### REPORTS

bution of those forcings to the warming of the early 20th century. However, these results do suggest that attempts to extract the response to solar forcing by correlating estimates of solar forcing with the observed temperature record can be misleading. Although some estimates of solar forcing do correlate with the observed record, they also correlate well with our experiment 3.

If the simulated variability and model response to radiative forcing are realistic, our results demonstrate that the combination of GHG forcing, sulfate aerosols, and internal variability could have produced the early 20th century warming, although to do so would take an unusually large realization of internal variability. A more likely scenario for interpretation of the observed warming of the early 20th century might be a smaller (and therefore more likely) realization of internal variability coupled with additional external radiative forcings. Additional experiments with solar and volcanic forcing, as well as with improved estimates of the direct and indirect effects of sulfate aerosols, will help to further constrain the causes of the early 20th century warming. Our results demonstrate the fundamental need to perform ensembles of climate simulations in order to better delineate the uncertainties of climate change simulations associated with internal variability of the coupled ocean-atmosphere system.

## References and Notes

- P. D. Jones, M. New, D. E. Parker, S. Martin, I. G. Rigor, Rev. Geophys. 37, 173 (1999).
- 2. B. D. Santer et al., Nature 382, 39 (1996).
- 3. G. C. Hegerl et al., Clim. Dyn. 13, 613 (1997).
- S. F. B. Tett, P. A. Stott, M. R. Allen, W. J. Ingram, J. F. B. Mitchell, *Nature* 399, 569 (1999).
- T. J. Crowley and K.-Y. Kim, Geophys. Res. Lett. 26, 1901 (1999).
- M. Free and A. Robock, J. Geophys. Res. 104, 19057 (1999).
- 7. S. Manabe and R. J. Stouffer, J. Clim. 7, 5 (1994).
- 8. \_\_\_\_\_\_, M. J. Spelman, K. Bryan, *J. Clim.* **4**, 785 (1991).
- J. F. B. Mitchell, T. C. Johns, J. M. Gregory, S. F. B. Tett, Nature 376, 501 (1995).
- J. F. B. Mitchell, R. A. Davis, W. J. Ingram, C. A. Senior, J. Clim. 8, 2364 (1995).
- J. M. Haywood, R. J. Stouffer, R. T. Wetherald, S. Manabe, V. Ramaswamy, Geophys. Res. Lett. 24, 1335 (1997).
- T. R. Knutson, T. L. Delworth, K. W. Dixon, R. J. Stouffer, J. Geophys. Res. 104, 30981 (1999).
- D. E. Parker, P. D. Jones, A. Bevan, C. K. Folland, J. Geophys. Res. 99, 14373 (1994).
- 14. For fully overlapping 35-year periods from model years 101 to 1000 (i.e., years 101-135, 102-136, ..., 966-1000), we projected the model output onto the same grid used for the observations. The model output was then sampled according to the temporal and spatial distribution of observed data over the period 1910-1944 to form global mean, annual mean time series from which linear trends are calculated. This vielded a set of 866 trends of duration 35 years. We then randomly selected six samples of nonoverlapping 35-year periods and computed the difference between the trend in the first sample and the mean of the trends for the other five samples. This process was repeated one million times to produce a distribution of differences between a single trend (realization) and five-member ensemble means. Using this

distribution, we then evaluated how likely the difference is between the trend corresponding to the observations (viewed as a single realization) and the five-member ensemble mean trend. Differences equal to or exceeding 0.32 K/year (the difference between the observed trend and the ensemble mean model trend) occurred in 4.8% of the cases, indicating the likelihood that the observed trend is consistent with the model ensemble. This assessment depends on the assumption that internal variability in the five transient runs is similar to that in the control run.

- 15. The ensemble mean trend from the five GHG-plus-sulfate experiments (n=5) was compared with the observed trend (n=1) at each grid point (with sufficient temporal coverage), using a local two-sided two-sample t test. The population variance for the t test was estimated from 35-year trends as simulated in the 900-year control integration. For the t test, we assumed 25 degrees of freedom, based on the number of nonoverlapping 35-year chunks in the control integration. Assuming only 20 degrees of freedom, the percent area rejecting the null hypothesis decreases only slightly (from 27 to 26%).
- 16. J. W. Hurrell, Science 269, 676 (1995).
- J. C. Rogers, J. Clim. Appl. Meteorol. 24, 1303 (1985);
   C. Fu, H. F. Diaz, D. Dong, J. O. Fletcher, Int. J. Climatol. 19, 581 (1999).

