

Fig. 2. Simplified representation of eggshell microstructural changes during incubation as the cassowary embryo resorbs the calcium it requires for growth (>80%) from the surrounding eggshell (77). As a result of this process of resorption, the surface structure of eggshell mammillary cones changes during incubation, and measurements of surface texture can be used to estimate the ontogenetic age of the embryo (3): (*A*) Male cassowary (*C. casuarius*), as males incubate eggs and tend to chicks; (*B*) green eggshell exterior (archaeological samples did not retain this green color; note that egg is not to scale); (*C*) enlarged view of eggshell interior surface and mammillary cones; (*D*–*G*) eggshell mammillary cones at "Early," "Middle," "Late," and hatched stages of development. Developmental timeline based on comparative study of Ostrich (*Struthio camelus*) embryo and eggshell microstructural changes during ontogeny (3).

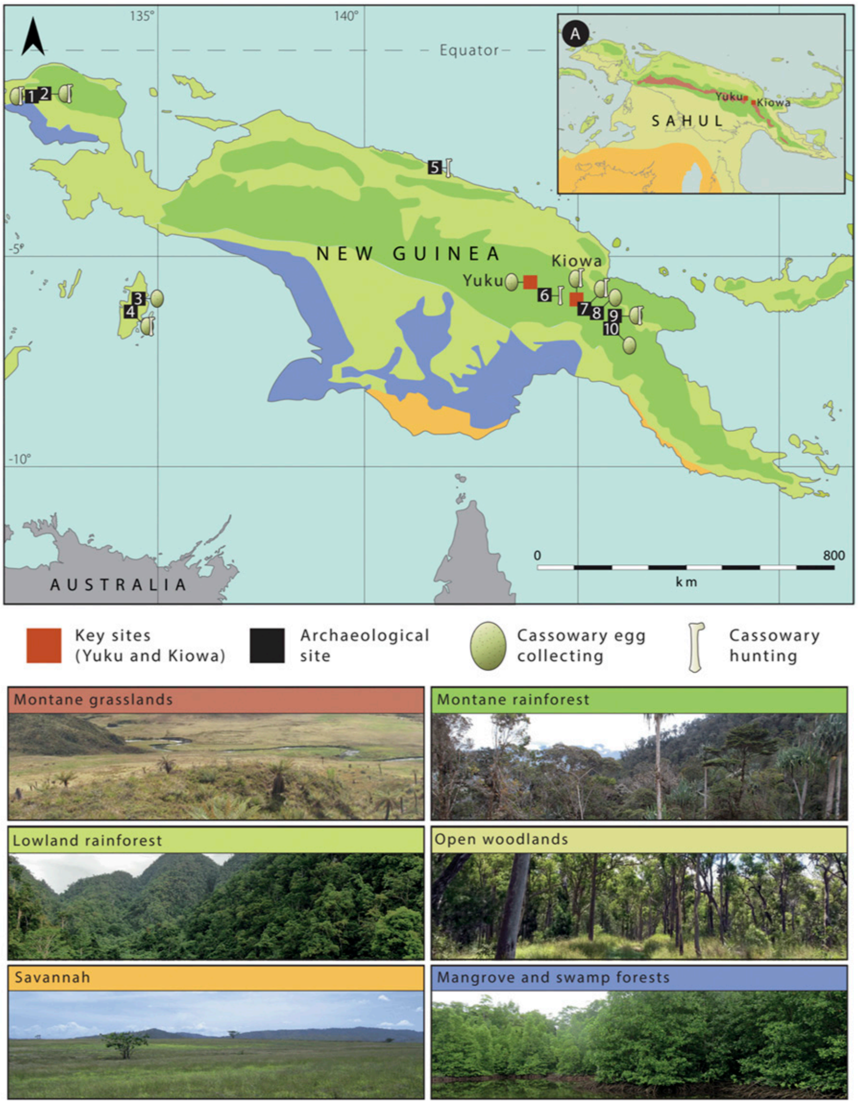

Fig. 3. Maps of the study region, ecology, and chronology of LP to mid-Holocene sites with evidence of human–cassowary interaction. 1: Toé, with eggshell from 30 to 10 ka and bone from 30 ka to the LH (34); 2: Kria, with eggshell and bone from 7 or 6 ka to more recently (34); 3: Liang Nabulei Lisa, with eggshell from 16 ka to recently (78); 4: Liang Lemdubu, with eggshell from 20 to 1.5 ka or later and bone from 20 to 1 ka (36); 5: Lachitu, with bone occurring sometime in the mid-Holocene (79); 6: Kamapuk, with bone present about 5 ka but no later (80); 7: Nombe with eggshell from 20 to 0.2 ka and bone from possibly 36 to 0.2 ka (25); 8: Kafiavana, with eggshell >5 ka (81); 9: Aibura with cassowary eggshell and bone dating to either 3.8 ka or 0.7 ka (81); and 10: Batari, with cassowary eggshell from 18 to 0.7 ka (81). Illustration: D. Gaffney; *Inset* A adapted from van der Kaars (82); photos courtesy of D. Gaffney, A. Ford, and B. Shaw.

other hominins on LP environments, support the possibility that LP extinctions of vertebrate fauna were driven by in-migration by more flexible populations of *H. sapiens* (11). More importantly, assumptions that foraging communities influence landscapes in minimal ways are inconsistent with the intergenerational knowledge of many Indigenous peoples, which indicates that traditional land owners and their ancestors have intentionally and intensively cultivated expansive landscapes, in some cases for millennia (12, 13).

