AMERICAN MUSEUM NOVITATES

Number 3807, 26 pp. June 30, 2014

# Mortality in a predator-free insular environment: the dwarf deer of Crete

ALEXANDRA A. E. VAN DER GEER,[1, 2] GEORGE A. LYRAS,[2] ROSS D. E. MACPHEE,[3] MARK LOMOLINO,[4] AND HARA DRINIA[2]

## ABSTRACT

Age-graded fossils of Pleistocene endemic Cretan deer (*Candiacervus* spp.) reveal unexpectedly high juvenile mortality similar to that reported for extant mainland ruminants, despite the fact that these deer lived in a predator-free environment and became extinct before any plausible date for human arrival. Age profiles show that deer surviving past the fawn stage were relatively long-lived for ruminants, indicating that high juvenile mortality was not an expression of their living a "fast" life. Although the effects on survivorship of such variables as fatal accidents, starvation, and disease are difficult to gauge in extinct taxa, the presence of extreme morphological variability within nominal species/ecomorphs of *Candiacervus* is consistent with the view that high juvenile mortality can function as a key innovation permitting rapid adaptation in insular contexts.

## INTRODUCTION

Discovering the factors that explain mortality and survival patterns in natural populations is a central preoccupation of ecology, and long-term studies of these phenomena are of great interest for life-history theory, population dynamics, wildlife management, and conservation biology. However, large mammalian herbivores have generally been considered unsuitable for

---

[1] Department of Geology, Naturalis Biodiversity Center, Leiden.

[2] Faculty of Geology and Geoenvironment, Department of Historical Geology–Palaeontology, National and Kapodistrian University of Athens.

[3] Division of Vertebrate Zoology (Mammalogy), American Museum of Natural History.

[4] College of Environmental Science and Forestry, State University of New York, Syracuse.

ISSN 0003-0082

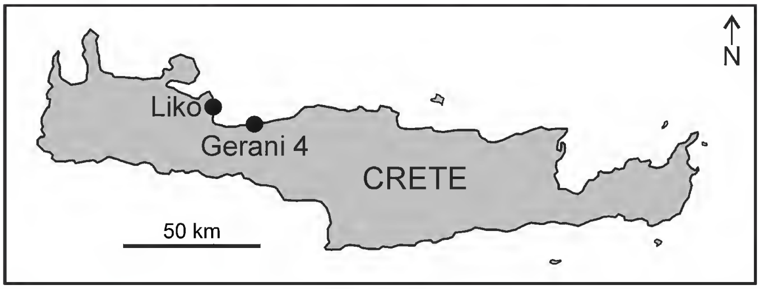


FIG. 1. Geographical position of cave localities Gerani 4 and Liko on Crete.

the study of population ecology because of their relatively long generation time (Gaillard et al., 1998). Yet such taxa are particularly interesting for demographic studies because many species are economically important or occupy a prominent place among conservation concerns. In addition, individual age—always a critical datum in population studies—is in general easier to reliably determine in long-lived species than in species like mice which generally live for only a year or so. Reflecting growing awareness of these advantages among investigators, a number of studies have been published during the past few decades that focus on large herbivores, starting with the pioneer study of Caughley (1966). Such studies are necessarily snapshots in geological time, covering at most a few decades or perhaps a century or so (e.g., feral goats in New Zealand; Parkes, 2005). A lengthier perspective is always desirable for testing time-dependent interpretations, and for this reason the fossil record—at least in specific circumstances—should be considered an essential adjunct to studies based primarily on extant taxa. Most significantly, in principle the fossil record can provide information on the dynamics of populations prior to, or independent of, any anthropogenic influence. Generally speaking, fossil assemblages do not represent natural, instantaneous populations but accumulations over time. Thus, reconstructed life tables are not time-specific but are instead long-term averages, the age composition of which reflects average age structure across time spans of indefinite lengths. In such cases the signal for year-by-year variation is inevitably dampened. Here we describe aspects of long-term population dynamics for the extinct deer *Candiacervus*, which inhabited the island of Crete, south of mainland Greece, during the Late Pleistocene.

Crete in something like its present form emerged in the Pliocene. As far as is now known, Plio-Pleistocene Crete lacked both large terrestrial carnivores and poisonous snakes, unlike the nearby mainlands of Greece and Asia Minor. Ancient Greeks attributed the absence of dangerous wild animals to Herakles, who was said to have destroyed all noxious species living on the island, the mythic birthplace of his father, Zeus. As appealing as this story may once have sounded to Crete's human residents, the real story is very different: poisonous and other potentially harmful animals were never eradicated because they had never arrived in the first place.

As is generally known, oceanic islands tend to be inhabited by unbalanced, impoverished faunas that are largely composed of species that managed not only to survive overwater dispersal but also to establish viable, continuing populations. Crete has been isolated from surrounding mainlands since the end of the Pliocene (van Hinsbergen and Meulenkamp, 2006). The main factor affecting the isolation of Crete is sea level change. The distance between Crete and mainland Greece is cur-

FIG. 2. Views of caves at Gerani (top) and Liko (bottom). These coastal caves are situated in Neogene limestones and contain richly fossiliferous sediments. Photographs: J. de Vos.

rently 90 km, but with a sea level drop of 100 m this would be reduced to 20 km. The distance between Crete and Rhodes is about 100 km, but for migrating terrestrial animals this overall distance could have been subdivided if Karpathos functioned as a stepping stone. The relative isolation of Crete can thus be defined as minimally 20 km or maximally 100 km, depending on direction.

Because of Crete's significantly long isolation, its Pleistocene biogeographical history resembles that of an oceanic island. Mammalian carnivores are rarely successful as island immigrants, and the Cretan case is no exception. Larger carnivores such as wolves and bears were never present, and the only documented mammalian carnivore of any sort was a Late Pleistocene otter (*Lutrogale cretensis*). Otherwise, the Late Pleistocene mammalian fauna consisted exclusively of deer (*Candiacervus* spp.), a dwarf elephant (*Palaeoloxodon creutzburgi*), a giant mouse (*Mus minotaurus*), and the Cretan shrew (*Crocidura zimmermanni*). All of these species were endemic, and all had disappeared long before the first ancient Greek ever set foot on the island—except for the Cretan shrew, currently listed as vulnerable by the *IUCN Red List of Threatened Species* (http://www.iucnredlist.org/).