- T. L. Delworth, S. Manabe, R. J. Stouffer, Geophys. Res. Lett. 24, 257 (1997).
- M. E. Schlesinger and N. Ramankutty, *Nature* **367**, 723 (1994).
- 20. M. E. Mann and J. Park, J. Clim. 9, 2137 (1996).
- 21. \_\_\_\_\_\_, R. S. Bradley, *Nature* **378**, 266 (1995); T. L. Delworth and M. E. Mann, *Clim. Dyn.*, in press.
- D. S. Battisti, C. M. Bitz, R. E. Moritz, J. Clim. 10, 1909 (1997).
- A. Kattenberg et al., in Climate Change 1995: The Science of Climate Change, J. Houghton et al., Eds. (Cambridge Univ. Press, Cambridge, 1996), pp. 285– 357.
- 24. T. P. Barnett et al., Bull. Am. Meteorol. Soc. 80, 2631 (1999).
- M. R. Allen, P. A. Stott, J. F. B. Mitchell, R. Schnur, T. L. Delworth, *Technical Report RAL-TR-1999-084* (Rutherford Appleton Laboratory, Chilton, Didcot, UK, 1999).
- P. A. Stott, S. F. B. Tett, G. A. Jones, M. R. Allen, W. J. Ingram, J. F. B. Mitchell, Clim. Dyn., in press.
- We thank M. Allen, J. Anderson, A. Broccoli, K. Dixon, G. Hegerl, I. Held, P. Kushner, J. Mahlman, S. Manabe, and R. Stouffer for helpful contributions at various stages of the work.

6 October 1999; accepted 11 February 2000

## Rapid Extinction of the Moas (Aves: Dinornithiformes): Model, Test, and Implications

R. N. Holdaway<sup>1\*</sup> and C. Jacomb<sup>2</sup>

A Leslie matrix population model supported by carbon-14 dating of early occupation layers lacking moa remains suggests that human hunting and habitat destruction drove the 11 species of moa to extinction less than 100 years after Polynesian settlement of New Zealand. The rapid extinction contrasts with models that envisage several centuries of exploitation.

All 11 species of the large (20 to 250 kg) flightless birds known as moas (Aves: Dinornithiformes) survived until the arrival of Polynesian colonists in New Zealand (1). Abundant remains of moas in early archaeological sites show that the birds were major items of diet immediately after colonization (2-5). Indeed, the presence of moa remains was formerly used to characterize the earliest or "Archaic" period of human occupation in New Zealand [the "Moa-hunter" period (3, 6)]. Polynesian hunting and habitat destruction were responsible for the extinction of all species of moa some time before European contact began in the late 18th century (1-4)7). Sites from the later, "Classic" Maori period lack evidence of moa exploitation. The Classic period is characterized by earthwork fortifications (the Maori term for which is pa) and occupation deposits indicating reliance on fish, shellfish, and plants for food.

Current interpretations of moa extinction implicitly or explicitly require a period of several hundred years of gradual population attrition by hunting and habitat loss: this is the orthodox model (2, 3, 5). The moa-hunting period has been estimated to have lasted some 600 years, peaking 650 to 700 years before the present (yr B.P.) and ending about 400 yr B.P. (2, 3). Anderson (2) estimated the duration of moa hunting from a radiocarbon chronology of moa hunting sites and from moa population parameters based on extant ratites and African bovids. It is difficult to estimate the time of moa extinction from a series of dates on moa bones and from moa hunting sites, because confidence intervals for calibrated ages are greater than those for conventional radiocarbon ages (8), and additional dates could be younger than the presently perceived limit.

Reassessment of some major archaeological sites has suggested that moas were becoming scarce by the end of the 14th century (9, 10). The earliest settlement sites date from the late 13th century (11), not the 10th or 11th century as previously thought (5). A later date for first settlement would imply that moa

<sup>&</sup>lt;sup>1</sup>Palaecol Research, 167 Springs Road, Hornby, Christchurch 8004, New Zealand. <sup>2</sup>Canterbury Museum, Rolleston Avenue, Christchurch, New Zealand.

<sup>\*</sup>To whom correspondence should be addressed. E-mail: piopio@netaccess.co.nz

extinction was much more rapid than suggested by the orthodox model. How might a human population have eliminated complete populations of large birds within a few decades? To explore the possibility of rapid extinction by human predation, we applied a standard Leslie matrix population model (12) to moas using parameters common to long-lived birds and the limited data that can be inferred from fossil evidence (such as clutch size) (13).

The objective was to explore the effects on the total moa population of low levels of exploitation concomitant with a small initial human population, coupled with the habitat loss induced by those people. For the model to be conservative and not to underestimate the time to moa extinction, we used an initial population of 100 people (14). We also selected low to medium human population growth rates, minimal rates of habitat removal in only two areas of the two main islands of New Zealand, and the lowest cropping rates suggested by Anderson (2). We estimated the total population of moas (all species) at the time of human settlement, from a regional analysis of distribution and abundance, to be 158,000 birds, which is about twice the population previously suggested (2). Only consumption of adult moas (>1 year old) was considered. Consumption of moa eggs, known to have been considerable (3), was ignored. At all stages, therefore, we chose population sizes and parameters that would minimize losses to the moa population, to ensure that the model would not underestimate the duration of the extinction process.