Montane New Guinea presents an important case study for clarifying forager impacts on forest landscapes over extended timescales. Humans had reached northern Sahul by at least 42,000 y ago, and the initial peopling of the region included rapid exploration of montane environments (14). The archaeological record demonstrates that early activities in the mountains involved the collecting of *Pandanus* nuts, transporting yams from the coast, forest burning, marsupial hunting, and the production of large "waisted" stone axes (15, 16). The highlands during this time were dominated by lower montane rainforests of beech trees (*Nothofagus*, *Lithicarpus*, and *Castanopsis*), with subalpine forests of pines (*Phyllocladus*) and conifers (*Dacrycarpus*, *Podocarpus*, and *Papuacedrus*) above that, and more open grasslands and shrubs at higher altitudes (17). Modern human genomic studies indicate Pleistocene populations frequenting the highland zone were in the order of a few hundred or thousand people (18). These populations were relatively stable until the end of the LGM when populations rapidly increased, with montane societies becoming relatively isolated from the lowlands by the start of the Holocene (19). These population increases co-occurred with climatic amelioration at the terminal Pleistocene (TP) and Early Holocene (EH), which saw average temperatures increase by about 7 °C in the montane zone and rainforests expanding further upslope, with the treeline shifting from 2,200 m asl to almost 4,000 m above sea level (asl) (20). Moreover, this period saw some groups increasingly focus their subsistence on wetland cultivation of tubers and tree crops in some intermontane valley systems (21). Despite these changes, montane rainforest foraging persisted as the primary mode of subsistence in other valley systems into the mid-Holocene (22), leading to regional variation in anthropogenic landscape modification and forest clearance (2, 23).

Although there is evidence that humans shared the montane zone with megafauna including giant kangaroos (*Protemnodon* spp.), Diprotodontids, the marsupial wolf (*Thylacinus cynocephalus*), and cassowaries (*Casuarius bennetti*) for several millennia (24, 25), it is unclear the extent to which these species were a focus of early hunting. There is no clear evidence that Pleistocene humans drove megafauna species to total extinction, but cassowaries are the only native large-bodied vertebrate species extant in the mountains today (26). Though the faunal record is patchy, some archaeological sites do provide evidence for local extirpation, including species of fruit bats (*Aproteles bulmerae*), marsupial wolves (*Thylacinus* sp.), and rodents from the Mount Elimbari area by the mid-Holocene, cuscus (*Phalanger* spp.) from the Mount Hagen area by the EH (2), and wallabies (*Thylogale christenseni* and *Thylogale brunii*) from the Nemangkawi mountains in western New Guinea sometime after the mid-Holocene (27, 28). These extirpations could have been driven by forest clearances, deliberate fires used for hunting, direct capture, trapping, and competition from introduced species, including pigs (*Sus scrofa*) and dogs (*Canis* sp.) (29).

Little is known about the nature of early exploitation, but cassowary hunting and rearing of chicks has been documented ethnographically, and on New Guinea the birds and their feathers are highly valued in trade and ritual today (30–32; Fig. 1). Regional evidence confirming early human–cassowary interaction (*SI Appendix*, Table S3) includes eggshell directly dated to around 20 ka B.P. from Toé cave (33, 34), around 16 ka B.P. (by association) on the Aru Islands formerly connected with Sahul (35, 36), and possibly dating to 25 ka B.P. (by association) at Nombe (25) (Fig. 3). Cassowaries are unmistakable, large ratites that inhabit the understory of wet, dense forests in northeastern Australia and New Guinea (37; Fig. 1). They are primarily frugivorous and are an important disperser of large-seeded plants (38–40). The three extant species of cassowary in Australia and on New Guinea are currently in decline due to human pressures, including habitat destruction, hunting, and predation on eggs and young by introduced predators (37, 41, 42). Nevertheless, cassowaries on New Guinea are notable in their persistence following human arrival, as most large flightless birds on islands—including Madagascar's elephant birds (Aepyornithidae) and Aotearoa/New Zealand's moa (Dinornithiformes)—were extinct by the LH (43, 44).

We investigate LP and Holocene patterns of human exploitation of cassowaries at two rock shelter sites—Yuku and Kiowa (Fig. 3 and *SI Appendix*, S1.1). These sites preserve deep zooarchaeological sequences that allow us to examine the temporal dynamics of hunting and faunal extirpation (45). Yuku in the Lanim Gorge on the northwest slope of Mount Hagen was occupied by at least the end of the LGM, 17,500 y ago until the recent past, while Kiowa near the Mae river valley on Mount Elimbari was occupied at the TP, 12,000 y ago until the last few centuries. Both sequences suggest early foragers supplemented a plant-rich diet with broad-spectrum hunting, leading to the capture of almost all available mammalian game. At Kiowa, fruit bats and cuscus were also captured in large quantities suggesting human hunters specialized in capturing a small number of reliable species (2). Polished axes traded in from nearby valley systems provide evidence for trade links connecting these sites with other areas in the mid-Holocene (23), and marine shell and pottery indicate exchange connections to the hilly lowlands and coast had formed by the last millennium B.P. (46, 47).