The terrestrial vertebrate fauna of Crete also included birds (Weesie, 1982, 1988). Although avian carnivores tend to be more successful as island invaders than their mammalian counterparts, the only one certainly represented in the Quaternary of Crete is the endemic near-flightless owl (*Athene cretensis*). Whether there was a second endemic raptor is controversial: on the basis of a single fragmentary bone Weesie (1988) asserted that *Aquila* had once existed on the island, but as this element has now been referred to Aves incertae sedis (Louchart et al., 2005) there is no remaining basis for asserting the presence of an eagle. The Quaternary herpetofauna includes a number of small to medium-sized lizards, snakes, and turtles, including the extinct endemic tortoise *Testudo marginata cretensis* (Bachmayer et al., 1976).

Judging from worldwide patterns, commitment to island life tends to have particular consequences for the species concerned. Some consequences are more obvious and amenable to interpretation than others, and for that reason have been widely studied. Thus, the island "rule" predicts that, in insular contexts, large mammals generally become smaller (dwarfism), while small mammals generally become larger (gigantism) (for a recent overview comprising extant as well as extinct forms, see Lomolino et al., 2013). Factors such as ancestral body mass, trophic strategy, competition, predation, dispersal abilities, bauplan, relative isolation, and island area all contribute to the speed and direction of body size evolution in island contexts (Lomolino, 1985, 2005; Lomolino et al., 2012; van der Geer et al., 2013a), and in some sense every case is unique to a certain degree. Not surprisingly, this conforms to what is also seen on mainlands, if we replace island area with distribution area. Identifying consequences of island life other than changes in size, however, may require a different approach. Thus, a study of the Middle Pleistocene Sicilian dwarf elephant (*Palaeoloxodon falconeri*) established that, compared to elephants on mainlands, its mortality profile showed excessively high loss of juveniles, especially in the three youngest size classes (Raia et al., 2003), despite the fact that it lived in a predator-free environment. Why this should be so in the absence of predation is both interesting and obscure. Although predation is considered one of the more important factors in driving body size evolution (e.g., Boekschoten and Sondaar, 1966; Sondaar, 1977; Smith, 1992; Dayan and Simberloff, 1998; Michaux et al., 2002; Raia and Meiri, 2006; see, however, Marris, 2014), what is the effect of a total lack of ecologically relevant predators on traits other than body size?

To examine these questions, in this paper we evaluate population structure and dynamics in two fossil dwarf deer taxa from the Late Pleistocene of Crete (*Candiacervus* sp. II and *Candiacervus ropalophorus*), described further in the next section. The purpose of this paper is to test the hypothesis that mortality profiles and survivorship curves of *Candiacervus* populations should differ characteristically from those of wild ruminants living on mainlands with ecologically relevant predators, and to determine whether any such differences can be attributed to the lack of predation.

## MATERIALS AND METHODS

### Localities, Fossil Occurrence, and Dating

Crete possesses an impressive number of Late Pleistocene fossiliferous localities (Iliopoulos et al., 2010), but only two such have yielded fossils of the target species in quantities large enough to warrant detailed study (fig. 1). These localities, Gerani 4 and Liko, are coastal caves situated in the Neogene limestones that drape the northwestern coast of Crete (fig. 2). Both contained richly fossiliferous cave sediments (de Vos, 1979) and were excavated in the early 1970s by teams from the University of Utrecht. Gerani 4 lies about 6 m above sea level, just off the New National Road (E 75) near the village of Gerani, ca. 6 km west of Rethymnon. Deer bones were found within a single fossil-bearing stratum, consisting of the upper 40 cm of the cave fill and capped by flowstone. Thanks to the unconsolidated nature of the clayey sediment, even the most delicate bones of juvenile animals could be collected whole and without difficulty.

Liko Cave is situated at the foot of a seacliff, about 3 m above sea level and 100 m south of the valley connecting the village of Likotinaréa with the Sea of Crete. Likotinaréa lies north of Georgiopoulos, which is in turn about halfway between Chania and Rethymnon. Because distinct layers could not be recognized stratigraphically at Liko, the collectors dug according to artificial units (A, B, C, D, and E) based on measured depths from surface. The majority of deer fossils came from units B and C. These fossils, on which we focus here, occurred predominantly within indurated silts and calcified breccias. The hardness of the sediments severely impeded collection, and fragile bones such as those of young animals were often unavoidably damaged. Thus, the Liko Cave material is useful mainly to estimate adult mortality and survivorship.

In both caves practically all material consisted of disarticulated bones, and no complete skeletons were encountered. However, the presence of a few elements still in articulation indicates minimal postmortem transport before final deposition. Furthermore, no element shows signs of erosion, and the taphonomy is consistent with the absence of transportation of material after burial. There were no signs of anthropogenic disturbance in either cave. Material from Gerani 4 and Liko Cave bear the acronyms RGM and AMPG respectively (table 1).

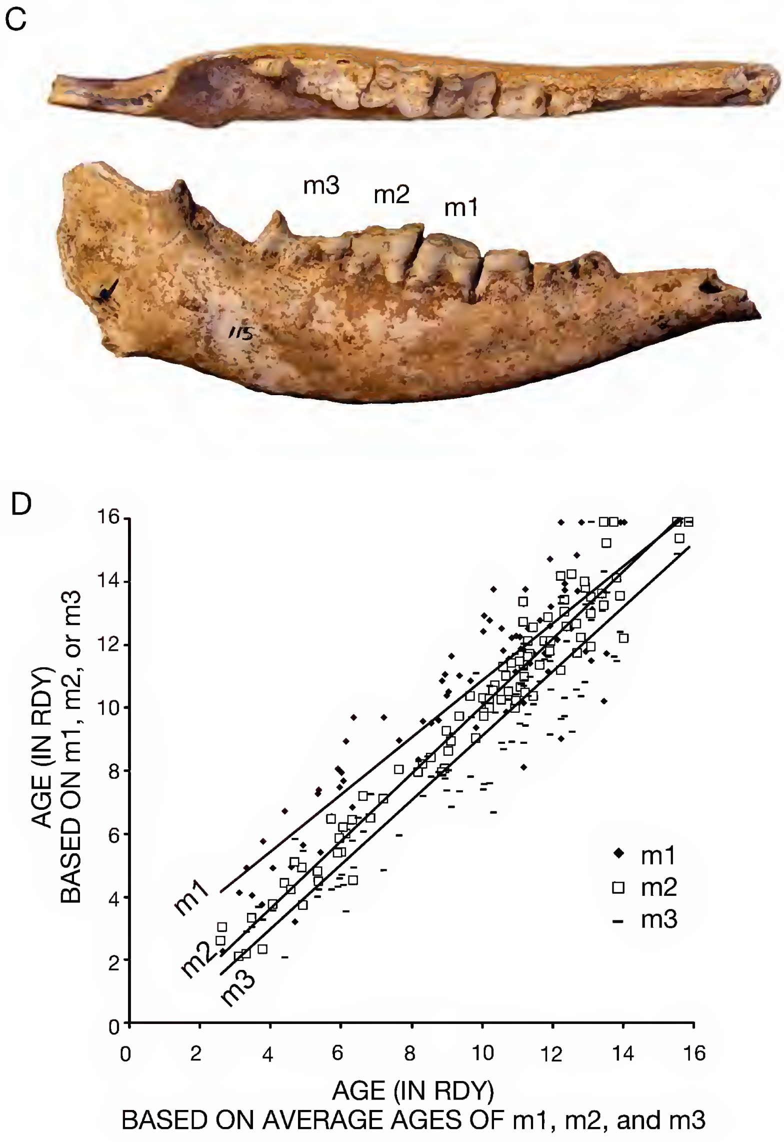
At present, the only chronometric ages available for these sites are based on amino acid racemization (AAR) estimates developed from *Candiacervus* tooth enamel. For Liko, AAR estimates range from 105,000 yr ± 20% (units B and C) to 87,000 yr ± 20% (unit D). For Gerani 4, the sole estimate is 70,000 yr ± 20% (Reese et al., 1996). Apparent date inversion at Liko indicates that the AAR estimates are problematic, and new efforts to date these deposits utilizing different dating methodologies are underway at both localities (Lee Arnold, personal commun.; Dirk Hoffmann, personal commun.).