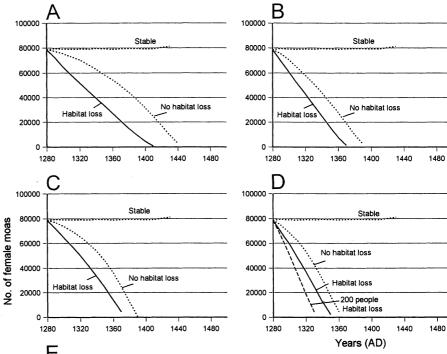
The simulations showed that moas, like most long-lived birds, were very vulnerable to any increase in adult mortality. When subjected to even a low level of human predation, moas required a disproportionate (and impossible) increase in recruitment to maintain their numbers (15). Time to extinction under all scenarios simulated was less than 160 years (Fig. 1, A through D). Even without habitat loss, the most conservative simulation suggested that moas were effectively extinct within 160 years of human colonization (Fig. 1A). Hence, the "no habitat loss" curves were useful in defining an upper bound for the duration of the exploitation/extinction process. Substantial areas of habitat were certainly lost early in the settlement period (16), together with their moa populations.

Habitat loss in areas II and V (Fig. 2) reduced the time to extinction for the whole fauna by decreasing adult moa survivorship before the human population had increased substantially (Fig. 1). Human population growth rate was more important in determining the time to extinction than was the rate of consumption of moas per individual. Doubling the founding human population to 200 reduced the time to extinction by

nearly a third under the same model conditions (Fig. 1D). In combination with habitat loss, this "most likely" scenario resulted in moa extinction 50 years after colonization (Fig. 1D). By then, the human population would have grown to nearly 600, which is much fewer than is presently thought necessary to seriously affect moa populations (2, 3).

The effect of the human population being

divided into separate groups in different areas was also explored. If 50 of an original 200 people settled in area V (the richest zone of moa distribution), they would have increased to 148 after 50 years at 2.2% per annum (p.a.). In that time, in concert with habitat destruction, they could have eliminated 56,000 adult moas. The time to extinction for the moas would have varied regionally with their abundance, which in turn depended on the terrain



Stable

Orthodox

Model

40000

200 people
Habitat loss

1000 1200 1400 1600 1800 2000

Years (AD)

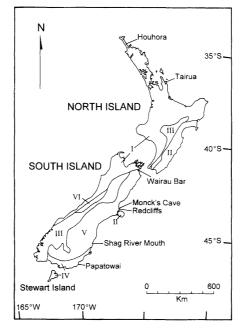
Fig. 1. Simulated declines in moa populations (the number of adult females) caused by human predation, with and without habitat loss, in areas II and V (Fig. 2). (A) One female moa per 20 people per week; human population 100, increasing at 1% p.a. (B) One female per 10 people per week; human population 100, increasing at 1% p.a. (C) One female per 20 people per week; human population 100, increasing at 2.2% p.a. (D) One female per 10 people per week; human population 100, increasing at 2.2% p.a. (solid line); one female per 10 people per week; human population 200,

increasing at 2.2% p.a. (long-dashed line). (E) Orthodox model of moa extinction versus maximum and minimum times to extinction from the Leslie matrix model. Leslie matrix analyses were done with RAMAS/Age (12), adapted to simulate "inverse density dependence" (increasing crop rates and decreasing prey population). Each simulation started with 78,800 adult females of all species (which is 3% above the population estimate). Survivorship values assumed are as follows (year class, survivorship): 0, 0.25; 1, 0.74; 2, 0.75; 3, 0.83; 4, 0.93; 5 and over, 0.95) based on the tendency of K-selected birds to live longer, have smaller clutches, have lower juvenile survival rates (14), and achieve a stable population given clutch size and assumed longevity. Fecundity rates based on a clutch size of 1 or 2 eggs (22) and an age of first breeding of 5 years, with full breeding potential reached in year 12, were as follows (year, chicks raised): 0 to 4, 0; 5, 0.05; 6, 0.10; 7, 0.15; 8, 0.2; 9, 0.25; 10, 0.50; 11, 0.8; 12 and over, 0.95. No immigration or emigration was assumed. The coefficient of variation (all parameters) is 2%. Predation of eggs and first-year birds was omitted. Starting values resulted in stable to slightly increasing mean populations (minimum, 57,900; maximum, 101,000 females after 50 years). Simulations were run in decadal blocks, and adult survivorship was recalculated after each decade and applied to a starting population of the mean end population (100 simulations for each mean) for the preceding decade. Adult survivorship was reduced from the initial value for the decade by the sum of the percentage loss to cropping (based on the annual crop required by the number of people at the start of each decade) and to habitat and the carrying capacity of the dominant vegetation. Times to extinction in areas with low moa numbers would have been so short that sequential occupation of sites in different regions could have occurred within the range of uncertainty in calibrating radiocarbon dates and hence be difficult to detect. In comparison to the orthodox model, both the longest and the most likely durations simulated here resulted in much steeper declines in the moa population (Fig. 1E). Another important difference is the impossibility of any prolonged initial phase of low-level exploitation or of residual survival of the moa as a resource, which are integral parts of most versions of the orthodox model (2, 3, 5) (Fig. 1E).