Results

Chronology. We obtained 15 new ^{14}C measurements on cassowary eggshell from Kiowa and Yuku and combined these with previous accelerator mass spectrometry (AMS) determinations (n = 10) derived from avian eggshell at these sites (*SI Appendix*, Table S1 and Fig. S10). These dates confirm that the human occupation and evidence for the exploitation of cassowaries at Yuku extends from the end of the LGM (ca. 17.8 k cal B.P.) through the EH (ca. 9.5 k cal B.P.), while Kiowa's occupation spans the TP through LH (48). Occupation of both sites was intermittent throughout this time span. Evidence for cassowary exploitation at Kiowa, however, derives from contexts that span the TP to mid-Holocene (ca. 12.5 k cal B.P. to 6.5 k cal B.P.; *SI Appendix*, Fig. S10). No evidence of egg harvesting was recovered for the LH.

Cassowary Bone. No cassowary bone was identified in the Yuku assemblage, despite comparable levels of bone preservation at both sites. All identifiable avian remains (Number of Identified Specimens [NISP] = 28) were recovered from Kiowa and are referable to the genus *Casuarius.* Of these, 15 could be identified to the species *C. bennetti* (Dwarf Cassowary). The smallest cassowary species and a montane forest resident, it would have been the locally available cassowary for Kiowa. The overwhelming majority (71%, NISP = 20) of cassowary bones were recovered from Unit EE and span the TP through mid-Holocene (ca. 12.5 k to 6.5 k cal B.P.; *SI Appendix*, Table S1 and Fig. S10). Within EE, Level 4 had the most cassowary elements (29% of EE, NISP 8; 7,169 to 6,984 cal B.P. [90.2%]). Unit SE contained 35% (NISP 7) of the cassowary bones, all but one of which were collected in mid-Holocene levels. Finally, Unit EB only produced one identifiable element (femur shaft fragment), recovered from a mid-Holocene deposit. All of the elements, with the exception of three fragments of a pelvis most likely from one individual, are from the hind limb. The vast majority (57%) are from the tibiotarsus. The femur and tarsometatarsus each make up 14% of the total NISP. In addition, there is one fibula and an ungual phalanx (claw). All elements are fully ossified (i.e., osteologically adult).

Cassowary Eggshell. A total of 1,019 fragments of eggshell assigned to *Casuarius* spp. were recovered from Kiowa (n = 31) and Yuku (n = 988). All stratigraphic associations and measurements pertaining to the eggshell assemblage are presented in Dataset S1. The vast majority of samples (n = 884)—about 87% of the overall assemblage—were recovered from layers dated to the TP and EH (*SI Appendix*, Fig. S11 and Table S2). Approximate eggshell fragment surface area—used here as a proxy for degree of fragmentation of the assemblage—and estimated minimum number of individuals (MNI) are given in Table 1. We observed little variation in the degree of eggshell fragmentation relative to chronological phase. Weathering, however, was not uniform across the two site assemblages (*SI Appendix*, Fig. S12), though no significant correlation was observed with regard to degree of weathering and chronological phase (*SI Appendix*, Table S4). Of the large proportion of samples dated to the TP and EH, about 65% (n = 571) displayed "light" or "medium-light" weathering (*SI Appendix*, Fig. S12).

Prediction of eggshell developmental stage using a modeling approach. NISP of eggshell according to predicted ontogenetic stage using the two statistical models (1-predictor and 4-predictor) are reported in *SI Appendix*, Table S5. Samples that were assessed as too weathered to distinguish morphological features were excluded (reference *SI Appendix*, S1.10). The majority of samples (~78%; n = 800) are predicted to be "Late" stage eggs according to the 1-predictor model. When using the 4-predictor model, however, this trend changes, and a large proportion of the eggshells are predicted to be "Middle" stage (~72%; n = 740;

Table 1. NISP, total and average sample surface area, and estimated MNI of Kiowa and Yuku cassowary eggshell assemblages

	NISP	Estimated total eggshell surface area in cm^2	Average sample area in cm^2	Estimated MNI
KIOWA	31	746.93	24.09	2.83
TP/EH	17	374.09	22.01	1.41
Mid-Holocene	14	372.85	26.63	1.42
YUKU	988	25,224.88	25.53	95.55
LGM	28	777.59	27.77	2.95
TP/EH	867	22,504.93	25.96	85.25
Unstratified	93	1,942.36	20.89	7.36

MNI is estimated by dividing total eggshell surface area (calculated using sample length and width measurements) by 264, which represents an estimate of the surface area of an intact dwarf cassowary egg.

Fig. 4). There is greater agreement between the models with regard to eggshells predicted to be in the “Early” stage.