## Determination of Age Classes

Discriminating age classes for the purpose of modeling mortality curves requires the analysis of suitable fossil material. For this study we utilized mandibles, not only because they are usually well preserved and available in large quantities, but also because they typically provide highly accurate information on individual age at death.

Age determination of a given mandible was based on rating the state of deciduous tooth replacement and the degree of tooth wear following the methods of Vorreyer (1957) and Fosse (1994, in González, 2003: 176). The anular structure of dental cementum was not used to estimate individual ages because we lack a sound basis for assessing diagenetic changes and the effects of seasonality on the formation of anular cementum in Late Pleistocene Crete.

FIG. 3. Three dental wear patterns found in *Candiacervus* mandibles (Gerani 4), with a graphical comparison of ages estimated per molar locus vs. average age based on all molars (A and B directly above, C and D on opposite page). **A,** Mandible in which all molars show a degree of abrasion that is closely correlated with their position in the eruption sequence, resulting in compatible age estimates. **B,** Mandible in which m2 shows greater wear than either m1 or m3, resulting in potential overestimation of age relative to the other molars. **C,** Mandible in which m3 shows greater wear than either m1 or m2, thus greatly overestimating age relative to m1. **D,** Comparison of ages estimated per m1, m2, and m3 tooth loci (symbols) and averages of separate m1, m2, and m3 ages (lines), for a sample of 88 mandibles.



We selected the European mainland red deer *Cervus elaphus* as the comparator taxon for our *Candiacervus* sample set because of the former's availability in collections and because *Cer. elaphus* is the only deer taxon for which extensive studies on population dynamics exist (such as the extensive data sets available for an uncontrolled population on the Isle of Rum [previously, Isle of Rhum], Scotland; see Nussy et al., 2007). In the text, reference to "non-Cretan" or "mainland" deer will always pertain to *Cer. elaphus* unless stated otherwise.

TABLE 1. Abbreviations.

| | |
|---|---|
| AMPG | Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Greece |
| RDY | red deer years (*Cervus elaphus* individual age in years) |
| RGM | Naturalis Biodiversity Center (formerly Rijksmuseum van Geologie en Mineralogie), Leiden, the Netherlands |
| dx | mortality, the number of individuals dying between stage x and stage x+1 |
| lx | survivorship, the percent of the original cohort that survives to stage x |
| m1, m2, m3 | first lower molar, second lower molar, third lower molar (permanent dentition) |
| qx | mortality rate, the percentage of the population dying between stage x and stage x + 1 |

For juvenile and subadult specimens up to 2 RDY (for abbreviations, see table 1), age determinations were based on tooth eruption and replacement patterns. In adult specimens we evaluated the stage of wear in combination with crown height. Wear was classified as varying from *unworn*, in which the distal cusps of the third molar show no evidence of wear, to *very worn*, in which molariform teeth are worn down to gum level. Gum level is assumed to have been reached when only 1–2 mm of the crown remains above the alveolar margin. We are aware that in nature considerable individual variation exists in both tooth eruption and wear patterns relative to actual individual age (Chapman and Chapman, 1970). We controlled for this by first surveying the material for major anomalies, and then establishing a methodology for minimizing their effect on assessment (see below).

For the estimation of the age of older individuals (2–16 RDY), we used the degree of molar abrasion assuming a constant rate of wear through time. Most mandibles used in this study are complete or nearly complete specimens that lack only a molar and/or the symphyseal region bearing the incisors and incisiform canine. It is important to note that, because of the high prevalence of irregular wear patterns in *Candiacervus*, our wear-based age determinations represent the average of assessments of each of the three molars. In the most unusual pattern, m3 displays a greater degree of wear than m2, which (if used exclusively) would result in an overestimation of age (see fig. 3). By averaging the three age assessments, we were able to control for one potential source of age misestimation without affecting sample size because anomalous jaws could be retained in the pool. We tested the effect of measuring one element (m1, m2, or m3) against taking the average and found that the average is a sound alternative for our samples (fig. 4). Major wear anomalies of this sort are not unique to Cretan deer; a comparable m3/m2 wear anomaly has been detected in the Balearic caprine *Myotragus* (wear class 4 of Bover, 2004).

Specimens were next binned into age classes because of the difficulty of establishing the age of any individual more precisely than in the form of a range of several months (or more). Wear classes were then combined with age predictions based on crown attrition in permanent teeth, following Klein (1982) and using his formula for permanent teeth:

AGE = AGEpel – ((AGEpel-AGEe)/CHo) × (CH), where AGE is estimated age, AGEpel is the age past which no individuals appear to survive (“potential ecological longevity”), AGEe is the age at which the permanent tooth erupts, CHo is initial (unworn) crown height, and CH