**Table 1.** Radiocarbon dates from occupation levels at Monck's Cave, Christchurch, New Zealand. All determinations were made on apatite from marine shell (*Austrovenus stutchburyi*) by the Waikato University Radiocarbon Laboratory (Wk). CRA, conventional radiocarbon age in years before the present (1950), with reference to the Old (Libby) Half-life; the calibrated age is given in calendar years (24).

Provenance	CRA	Calibrated age	δ <sup>13</sup> C	Lab no. (Wk)
		Cave interior		
G13 layer 2, lens 1	$980 \pm 40$	1σ, 1321–1410; 2σ, 1300–1434	$1.0 \pm 0.2$	6769
G13 layer 2, lens 2	910 ± 70	1σ, 1351–1458; 2σ, 1306–1506	$1.6 \pm 0.2$	6770
G14 layer 2, spit 1	900 ± 40	$1\sigma$ , $1406-1450$ ; $2\sigma$ , $1342-1476$	$1.1 \pm 0.2$	6771
G14 layer 2, spit 2	950 ± 45	$1\sigma$ , $1334-1428$ ; $2\sigma$ , $1308-1451$	$1.2 \pm 0.2$	6772
G14 layer 2, spit 3	960 ± 40	1σ, 1332–1420; 2σ, 1308–1443	$1.2 \pm 0.2$	6773
L14 layer 2	900 ± 45	1σ, 1403–1452; 2σ, 1335–1482	$0.6 \pm 0.2$	6779
•		Cave exterior		
K39 layer 2, spit 2	$780 \pm 45$	1σ, 1464–1531; 2σ, 1441–1625	$1.3 \pm 0.2$	6778
K39 layer 2, spit 4	$830 \pm 45$	1σ, 1440–1494; 2σ, 1414–1530	$0.7 \pm 0.2$	6777
K39 laver 2, spit 6	$1000 \pm 45$	$1\sigma$ , $1308-1402$ ; $2\sigma$ , $1287-1428$	$0.9 \pm 0.2$	6776
145 fire scoop	$750 \pm 40$	1σ, 1487–1558; 2σ, 1458–1642	$1.4 \pm 0.2$	6774
145 natural shell lens	$2410\pm50$	1σ, 180–44 B.C.; 2σ, 251–14 B.C.	$0.9 \pm 0.2$	6775

Fig. 2. Map of New Zealand archaeological sites with radiocarbon dates that are relevant to the duration of moa hunting and of habitat areas used for the estimation of total moa abundance before human colonization. Area I (130,000 km<sup>2</sup>): tall wet forest dominated by trees of the Podocarpaceae; area II (21,000 km2): drier forest dominated by Podocarpaceae; area III (53,000 km²): high-altitude (>800 m) southern beech (Nothofagus) forest; area IV (12,500 km²): southern South Island mixed forests and shrublands dominated by Podocarpaceae; area V (65,000 km<sup>2</sup>): drier eastern forest/shrubland/grassland mosaic with abundant Podocarpaceae; area VI (6,200 km2): montane shrubland, herbfield, bare rock, and glaciers. The total moa population was based on current carrying capacities for emus (Dromaius novaehollandiae) (worst, 2.5 kg km<sup>-2</sup>; medium, 9.1 kg km<sup>-2</sup>; best, 16.8 kg km<sup>-2</sup>) (2). Moa species were assumed to occupy habitat independently, and biomass per square kilometer was taken as the sum of that for the dominant species present, using representative species body masses of the following species: Megalapteryx didinus (MEDI), 20 kg; Anomalopteryx didiformis (ANDI), 40 kg; Eury-