Agreement between the two models is (13 + 165 + 231) / 969 = 42% (*SI Appendix*, Table S6). For example, a total of 545 samples that are predicted to have been harvested in the “Middle” stage using the 4-predictor model are predicted as “Late” stage using the 1-predictor model. This could be due to the fact that the 4-predictor model is picking up additional variation between the samples because it incorporates more surface roughness parameters (Sa, Ssk, Sku, and Sz) than the 1-predictor model (Sa only; reference *SI Appendix*, S1.6, S1.7, and S1.9).

Our two predictive models of eggshell developmental stage each resulted in three marginal probability values, which represent the likelihood that each sample was harvested in the “Early,” “Middle,” or “Late” stage of development (Dataset S1). The three probability values for each sample run through one of our models add up to 100%, and the highest probability value of the three is the identified stage of development. For example, an eggshell sample with marginal probability values of 60% for “Early,” 30% for “Middle,” and 10% for “Late” is identified by the model as having been sampled in the “Early” stage of embryonic development. For eggshells predicted to have been harvested during the “Late” stage by the 1-predictor model, the marginal probabilities for “Late” stage are significantly higher on average than the probabilities for “Middle” and “Early” stage, providing a degree of confidence in the predictions (*SI Appendix*, Fig. S13).

The dominance of the highest marginal probability value is less pronounced for the predictions using the 4-predictor model, suggesting that the model is somewhat less “confident” in its predictions than the 1-predictor model (*SI Appendix*, Fig. S14). In other words, because the 4-predictor model may be picking up additional variation in surface roughness compared to the 1-predictor model, the difference between the predicted probabilities for the “Late” and “Middle” stages is less pronounced than in the 1-predictor model.

Identification of eggshell developmental stage using visual assessment. Visual assessment of microstructural features for each cassowary eggshell sample in the overall assemblage (n = 1,019) was conducted using a set of four high-resolution images (Fig. 5) and four cross-sectional profiles (*SI Appendix*, Fig. S15; n = 8,152 total visualizations). NISP of eggshell identified as having been harvested in the “pre-pitting” (equivalent to the “Early” stage in the predictive models) versus “pitting” stage (equivalent to the later part of the “Middle” stage and to the “Late” stage in the predictive models) are reported in *SI Appendix*, Table S7. The vast majority of eggshells displayed pitting (cone microstructure erosion [CME] categories 2 and 3; Fig. 4). For example, in the TP/EH assemblage, pitting was evident in ∼62% of the samples (n = 548), while ∼19% (n = 166) showed intact mammillary cones with no signs of resorption, and ∼15% were too weathered to distinguish visually whether pitting had commenced. Samples assigned to CME category 3 clearly displayed pits, though some of the morphology showed signs of weathering that could affect the roughness measurements used in the predictive models.

Comparisons of modeling approach and visual inspection. Agreement between the two models and the visual inspection can be assessed by considering counts of “Middle” and “Late” stage predictions versus counts for CME categories 2 and 3 (green values in *SI Appendix*, Tables S8 and S9 and Fig. 4). These counts suggest broadly similar levels of agreement between these approaches. Of the samples where pitting was visible, 99% (596/603) were

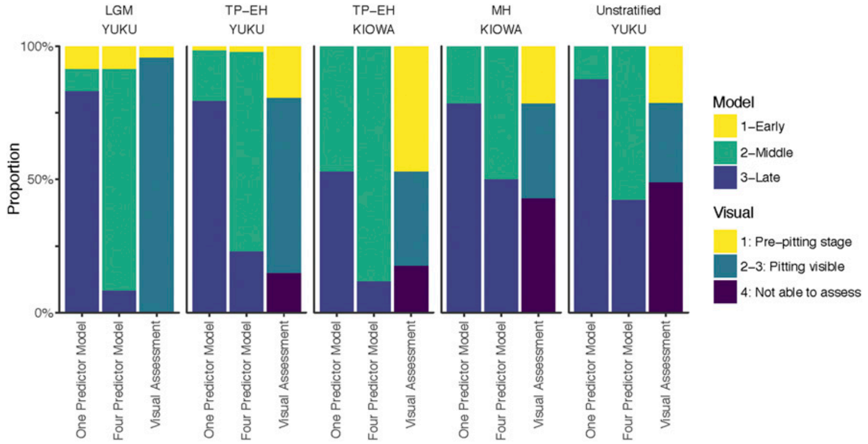

Fig. 4. Overall proportions of the Kiowa and Yuku assemblages predicted to have been harvested at “Early,” “Middle,” and “Late” stages of ontogeny using the 1-predictor and 4-predictor models and identified through visual assessment of CME as having been harvested in the “pre-pitting” (equivalent to the “Early” stage in the predictive models) versus “pitting” stage (CME categories 2 and 3, equivalent to the later part of the “Middle” stage and to the “Late” stage in the predictive models), across chronological phases.