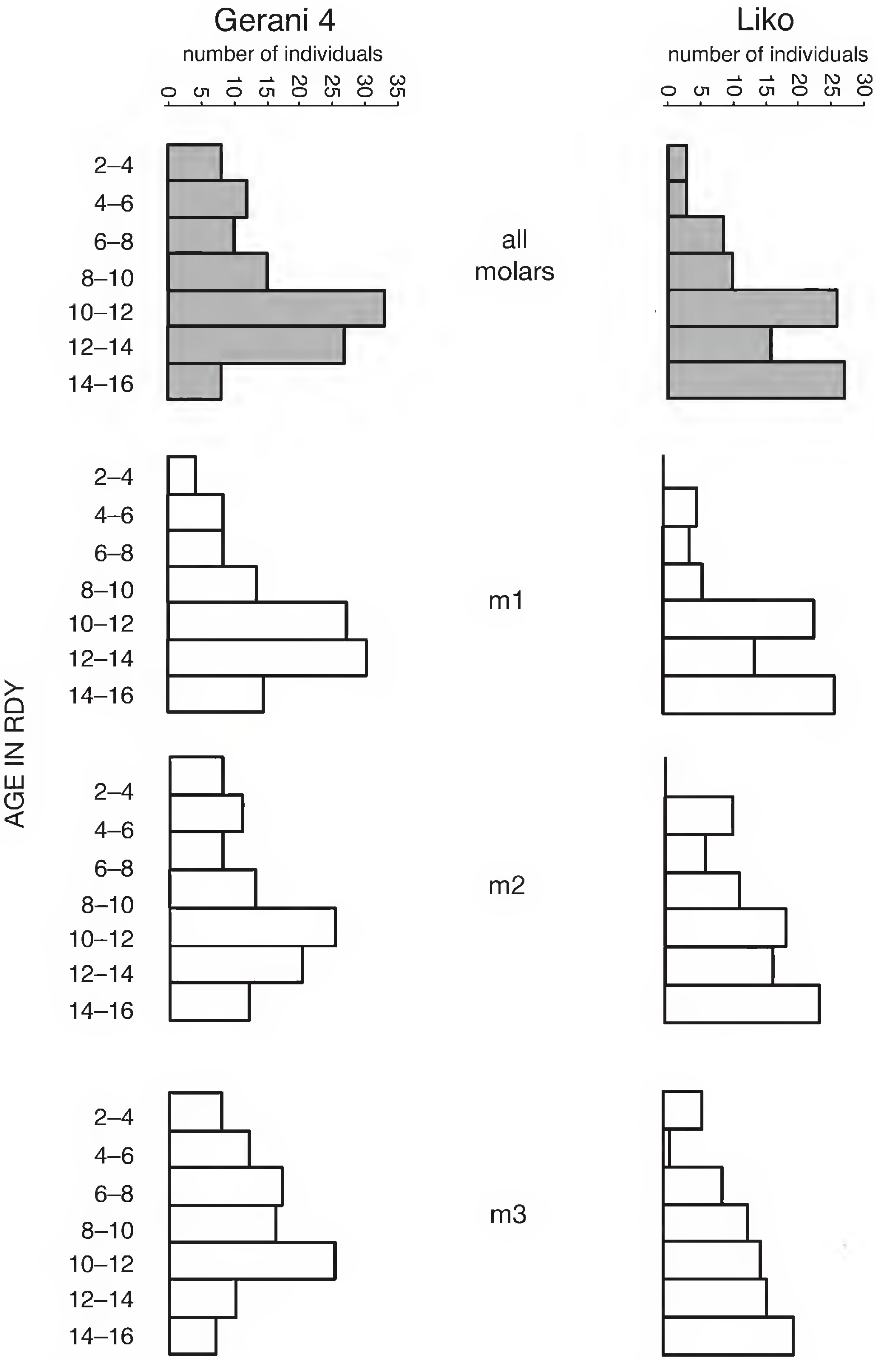


FIG. 4. Mortality profiles (dx) for *Candiacervus ropalophorus* from Gerani 4 (left) and *Candiacervus* sp. II from Liko (right), based on age estimations inferred from wear stages of all molars (top histograms) or of m1, m2, or m3 considered singly (other histograms). Although some differences can be observed between the profiles, patterns are essentially the same.

is measured crown height. Age of individual *Candiacervus* and its potential ecological longevity are cited in terms of RDY.

The mandibular dental formula (mDF) of *Candiacervus* conforms to that of most deer (Geist, 1998). For the deciduous dentition, dmDF = di, dc, dp. For the permanent dentition, pmDF = i, c, p, m, and there is a large diastema between the incisiform canine and the proximal premolar (p2). The order of tooth eruption of the permanent dentition in *Candiacervus* is m1, i1, m2, i2, i3, c1, m3 (p4, p3, p2), again as in most deer.

In extant deer, fawns are born with the deciduous dentition fully erupted, and we assume that this was also the case in *Candiacervus*. Specimens showing only a partially erupted deciduous dentition were considered prenatal.

## Survivorship Curves

The data for constructing *Candiacervus* survivorship curves are based on the composite life table approach for each population (sensu Kurtén, 1953). In such a table, the number of individuals in a given age class is assumed to represent the mortality ($d_x$) within that class. Survivors ($l_x$) are calculated by subtracting $d_x$ from the $l_x$ of the preceding group, starting with an initial number of 1000 individuals. A survivorship curve is produced by plotting survivors ($l_x$) against age classes; for a given species, curve shape may point to its basic survival strategy (i.e., *K* vs. *r* selection) (Shipman, 1981; Pianka, 2000).

## Taxonomic Issues

The alpha taxonomy of Pleistocene Cretan deer is poorly resolved. Considerable variation occurs in certain features, such as antler morphology and estimated body size, which in mainland contexts might arguably justify the recognition of several species—perhaps as many as eight (fig. 5). However, given the dimensions of Crete during the Late Pleistocene (ca. 10,000 km$^2$), such a high level of specific diversity seems improbable, which in turn suggests that some or most of this variation is ecomorphological (de Vos, 1979, 1984). As systematic resolution within *Candiacervus* is not directly relevant here, for our purposes it is sufficient to adopt a simplifying assumption to the effect that a single ancestral deer lineage reached the island some time during the late Middle to early Late Pleistocene. All Late Pleistocene deer "species" are held to derive from this lineage and are thus strictly monophyletic (de Vos, 1979, 1984, 1996, 2006; de Vos and van der Geer, 2002; van der Geer et al., 2006b; van der Geer et al., 2013b). We note here that an alternative hypothesis (Capasso Barbato and Petronio, 1986; Capasso Barbato, 1992, 1995) assumes colonization by two different ancestors, a large deer from the *verticornis* group within *Praemegaceros* and a small-sized deer within *Pseudodama* (now *Metacervoceros*; see Croitor and Bonifay, 2001; Croitor, 2006). This scenario would make the Late Pleistocene diversity of Cretan deer formally polyphyletic. Somewhat counterintuitively, this view requires in addition that the large ancestor evolved into small-sized species while the small ancestor gave rise to three large-sized species. Fortunately, the difference between the two hypotheses—one versus two ancestors—has no direct bearing on our results because our two