apteryx geranoides (EUGE), 95 kg; *E. curtus* (EUCU), 20 kg; *Emeus crassus* (EMCR), 50 kg; *Pachyornis elephantopus* (PAEL), 145 kg; *P. australis* (PAAU), 120 kg; *P. mappini* (PAMA), 20 kg; *Dinornis struthoides* (DIST), 100 kg; *D. novaezealandiae* (DINO), 150 kg; and *D. giganteus* (DIGI), 200 kg. The dominant species in each region were as follows (species, total birds of all species km<sup>-2</sup>, total birds). Area I: EUCU (North Island only), PAMA (North Island only), DIST, DINO, and MEDI (South Island only); 0.425; 48,025. Area II: ANDI, DINO, DIST, PAMA, and DIGI; 1.54; 31,724. Area III: MEDI (South Island), PAAU (South Island), DINO, DIST, and ANDI; 0.146; 7621. Area IV: DIGI, EUGE, DIST, ANDI, DINO, EMCR, and PAEL; 0.532; 6650. Area V: PAEL, EUGE, EMCR, DIST, and DIGI; 0.88; 57,625. Area VI: PAAU and MEDI; 0.146; 905. Habitat destroyed in areas II and V = 0.9% p.a., with human population increasing at 1.6% p.a., respectively, for the first 100 years of human settlement, with a complete loss of moas occupying the area destroyed each year (that is, no emigration of displaced birds). The actual rate of loss in both areas is about 3% p.a.; a 50% reduction (*16*) is taken to have occurred within 100 years of colonization.

To test the conflicting models, it was necessary to determine when moa hunting ceased. Evidence supporting the Leslie matrix model was found in a series of radiocarbon dates establishing a chronology for Monck's Cave (Figs. 2 through 4). The artifacts found in the cave and the materials from which they were made indicate that the site was transitional between moa-hunter and Classic sites (17). In addition, although it is in an area where moa hunting had been intensively practiced (and is close to a major moa-hunter site), Monck's Cave lacked evidence of moa consumption (17). Hence, dating the occupation layers could provide a local terminal date for the moa, assuming that people were likely to eat moa meat if it was available within human foraging range of the site.

A series of radiocarbon determinations (Table 1) from marine shell (Fig. 3) shows that the site was occupied in the mid-to-late 14th or early 15th centuries inside the cave and perhaps into the 16th century outside (Fig. 4). The dates from Monck's Cave bridged the time between when people unequivocally hunted moas and when they clearly did not, relying instead on other foods, and built fortified pa (Fig. 4). The dates therefore showed that moas were not available to people in the area from the late 14th century onward. The evidence for human arrival in the late 13th century (11), and the evidence presented here for the absence of moas from the environment in a major moa-hunting area by the late 14th century, strongly support the rapid extinction model. Gradual extinction models are not supported.

Data from major moa-hunting sites such as Houhora and Tairua in the North Island, and Wairau Bar, Shag River Mouth, and Papatowai in the South Island (Fig. 2) also support the short extinction chronology. Very early sites, such as Wairau Bar, Houhora, and Papatowai show that moa were hunted from the earliest settlement phase. At the Shag River site, 265 km south of Monck's Cave, radiocarbon dates suggest a brief (<50 years) occupation in the middle of the 14th century (9, 18). Moas represented about 50% of the food remains in the lower layers but only about 20% by the end of occupation there. We conclude that moas had been severely depleted in the area by this time.

The Leslie matrix model suggests that a protracted period of moa exploitation was not possible, given the life history parameters of the birds, even with the lowest conceivable numbers of Polynesian colonists. Minimal cropping rates (2) initiated a sudden precipitate population collapse, because the birds had little capacity to make good constant losses of adults. Dates for the earliest sites and the end of moa hunting imply that the period of moa-hunting was brief in comparison to the duration of Polynesian occupation

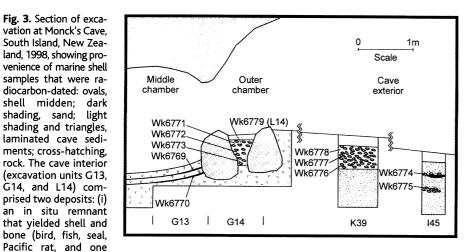
of New Zealand. The small founding human population achieved a very high archaeological visibility. Because the hunters moved to new sites shortly after the supply of moas was exhausted, most sites remained intact. The high visibility of massive moa bones on the surface in sites shows that there can have been no "pre-visibility" occupation phase nor a period of slow, archaeologically cryptic, population growth from a small founding human population. Previous suggestions that proxy indicators show anthropogenic environmental change well before 1000 A.D. can be discounted (19). Any occupation of more than 5

vears would be visible, both as archaeological remains and as environmental damage (16).

Rapid extinction implies that the number of moas preserved in a site could be directly related to the moa population in that area. Indeed, where the population was small enough to be exterminated in less than 10 to 20 years (as in most parts of the North Island), a site could contain most of the moa population alive in that area when people arrived.

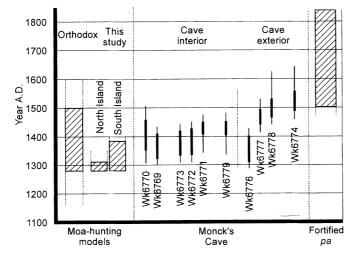
Long-lived birds are very vulnerable to human predation of adults (20). Although habitat destruction by fire (16) increased the effective predation rate on moas, even minimal levels of human hunting pressure caused an irreversible decline in the moa population. Our relatively simple Leslie matrix simulations agreed closely with archaeological data on the beginning and end of moa hunting. The consequences for understanding the pattern and process of the peopling of the last major habitable land mass to be reached by humans are far-reaching. The elimination of the moa by Polynesians was the fastest recorded megafaunal extinction, matched only by the predictions of the "Blitzkrieg" model for North American late Pleistocene extinctions (21).