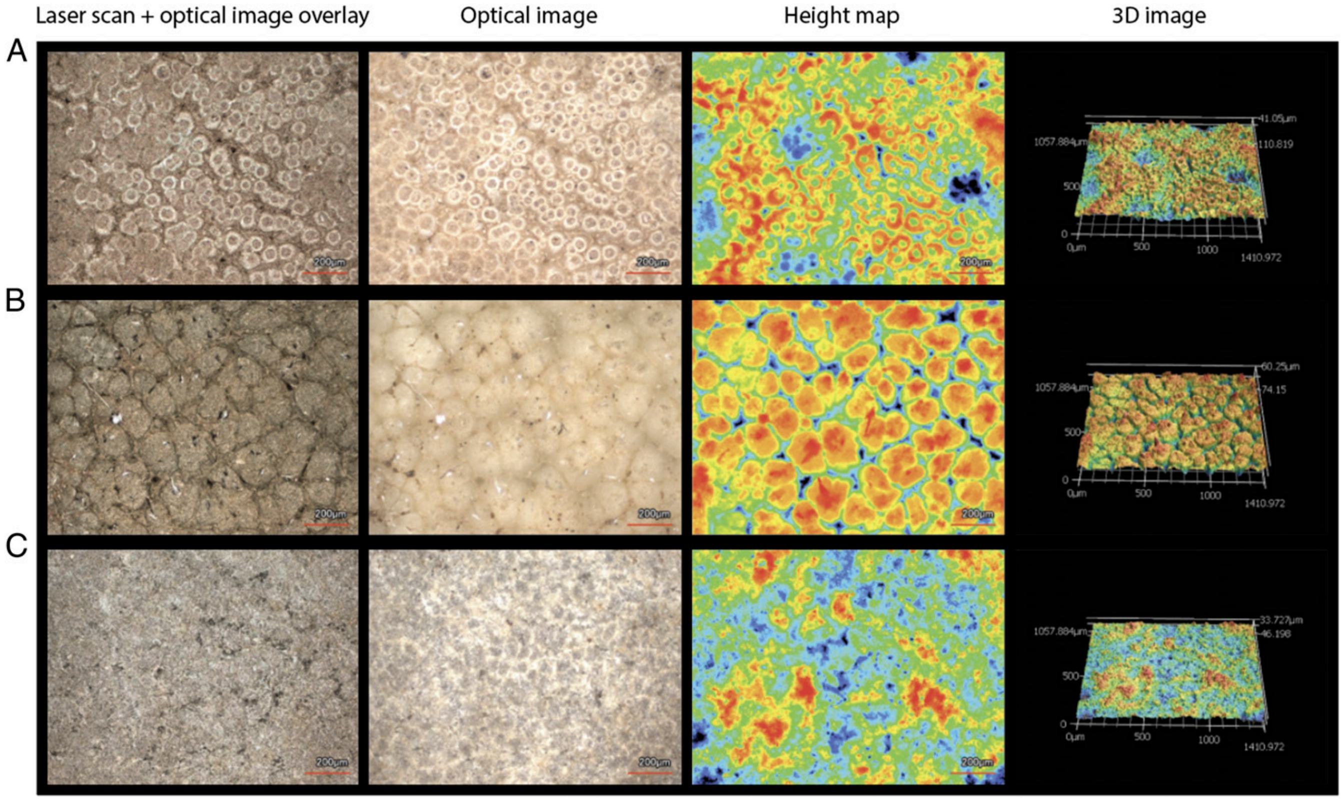

Fig. 5. Images rendered through high-resolution laser microscopy scanning of cassowary (*Casuarius* spp.) eggshell interior surfaces: (*A*) sample displaying light weathering and clearly defined pitting of mammillary cones (sample identification number [ID]: 1249); (*B*) sample displaying medium-light weathering and no pitting (prepitting stage; sample ID: 1245); and (*C*) sample displaying extreme weathering. Diagnostic features too weathered to assess mammillary cone erosion stage (sample ID: 1253). All examples derive from Yuku LP/EH layers.

recognized as "Middle" or "Late" stage by the 1-predictor model versus 98% identified as "Middle" or "Late" (591/603) by the 4-predictor model.

Eggshell Color and Burning. Eggshell fragments in both assemblages varied in color (*SI Appendix*, Fig. S16). Color variation reflects both depositional context and sometimes degree of burning. Burning of eggshell exteriors was observed on 58% of the total assemblage, while interior burning was observed on 48% of samples. Excluding unstratified samples, exterior and interior burning were most prevalent on eggshells dated to the TP and EH (*SI Appendix*, Table S10). Burning was also observed on a greater proportion of the assemblage from Yuku than from Kiowa.

Paired observations of exterior and interior burning on samples predicted to have been harvested at different stages of development reveal some diachronic patterns, including burning on the exterior and interior of the majority of "Early" stage eggshells during the LGM and LP/EH (*SI Appendix*, Fig. S17 and Fig. 6). During the LP/EH there is an increase in the occurrence of samples with no indications of burning, especially for those predicted to have been harvested in the "Middle" and "Late" stages of development.

We tested whether incidence of exterior and interior burning was correlated with eggshell developmental stage (*SI Appendix*, Tables S11 and S12). Both tests of independence revealed a significant association between incidence of burning and developmental stage.