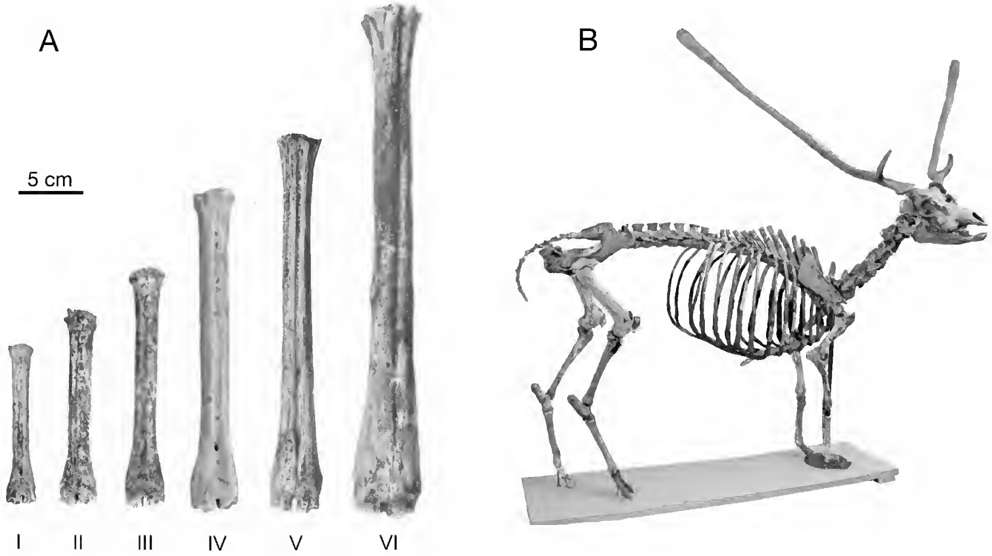


FIG. 5. Long bone elements of Late Pleistocene Cretan deer (*Candiacervus*) are remarkably variable in both size and shape. **A,** Six metapodial size classes as determined by de Vos (1979, 1984); size class 2 includes three different antler types, resulting in a total of at least eight groupings (whether these are considered species or ecomorphs). **B,** Composite mount representing size class 2 (*Candiacervus* sp. II) from Liko Cave. Shoulder height and withers height in life would be about 55 and 58 cm respectively.

populations belong to the smallest species/morph and thus share an implied common ancestry in both scenarios. De Vos (1979, 1984) found a significant difference in the size ranges of the Gerani 4 and Liko populations, and on that ground attributed them to two different species. In the view of Capasso Barbato (1992), the next-to-smallest species, *Candiacervus* sp. II, is not valid and should be included in the species *Candiacervus ropalophorus* (= *Megaceroides* "*ropalophorus*" of Caloi and Palombo, 1996). In that scenario, our two populations would represent a single species, but are not necessarily of the same geological age.

With regard to the material from Gerani 4, we are confident that it represents only a single species (*Can. ropalophorus*), as only one type of antler and only one adult size class have been recorded there (de Vos, 1979). By contrast, the material from Liko contains four size classes and several antler types (de Vos, 1984). Accordingly, we restricted our analysis to size class 2 (nominally *Candiacervus* sp. II), which is the one to which the majority of specimens belong (de Vos, 1979).

## RESULTS

A high number of juveniles were present at both localities (table 2). If we calculate separate mortality profiles for the two localities, results are as follows. For Gerani 4 (fig. 6), the all-ages mortality profile shows a large peak within the youngest age stage (0–2 RDY), followed by a steep dip in early adulthood and an irregular but progressive increase thereafter until 10–12 RDY, after which the mortality level drops again. Peak mortality in adults is situated at about 70% of maximum longevity. The juveniles-only profile (fig. 6) displays a large peak within the

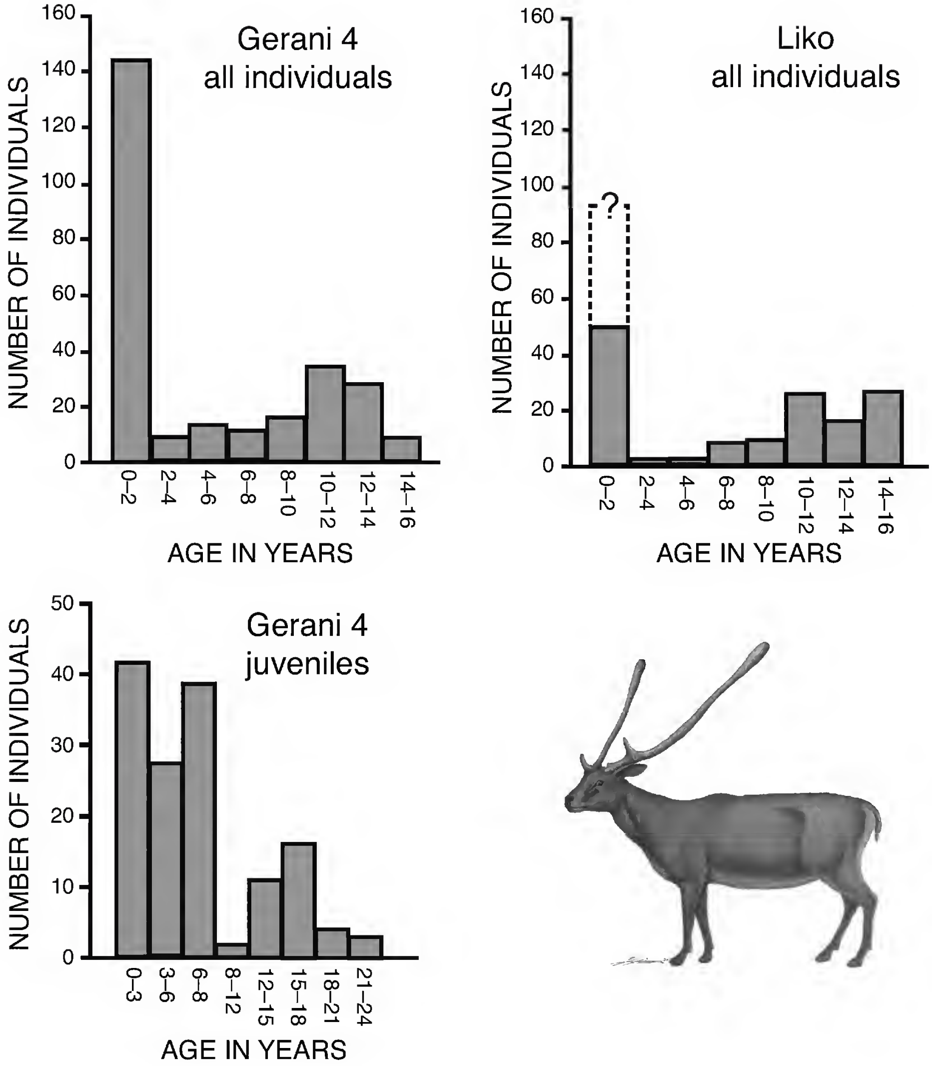


FIG. 6. Mortality profiles (dx) for *Candiacervus ropalophorus* from Gerani 4 (top left, actual numbers for all ages; bottom left, juveniles only) and *Candiacervus* sp. II from Liko (top right, all ages). Bottom right, reconstruction of *Can. ropalophorus* by Alexis Vlachos.

first three months of life. The subsequent two peaks are lower and coincide roughly with winter (assuming spring was the normal birth season, as in all other deer living in the northern hemisphere). This winter peak is not present in the second column. The lowest dip at 8–12 months seems to coincide with spring. The overall death rate for juveniles at Gerani 4 is much higher in the first year than the second.