### vation at Monck's Cave, South Island, New Zealand, 1998, showing provenience of marine shell samples that were radiocarbon-dated: ovals, shell midden; dark shading, sand; light shading and triangles, laminated cave sediments; cross-hatching, rock. The cave interior (excavation units G13, G14, and L14) com-



worked fragment of moa bone) in a cleft between two rocks in G14 and in L14; and (ii) two layers interspersed between earlier and later, washed-in, laminated microstrata (black layers in G13, clearly derived from the cultural deposit in G14). Dating samples were submitted from three arbitrary levels in G14 and from both black layers in G13 to test whether more than one occupation was indicated. The results show that the cave was occupied only once, and probably briefly. The cave exterior (excavation units K39 and I45) comprised a single, nonstratified, marine shell midden layer (not necessarily contiguous between these units). K39 is  $\sim$ 350 mm of shell midden overlying clean sand. K39 was excavated in arbitrary 50-mm levels; the top, middle, and bottom levels were dated. 145 is a fire-scoop feature with marine shell associated, 200 to 400 mm below the surface. A natural shell lens, at 500 to 550 mm, returned an age of 2410  $\pm$  50 years before the present (Wk 6775) (Wk, lab number from the Waikato University Radiocarbon Laboratory). The cave was sealed by a landslide, almost certainly at the time of occupation; later dates for the cave's exterior may reflect the earlier abandonment of the cave itself.

Fig. 4. Comparison of radiocarbon ages from early sites with abundant evidence of moa hunting (Wairau Bar, Houhora, Papatowai, and Shag River Mouth), Monck's Cave, and Classic fort (pa) sites. Dates for moa exploitation sites (Orthodox) are expressed as a band encompassing the range of calibrated dates on charcoal, marine shell, and moa bone collagen accepted by Anderson (11). Dates for Monck's Cave are shown as 68% confidence limits (thick line) and 95%



confidence limits (thin line) for calibrated dates (24). The band signifying dates for fortified pa summarizes available calibrated dates on various materials (25).

### References and Notes

- 1. Climate was not a factor in the New Zealand Holocene extinctions. No New Zealand vertebrates are known to have gone extinct at the end of the Otiran Glacial, and climatic fluctuations within the past 1000 years were minor in comparison to that event [R. N. Holdaway, in Extinctions in Near Time: Causes, Contexts, and Consequences, R. D. E. MacPhee, Ed. (Kluwer Academic/Plenum Press, New York, 1999), pp. 189-238.].
- 2. A. J. Anderson, J. Archaeol. Sci. 16, 137 (1989).
- \_, Prodigious Birds: Moas and Moa Hunting in Prehistoric New Zealand (Cambridge Univ. Press, Cambridge, 1989).
- 4. R. Cassels, in Quaternary Extinctions: a Prehistoric Revolution, P. S. Martin and R. G. Klein, Eds. (Univ. of Arizona Press, Tucson, AZ, 1984), pp. 741-767
- 5. J. M. Davidson, The Prehistory of New Zealand (Longman Paul, Auckland, New Zealand, 1984).
- R. S. Duff, The Moa-hunter Period of Maori Culture (Canterbury Museum bulletin no. 1, New Zealand Government Printer, Wellington, New Zealand,
- 7. A. J. Anderson, in Quaternary Extinctions: A Prehistoric Revolution, P. S. Martin and R. G. Klein, Eds. (Univ. of Arizona Press, Tucson, AZ, 1984), pp. 728-740.
- 8. R. E. Taylor, M. Stuiver, P. J. Reimer, Quat. Sci. Rev. (Ouat. Geochronol.) 1, 655 (1996).
- 9. A. J. Anderson and I. G. Smith, World Archeol. 27, 359 (1996).
- 10. A. J. Anderson and I. G. Smith, in Shag River Mouth: the Archaeology of an Early Southern Maori Village, A. J. Anderson, B. Allingham, I. G. Smith, Eds. [Archaeology and Natural History (ANH) Publications, Research School of Pacific and Asian Studies (RSPAS), Australian National University, Canberra, Australia, 1996], chap. 20.
- 11. A. J. Anderson, Antiquity 65, 767 (1991); T. Higham, A. Anderson, C. Jacomb, Antiquity **73**, (1999).
- 12. S. Ferson and H. R. Akçakaya, RAMAS/Age: Modelling Fluctuations in Age-structured Populations (Applied Biomathematics and Exeter Software, Setauket, NY,
- 13. J.-D. Lebreton and J. Clobert, in Bird Population Studies: Relevance to Conservation and Management, C. M. Perrins, J.-D. Lebreton, G. J. M. Hirons, Eds. (Oxford Univ. Press, Oxford, 1991). pp. 105-125.
- 14. An analysis of mitochondrial DNA diversity in the present Maori population suggests that there were 50 to 100 women in the colonizing population [R. P. Murray-McIntosh, B. J. Scrimshaw, P. J. Hatfield, D. Penny, Proc. Natl. Acad. Sci. U.S.A. 95, 9047 (1998)]. We used an initial population at the low end of the range implied by these data.
- 15. C. M. Perrins, in Bird Population Studies: Relevance to Conservation and Management, C. M. Perrins, J.-D. Lebreton, G. J. M. Hirons, Eds. (Oxford Univ. Press, Oxford, 1991). pp. 190-206.
- 16. M. S. McGlone, N.Z. J. Ecol. 12 (suppl.), 115 (1989); and J. M. Wilmshurst, Quat. Int. 59, 5 (1999).
- 17. Monck's Cave (Figs. 2 and 3) was discovered and first excavated in 1889 [H. O. Forbes, Trans. Proc. N.Z. Inst. 23, 373 (1891)]. A few fragments of moa bone and eggshell were found, and some shell fragments retained chorioallantoic membranes. The bone appeared to be industrial rather than food remains;