Discussion

Human use of avian eggs has been documented in some of the earliest deposits attributed to *H. sapiens*, and avian eggshell is thus a key material for understanding the evolution of complex human behaviors (49). The method we have developed to analyze eggshell microstructural variation has great potential to clarify past human interactions with avian species and can be applied to new as well as legacy collections of eggshell from diverse time periods and contexts. Analysis of eggshell surface microstructures can offer insights into resource management decisions, as it can reveal patterns in the timing of egg harvesting, which itself can shed light on foraging strategies and seasonality, as well as dietary preference (e.g., consuming primarily yolk and albumin versus balut) and even the management of avian breeding (3, 50). Additionally, the method we present can be used to investigate the use of eggs—such as ostrich eggs in Pleistocene contexts (49)—as secondary products (e.g., liquid containers), which presumably would have required selection of "Early" stage eggs with liquid contents that could be extracted without excessively damaging the shell.

The overarching question posed in this paper is whether cassowary bone and eggshell assemblages recovered from Kiowa and Yuku reflect strategic harvesting and management of cassowaries by mobile foragers in the montane rainforests of eastern New Guinea beginning as early as the LGM. Growing archaeological evidence in the region suggests that the persistence of LP and Holocene foraging communities in montane rainforest environments was facilitated by their flexible use of diverse forest resources (2) and that resource use strategies differed by valley system (48). Cassowary exploitation presents a unique opportunity to investigate human management of a keystone rainforest species and the region's largest vertebrate, whose feathers, meat, bone, and eggs are all highly valued by people today and may have been important to early foragers.

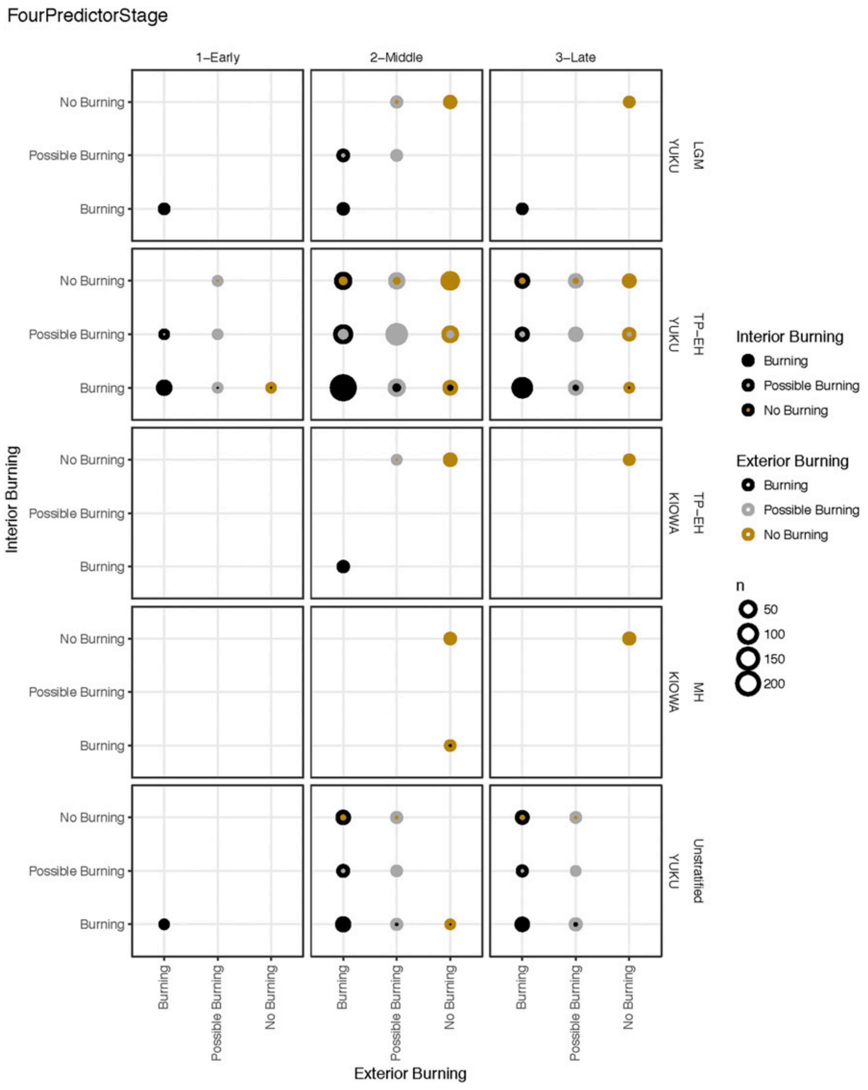

Fig. 6. Density plot showing eggshell interior and exterior burning according to eggshell ontogenetic stage (1 = "Early," 2 = "Middle," and 3 = "Late") prediction using the 4-predictor model and according to chronological phase at Kiowa and Yuku.