For Liko (fig. 6), the mortality profile also shows a prominent peak in the youngest age class, followed by a marked dip at 2–6 RDY and a gradual increase until 10–12 RDY, after which mortality remains rather constant with perhaps a minor dip at 12–14 RDY. Thus, after high initial mortality in the first two years, the mortality rate drops, and remains very low until about 10–12 RDY after which it either drops gradually till the end of the series (Gerani 4) or remains more or less constant (Liko). As explained in the Introduction, juvenile mortality at Liko may have been much higher than the profile reveals because the youngest specimens are underrepresented for taphonomic reasons. The Liko profile is thus meaningful only for interpreting adult mortality and survivorship.

The survivorship curve of *Candiacervus* at Gerani 4 (fig. 7) at first drops sharply, to a point at which more than half of the fawns are dead, then decreases gradually thereafter until ~10–12 RDY. The slope becomes progressively steeper until the last age stage, when the whole population is deceased. The survivorship of Liko *Candiacervus* also shows a change in steepness at 2 RDY, after which the slope is almost horizontal until about 10–12 RDY. Thereafter the slope drops steeply toward the end stage, as in the case of Gerani 4. The actual position of the Liko survivorship curve relative to the starting point is unknown as juveniles are likely underrepresented. In summary, after a high initial mortality during early postnatal life, mortality rates drop at both sites and reach a minimum value at 2–4 RDY (fig. 7). After about 10 RDY, the mortality rate increases gradually in the case of Gerani, more sharply in the case of Liko as the maximum longevity level is approached.

## DISCUSSION

### Type of Profile

An initial problem is to decide whether the age distributions of the *Candiacervus* samples correspond to an attritional (mortality) profile or a catastrophic (survivorship) profile (fig. 8A, B). Attritional profiles imply that individuals mostly die as a result of factors like fatal accidents or chronic diseases, which ordinarily have their greatest impact on the very young and/or very old. By contrast, catastrophic profiles tend to be generated by unique events of unusual magnitude, such as a volcanic eruption or outbreak of virulent epizootic disease that kills individuals of all ages at roughly the same rate (Klein, 1982). Had the *Candiacervus* age profiles been catastrophic in form, one would have expected to see a discontinuous age distribution with discrete age classes, because deer are seasonal and give birth (normally to singletons) only once a year and in the same season.[5] This pattern would be particularly noticeable if most deaths were restricted to a certain period, perhaps due to factors such as dry-season bush fires or starvation before the autumn rains. These possibilities can be excluded for both Liko and Gerani 4, as we shall now show.

Although earlier studies refer to the Gerani 4 profile as belonging to a single population that died as a result of a natural catastrophe (Sondaar, 1977; Biskop, 1978; van der Geer et al., 2006a), the results presented here reveal that this conclusion is invalid because the age profile

---

[5] Theoretically, seasonality of reproduction and number of offspring per birth in *Candiacervus* could have changed during its evolution. However, as we emphasize elsewhere all extant plesiometacarpal (i.e., Old World) deer, of which *Candiacervus* is an example, give birth to one fawn per season (twins are rare to very rare). This includes the insular Philippine species *Rusa marianna*, which has lived on these islands for at least 70 ka (as indicated by fossils collected at Callao Cave, Luzon; Mijares et al., 2010) but has not changed pattern. The likely divergence time for *Candiacervus* is not appreciably longer (126 ka).

Table 2. Specimens Utilized in This Study. Number of mandibles of *Candiacervus* for each class for the localities Gerani and Liko.

| Gerani 4 | | Liko | |
|---|---|---|---|
| Age classes in RDY | *N* | Age classes in RDY | *N* |
| 0–2 | 145 | 0–2 | 49 |
| 2–4 | 8 | 2–4 | 2 |
| 4–6 | 12 | 4–6 | 2 |
| 6–8 | 10 | 6–8 | 8 |
| 8–10 | 15 | 8–10 | 9 |
| 10–12 | 33 | 10–12 | 26 |
| 12–14 | 27 | 12–14 | 16 |
| 14–16 | 8 | 14–16 | 27 |

does not correspond to a survivorship model. This is also evident from comparison with examples of definitely catastrophic profiles in the paleontological literature, such as those derived for the prongbuck *Cosoryx* (= *Merycodus*) *furcatus* and the horse *Protohippus perditus* from Late Miocene deposits in Nebraska (Voorhies, 1969), as well as those for the early ovibovine *Plesiaddax depereti*, the spiral-horned antelope *Urmiatherium intermedium*, and the gazelle *Gazella dorcadoides* from Late Miocene deposits in northern China (Kurtén, 1953). A relevant cervid example of an attritional profile is that presented by Kubo et al. (2011) for the deer *Cervus nippon* from Kinkazan Island, Honshu (fig. 8B) and *Cervus astylodon* from Late Pleistocene deposits on the Ryukyu Islands (Kubo et al., 2011: fig. 6).

The mortality profiles of the two *Candiacervus* populations strongly resemble those computed for free-ranging bovids and hippos in Africa (Klein, 1982) as well as *Cervus elaphus* from the Isle of Rum (Nussy et al., 2007). As in these cases, the major peaks observed for the earliest age classes in the *Candiacervus* profiles are largely due to the presence of fawns and (very) old animals; only a small proportion represent individuals in their prime. For populations of Burchell's zebra (*Equus burchelli*), and, less obviously, for the African elephant (*Loxodonta africanus*) presented by Klein (1982), the initial major peak also coincides with juvenile life, after which a relatively stable mortality rate affects all age groups, with some irregular but minor rises and dips, unlike what we see in the *Candiacervus* populations. Instead, the Liko and Gerani 4 curves conform to the mortality pattern expected for a hypothetical population given by Klein (1982: fig. 1) in which females are assumed to have at most one young per year. The Cretan populations also contrast with highly prolific species like the warthog (*Phacochoerus aethiopicus*), in which the majority of individuals die during the first three to five years, with the few surviving adults continuing on at a constant death rate.