REPORTS

eight artifacts from the site were manufactured from the same material. Originally cataloged as "subfossil," their appearance and condition, especially in comparison to bone of other species from the cave, suggest that they had been "mined" from elsewhere, perhaps the nearby Redcliffs site, where moa bones were very common. The many artifacts found in 1889 [H. D. Skinner, Rec. Canterbury Mus. 2, 151 (1924)] included a few types that can be attributed to the Archaic [J. Golson, in Anthropology in the South Seas, J. D. Freeman and W. R. Geddes, Eds. (Avery, New Plymouth, New Zealand, 1959), pp. 29-74], including a fragment of a one-piece fish hook and 2 of the 17 adzes in the collection. However, most do not fit well into either the Archaic or Classic assemblages as currently understood. Monck's Cave is one of a group of northeastern South Island sites that are neither typically Archaic nor Classic in material culture, economic focus, or settlement pattern but appear to be transitional between the two [C. Jacomb, thesis, Department of Anthropology, Otago Univ., Dunedin, New Zealand (1995)]. Excavations in 1998 revealed extensive deposits of marine mollusk shell; some fish bone; sparse bird, seal, and Pacific rat bone; and a fragment of worked moa bone and three small pieces of moa eggshell.

- A. J. Anderson, B. Allingham, I. G. Smith, Eds., Shag River Mouth: the Archaeology of an Early Southern Maori Village (ANH Publications, RSPAS, Australian National Univ., Canberra, Australia, 1996).
- D. G. Sutton, N.Z. J. Archaeol. 9, 135 (1987); N. J. Enright and N. M. Osborne, N.Z. J. Archaeol. 10, 139 (1988); M. S. McGlone, A. J. Anderson, R. N. Holdaway, in The Origins of the First New Zealanders, D. G. Sutton, Ed. (Auckland Univ. Press, Auckland, New Zealand, 1994).
- J. P. Croxall, Ardea 67, 15 (1979); J. P. Croxall, P. Rothery, S. P. C. Pickerin, P. A. Prince, J. Anim. Ecol. 59, 775 (1990); H. Weimerskirch and P. Jouventin, Oikos 49, 315 (1987).
- J. E. Mosimann and P. S. Martin, Am. Sci. 63, 304 (1975).
- G. E. Hamel, in *Birds of a Feather*, A. Anderson, Ed. (British Archaeological Reports International Series 62, Oxford, 1979), pp. 61–66; R. A. Falla, in *A New Dictionary of Birds*, A. Landsborough Thomson, Ed. (Nelson, London, 1964), pp. 477–479; W. H. Hartree, *Notornis* 46, 457 (1999).
- 23. J. P. Croxall and P. Rothery [in Bird Population Studies: Relevance to Conservation and Management, C. M. Perrins, J.-D. Lebreton, G. J. M. Hirons, Eds. (Oxford Univ. Press, Oxford, 1991), pp. 272–296] demonstrated the effects of a small reduction in adult survivorship in a long-lived slow-breeding bird. In the wandering albatross (Diomedea exulans), the breeding population declined even with 94% adult survivorship.
- Marine shell was cleaned, washed in 2 M HCl for 100 s, rinsed, and dried. Samples were not assessed by x-ray diffraction, because New Zealand marine shell very rarely exhibits significant recrystallization [T. Higham, Quat. Geochronol. 13, 163 (1994)]. Radiocarbon determinations were calibrated to calendar years using OxCal {C. Bronk Ramsay, Radiocarbon 37, 425 (1995); the marine curve was as modeled by M. Stuiver, P. J. Reimer, and S. Braziunas [Radiocarbon 40, 1127 (1998)]; R was set at -25 ± 15 years, according to T. F. G. Higham and A. G. Hogg [Radiocarbon 37, 409 (1995)]].
   M. Schmidt, "Few have been tested by the spade. . . ."
- M. Schmidt, "Few have been tested by the spade. . . . "
   Pa Excavation and Radiocarbon Dating in New Zealand Archaeology (research essay, Department of Anthropology, Auckland Univ., Auckland, New Zealand, 1993).
- 26. We thank Te Ngai Tuahuriri Runanga of Ngai Tahu for permission to excavate at Monck's Cave; the New Zealand Foundation for Research, Science & Technology (R.N.H.) and the Canterbury Museum (C.J.) for financial support; the Christchurch City Council for financial support for excavations in Monck's Cave; and the Mason Foundation for funding radiocarbon dates. M. S. McGlone, J. M. Wilmshurst, P. S. Martin, and M. J. Winterbourn provided valuable criticism of earlier drafts of the manuscript.