Evidence for hunting of cassowaries is limited. There is no evidence that foragers at Yuku hunted cassowaries, though they collected cassowary eggs, while some hunting of adults is evidenced at Kiowa in the mid-Holocene. At Kiowa, cassowary hunting does not appear to have been intensive given the relatively small assemblage, but carcasses may have been initially processed offsite. Although screens were not used during the excavations, bones of small mammals were recovered (48), suggesting that taphonomy or human behavior may explain the absence of certain cassowary skeletal elements. The absence of wing and skull elements could be explained by taphonomy as these elements are less dense than the hind limb and pelvis and could more easily have been crushed and/or washed away. The lack of sternum, which is quite large and dense in cassowary, is less easily explained by taphonomic processes. In contemporary communities on eastern New Guinea, the sternum is often displayed on the outside of houses or hung inside in the thatch as hunting trophies, but we have no basis for inferring this practice in deeper time. Being a flightless bird with extremely reduced wings, the femur and tibiotarsus (the thigh and drumstick) of a cassowary would provide the most meat. Because Dwarf Cassowaries are quite heavy birds (15 to 25 kg), it is possible that carcasses were processed where they were caught (51) and only the meatiest parts (i.e., the hind limb) were brought to Kiowa.

Evidence for egg harvesting provides insight as to seasonality of foraging rounds and interactions between cassowary populations and people. Cassowaries are polyandrous with male parental care (Fig. 7; 37). Female cassowaries mate and lay several clutches with several different males. Male cassowaries alone build nests of shallow depressions in the ground lined with leaves, incubate the three to five eggs for 7 to 8 wk (~50 d) and then care for the chicks for up to 9 mo after hatching. Southern Cassowary (*Casuarius casuarius*) and Northern Cassowary (*Casuarius unappendiculatus*) breed from June to October, while Dwarf Cassowary (*C. bennetti)* breed in some parts of New Guinea from February to April (52–55). But seasonality varies across the island (56), and dwarf cassowary breeding seasonality is not narrowly predictable (57).

Field biologists report that nests are difficult to find, do not appear to be located in the same site each year, and tend to be located in closed understory (58). Males appear to leave the nest unattended for lengths of time during the laying stage, but once incubation begins, males do not leave the nest and remain predominantly inactive as they continuously incubate for ~50 d (58).

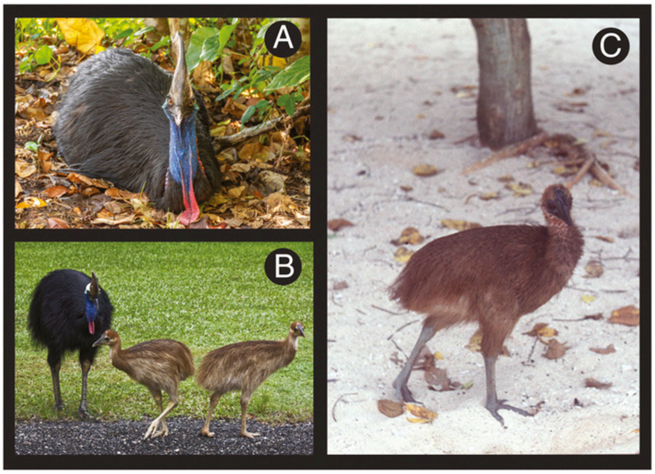

Fig. 7. Cassowary reproductive ecology featuring male parental care: (*A*) Male cassowary (*C. casuarius*) sitting on the forest floor; (*B*) Male cassowary (*C. casuarius*) and two juveniles; and (*C*) young cassowary chick (*Casuarius* spp.).

Once the chicks hatch, males apparently do not remove the eggshell from the nest or consume the eggshell fragments (58). Cassowary chicks are precocial and leave the nest to follow the male within a few days of hatching (58). Male Dwarf Cassowaries at Crater Mountain, eastern New Guinea, appear to incubate in the fruiting lean season, rarely leaving the eggs, and females appear to shift altitudes at this time to track greater fruit availability (52).

The intersite pattern for hunting described above reverses with regard to egg harvesting. The eggshell assemblage from Kiowa is relatively small compared to that of Yuku, where egg harvesting begins in the LGM and intensifies in the TP and EH. No pattern of intensification of egg harvesting is discernible at Kiowa. Our expectation is that if people are using the rock shelters seasonally and/or are managing their exploitation of cassowary nests, then eggshell assemblages should exhibit patterns in the developmental stage of harvested eggs and incidences of eggshell burning. The two modeling approaches combined with the visual inspection of eggshell development confirm that a majority of eggs were harvested during later stages of ontogeny (Fig. 4; *SI Appendix*, S1. 9–10). This pattern holds across both sites and through time, though the proportion of earlier stage eggs is slightly higher in the TP/EH at Kiowa. These data indicate that people at these two sites—and especially at Yuku—were preferentially harvesting eggs that contained cassowary embryos with fully formed limbs, beaks, claws, and feathers (3, 59–61). Furthermore, while there is overall agreement between our two models and visual inspection in the identification of later stage eggshells, the 4-predictor model appears to be picking up further microstructural variation that allows us to improve the resolution of our identifications. Results of the 4-predictor model indicate that people were regularly collecting cassowary eggs in the very latest stage of embryonic development, only a few days prior to hatching. This pattern is most pronounced in the LP and EH and supports the possibilities that foragers were collecting eggshell from eggs that had already hatched, preferred consuming eggs with fully formed embryos—considered a delicacy in some parts of the world—and/or that they were collecting eggs that they then allowed to hatch.