## JUVENILE MORTALITY

In a predator-free environment, and with other things being equal, the expectation is that most young animals should survive into adulthood. Yet judging from the initial high peaks in

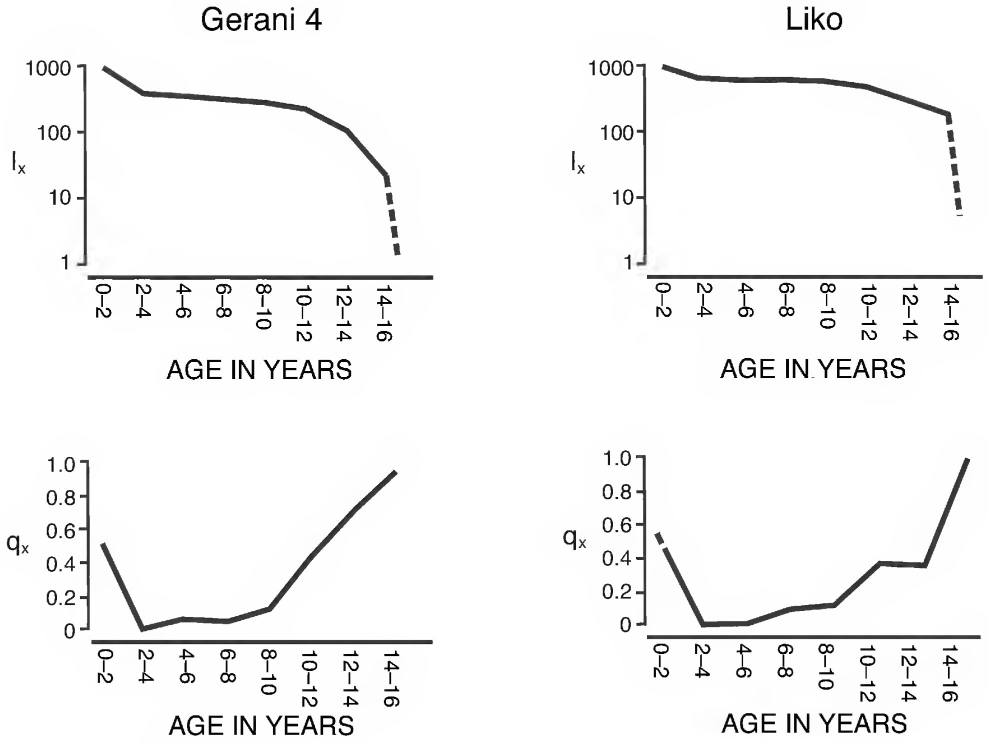


FIG. 7. Survivorship curves (lx) and mortality rates (qx) (top and bottom, respectively) for *Candiacervus ropalophorus* (Gerani 4) and *Candiacervus* sp. II (Liko).

the Gerani 4 profiles, it appears that fawns of *Candiacervus* suffered rates of mortality as high as those affecting mainland herbivores today. The superabundance of juvenile remains is very evident in postcranial material from other *Candiacervus* sites as well, in which about half the material is subadult or younger (de Vos, 1979; van der Geer et al., 2006a).

As already noted, in actuality the juvenile peaks in our profiles might have been even higher, as very young individuals (first age class) are less likely to be preserved and are therefore statistically undersampled (cf. Damuth, 1982). In extant wild ruminants, mortality rates are highest during the first weeks postpartum; in general, most juvenile deaths occur during the first half-year of life (Sarno et al., 1999). Causes of juvenile mortality in the wild today are many, but the ones most frequently mentioned in relevant studies include accidents, starvation and malnutrition, diseases including congenital defects, extreme weather conditions, low neonatal body weight, inadequate maternal protection, high population density, and predation (Sarno et al., 1999). With regard to accidents, a study of mortality associated with wire fences in the western United States (Harrington and Conover, 2006) showed that juveniles of pronghorn (*Antilocapra americana*), mule deer (*Odocoileus hemionus*), and elk (*Cervus elaphus*) were eight times more likely to die from fence-related accidents than adults. Interestingly, the highest mortality associated with wire fencing was observed during August, coinciding with the wean-

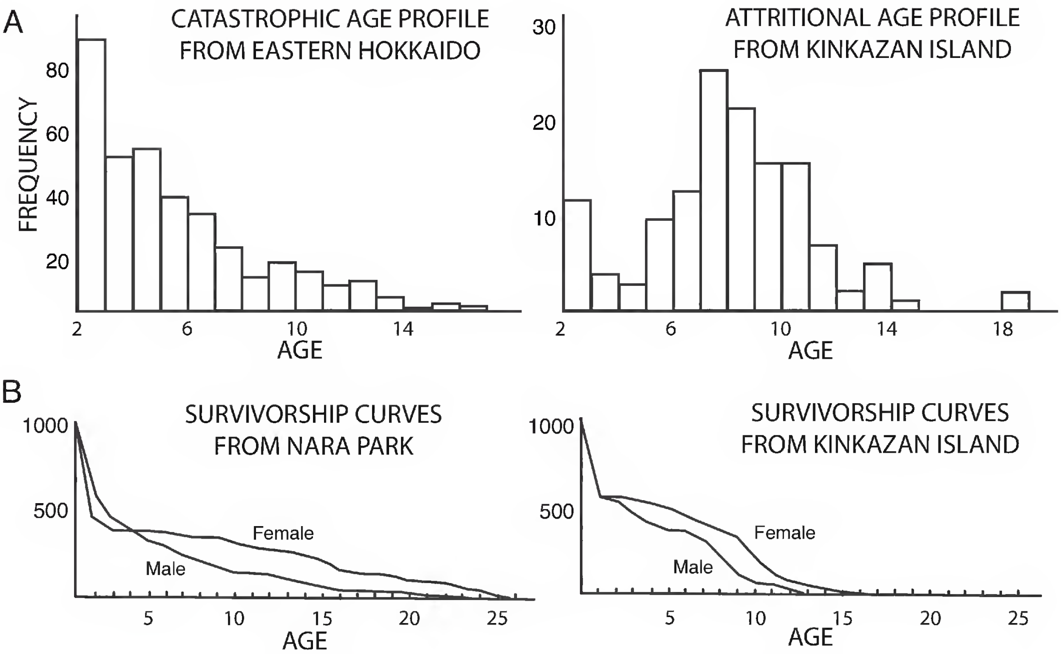


FIG. 8. **A,** Examples of catastrophic (left) and attritional (right) age profiles for sika deer (*Cervus nippon*), adapted from Kubo et al. (2011). The catastrophic profile is based on randomly harvested deer from eastern Hokkaido, while the attritional profile is based on field-collected carcasses from Kinkazan Island, Honshu. **B,** Examples of survivorship curves for sika deer from Nara Park (left) and Kinkazan Island (right), adapted from Koike and Ohtaishi (1987). Both curves represent populations that are not hunted. Note that the scale in B is arithmetic.