20 October 1999; accepted 20 January 2000

# The Initial Domestication of Goats (*Capra hircus*) in the Zagros Mountains 10,000 Years Ago

Melinda A. Zeder<sup>1\*</sup> and Brian Hesse<sup>2</sup>

Initial goat domestication is documented in the highlands of western Iran at 10,000 calibrated calendar years ago. Metrical analyses of patterns of sexual dimorphism in modern wild goat skeletons (*Capra hircus aegagrus*) allow sexspecific age curves to be computed for archaeofaunal assemblages. A distinct shift to selective harvesting of subadult males marks initial human management and the transition from hunting to herding of the species. Direct accelerator mass spectrometry radiocarbon dates on skeletal elements provide a tight temporal context for the transition.

The fertile crescent region of the Near East was the center of domestication for a remarkable array of today's primary agricultural crops and livestock animals. Wheat, barley, rye, lentils, sheep, goats, and pigs were all originally brought under human control in the broad arc that stretches from the southern Levant through southeastern Turkey and northern Syria, to the high Zagros mountain pastures and arid lowland plains of Iraq and Iran. For more than 50 years researchers have sought to define the sequence, temporal placement, and social and environmental context of domestication (1). Central to addressing this process is the ability to identify early domesticates in the archaeological record, and to place them within a secure temporal context. Here we describe recent research that uses a study of modern wild goats (Capra hircus aegagrus) to develop an unequivocal marker of early goat domestication, which we apply to assemblages that lie both within and outside the natural range of wild goats in the eastern fertile crescent region—a region long thought to be the initial heartland of goat domestication (2).

Two markers have been used to identify domestication in goats. It has been proposed that changes in skeletal morphology, particularly population-wide reduction in body size, quickly follow human controlled breeding (3, 4). Uncertainty over the pace and causal connection between body size reduction and human control limits the utility of this marker, however, as does difficulty in distinguishing between human-in-

duced changes and those resulting from other biological or environmental factors (5). Alternatively, changes in age and sex profiles that resulted from controlled breeding and selective harvesting of young males have been proposed as providing a better early marker of domestication (6). Difficulty in distinguishing between various selective hunting strategies and those that reflect deliberate herd management and domestication has been the main perceived limitation of this demographic profiling approach (4). Until now a key obstacle has been an inability to construct the separate male and female age profiles necessary to detect the distinctive sex-specific harvest patterns of managed herds.

Recent metrical analysis of a skeletal collection of 37 modern wild goats, curated by the Field Museum of Natural History, from different habitats in Iran and Iraq provides an empirical basis for assessing the utility of these different markers of early goat domestication (7). In all measurements taken on nine different postcranial skeletal elements, sex was the single most significant factor influencing size (Fig. 1). Even the unfused bones of young males older than 1 year were absolutely larger than the fully fused bones of older, adult females. Environment also influenced body size, with a clear pattern of size reduction from the cooler, wetter regions in northern Iran and northwestern Iraq (Fig. 1A) to the arid, hotter, and sparser pastures of southern Iran (Fig. 1C). While the available sample of domesticated goats (C. h. hircus) from the region was too small to draw firm conclusions, domestic status does not appear to be a major factor influencing size in this modern sample, especially in female goats (Fig. 1, A and B).

This modern reference class of goat skeletons provides a baseline of comparison for analysis of goat bone assemblages

<sup>&</sup>lt;sup>1</sup>Archaeobiology Program, Department of Anthropology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0112, USA. 
<sup>2</sup>Department of Anthropology, University of Alabama at Birmingham, Birmingham, AL 35294-3350, USA.

<sup>\*</sup>To whom correspondence should be addressed. E-mail: zeder.melinda@nmnh.si.edu