The correlation we found between incidences of eggshell burning and developmental stage is also noteworthy, particularly in terms of exterior burning (*SI Appendix*, Table S11). Early stage eggs featured higher incidences of exterior burning than expected if burning and developmental stage were independent, whereas later stage eggs displayed lower incidences of burning than expected. This could indicate that early stage eggs that contained primarily liquid contents (yolk and albumin) were preferentially cooked intact over an open fire or in an earth oven. Interestingly, Majnep reports his people cooked eggs on *Ficus dammaropsis* leaves on hot rocks and specifically says other leaves were not strong enough (62). *F. dammaropsis* is currently a lower to midmontane taxon (850 to 2,500 m asl). It is possible that the TP/EH habitat would not have supported *F. dammaropsis*, such that cooking in the eggshell would have been more prevalent, and the use of leaves (with less shell burning) became more common as treeline and montane vegetation moved up.

Eggshells assigned to the “Middle” stage by the 4-predictor model displayed a higher incidence of burning (both interior and exterior) than “Late” stage eggs, consistent with the possibility that some “Late” stage eggs were not cooked or consumed and were instead allowed to hatch (Fig. 6). This pattern is visible both in the larger Yuku assemblage and at Kiowa. At Kiowa, however, no eggshells assigned to the “Late” stage by the 4-predictor model display any signs of burning whatsoever.

The possibility that LP/EH foragers in montane New Guinea were hatching and rearing cassowary chicks is consistent with modern occurrences of cassowary chick rearing and translocation (63, 64), as well as a known history of plant and animal translocations in the region more broadly since the LP (65–67). These translocations primarily involved people trading or directly transporting tubers and medium-sized marsupials; however, Dwarf Cassowaries were imported prehistorically from mainland New Guinea to New Britain, presumably as docile juveniles (Fig. 7*C*; 63). These early forms of animal husbandry were a component of wider niche construction practices in New Guinea’s tropical forests (68) that did not just involve the domestication of these spaces (69, 70) but also encouraged humans to attune their foraging strategies to these managed forest ecologies (71).

Although there is some evidence of a commensal relationship between early humans and rock doves possibly as early as 67 ka B.P. in Gibraltar (72), the data presented here may represent the earliest indication of human management of the breeding of an avian taxon anywhere in the world, preceding the early domestication of chicken (*Gallus gallus*) and geese (*Anser anser*) by several millennia (73, 74). This is particularly intriguing given the large size and behavioral characteristics of cassowary and other ratites generally—such as territoriality and aggression—that make them more surprising candidates for close interaction with humans, as compared to early avian domesticates, such as chickens and geese. However, cassowary chicks imprint readily to humans and are easy to maintain and raise up to adult size (Fig. 1). Cassowary chicks are a traded commodity in parts of Papua New Guinea today (42).

Our findings highlight the importance of clarifying human interactions with keystone species, as these likely had ecological impacts at the landscape scale. As important seed dispersers, large K-reproducing ratites like cassowaries can be used as a deep-time proxy for human impacts on tropical forests. Research on modern cassowary populations in Australia indicates that their reproductive ecology (e.g., substantial male parental investment and low annual productivity) makes them extremely sensitive to predation and habitat disturbance and unlikely to successfully recolonize areas where they have previously been extirpated (58). Egg collecting at Kiowa and Yuku may have had more significant impacts on local cassowary populations compared to cassowary hunting. However, the persistence of cassowary eggshells in archaeological sites throughout montane New Guinea during the LGM to EH (*SI Appendix*, Table S3) suggests that cassowaries—and rainforest biota more broadly—were relatively resilient to human exploitation and land-use pressures of the time (Fig. 1). Although forest clearance has occurred on New Guinea since the Pleistocene (75), there have always been large tracts of suitable forest habitat. Further research is needed to shed light on the coevolutionary dynamics between people, cassowaries, and New Guinea’s tropical forests, especially through the investigation of additional records of human–cassowary interaction paired with the study of long-term, high-resolution records of climate and vegetation change.

Materials and Methods

Excavations. Yuku was excavated in 1959 and Kiowa in 1960 by the late Susan Bulmer and local field assistants. The excavations produced a sequence replete with stone tools and flaking debitage, vertebrate faunal remains, and occasional bone tools, shells, exotic objects, and eggshell fragments. Excavation followed natural sedimentological boundaries, with each context being designated an archaeological level. Detailed description of the excavations, stratigraphy, AMS dating, and materials analysis are presented in *SI Appendix*, S1.

Bone. Vertebrate remains from Kiowa and Yuku were analyzed following established zooarchaeological standards and methods (76). Sorted materials were weighed and recorded according to size class, and a full report of noncassowary vertebrate remains is presented by Gaffney et al. (48). *Casuarius* spp. elements were identified using comparative skeleton collections housed in the Smithsonian's National Museum of Natural History's Bird Division.

Eggshell. Eggshell fragments were weighed, measured, and coded based on Munsell color guides. In addition, high-resolution scans of eggshell surfaces were collected using a Keyence VK laser scanning microscope, and measurements of eggshell surface roughness were generated for analysis of eggshell developmental stage. Detailed methods of eggshell analysis, including predictive model parametrization, are presented in *SI Appendix*, S1.4–S1.9.

Data Availability. All study data are included in the article and/or supporting information.

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