ing of fawns. Our age profile for Gerani 4 appears to indicate a similar increase in juvenile mortality at an equivalent age. In extant mammals, weaned juveniles are more prone to accidents because of stresses stemming from a change in diet: food-stressed individuals accept higher risks in order to avoid starvation. The nature of fatal accidents that might have affected deer in Pleistocene Crete is unknown, but could have included falling into crevices and pits in the irregular and often steep limestone substrate, or seriously damaging legs while climbing that substrate. That the latter type of accidents indeed took place can be inferred in the Gerani sample from healed fractures in distal elements (two metatarsals, one metacarpal) as well as from evidence of arthrosis in joints (one ankle joint, one hip joint, one tarsal joint), although these latter presentations may have been caused by age-related arthritic processes. Broken bones in juveniles that did not survive long after the accident and thus show no healing are difficult to recognize with certainty in the fossil record.

Predation as a cause of mortality in juvenile large herbivores can be very significant (Linnell et al., 1995; Long et al., 1998), but its effect may be magnified by other factors. In a large-scale study of juvenile mortality in wild guanaco (*Lama guanicoe*; Sarno et al., 1999), it was found that puma predation was most intense during times of winter snowfall, suggesting that conditions forced by bad weather conditions (heightened malnutrition, disease, metabolic demands) only indirectly led to increased death by predation, because the pumas selected individuals that were seriously weakened. Similar results have been found for red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) during winter (Jedrzejewski et al., 1992). That the absence of predation as a factor may have no obvious effect on the mortality profile is shown by studies of the red deer of Rum. For this population, the most important causes of death are starvation, weather-related factors (including natural winter mortality), accidents, and parturition (not relevant to juvenile mortality), yet the mortality profile (Nussey et al., 2007) is very similar to that of continental African large herbivores. In some years, juvenile mortality on Rum has run to nearly 60% (Clutton-Brock et al., 1985). This closely compares to some New Zealand records (59% mortality in female red deer fawns [Caughley, 1971], and 57% in kids of feral goats living on Macauley Island [Williams and Rudge, 1969]). Other examples from New Zealand include feral thar (*Hemitragus jemlahicus*) and domestic sheep (*Ovis aries*), for which survivorship curves inferred from live counts and random shooting do not differ in any essential way from those of mainland wild bovids—even though predation is not a factor in New Zealand (Caughley, 1966). Indeed, the mortality curve for feral New Zealand sheep is notably similar to that of wild Dall sheep (*Ovis dalli*) from Alaska. Juvenile mortality during the first year was also very high for sika deer in Nara Park, Honshu, which is a protected area (42% of males and 55% of females; Koike and Ohtaishi, 1987), but less so on Kinkazan Island (31% of males and 23% of females; Minami et al., 2009a). In the latter case, fawn mortality was due to accidents and attacks by crows (*Corvus macrorhynchos*) immediately after birth or starvation during the first winter after birth.

The observations provided above imply that, although predation may be an important factor in certain circumstances, in general its net effect on age profiles appears to be negligible because young animals usually die for other reasons. One explanation could be that predation might accelerate death to a certain extent but does not influence age (in years) at death (Hutchinson, 1978). That, in turn, raises the suspicion that perhaps not all cases for which predation is highlighted as the main cause of juvenile mortality are actually natural. For example, the importance of the coyote (*Canis latrans*) as a leading cause of death among fawns of white-tailed deer (*Odocoileus virginianus*) in the southeastern United States may be partly ascribed to the fact that coyotes are a recent addition to the local ecological assemblage (Jackson, 2011). Coyotes were once limited to the Great Plains and western North America, but in many areas where they were not previously resident they now fill the vacuum left by the disappearance of wolves and pumas (Gompper, 2002). Here *Canis latrans* should be seen as an invasive species, to whose presence the herbivores have not yet fully adapted (cf. study of Long et al. [1998] concerning mortality among white-tailed deer fawns on Desert Island, Maine). To conclude, juvenile survivorship in wild ruminants appears not only to be comparable between islands and continents (e.g., Linnell et al., 1995; Sarno et al., 1999), but also between predator-free and more balanced ecological assemblages.

## Adult Mortality and Longevity

With regard to the interpretation of the second peak (10–12 RDY) detected in the two cave samples, it first needs to be noted that there is some uncertainty connected with how one judges which individuals should be considered “aged” in large mammalian herbivores. In

Klein's (1982) diagrams for Dall sheep (*Ovis dalli*, *n* = 608), waterbuck (*Kobus ellipsiprymnus*, *n* = 99), and hippopotamus (*Hippopotamus amphibius*, *n* = 207), substantial increases in mortality rates occurred in adults that were at 60%–70% of estimated longevity for the species in question, whereas in Cape buffalo (*Syncerus caffer*, *n* = 703), impala (*Aepyceros melampus*, *n* = 355) and black rhinoceros (*Diceros bicornis*, *n* = 477) the rate intensified at 40%–50% of species' longevity. Our data suggest that *Candiacervus* approximated the first scenario, with perhaps a slight shift toward a higher percentage of very old individuals in the population. It is difficult to be certain because our age estimations for *Candiacervus* adults are inferential (based on transferred wear patterns in red deer) rather than truly actualistic (based on wear rates of known-age animals in the target taxon). Thus, it is possible that we have either over- or underestimated longevity. However, even if this were the case, misestimation would not influence the height of the histograms but would only compress adult size classes. The second peak would still lie at ~70% of estimated longevity, comparable to what Kubo et al. (2011) observed in a sample of the Late Pleistocene Ryukyu deer *Cervus astylodon*, in which the large number of individuals with very worn third molars skewed the histogram toward older age. A juvenile peak could not be recognized for this taxon because only fully erupted third molars were taken into account in this study (m3 does not erupt until two years of age).

*Cervus astylodon* evolved increased longevity (Kubo et al., 2011), but not to the extreme degree seen in the dwarf bovid *Myotragus balearicus* according to Köhler and Solà (2009; Jordana et al., 2012). However, the conclusion of Köhler and Solà (2009) concerning *Myotragus* was based on the presence of lines of arrested growth (LAG), otherwise exclusive to ectotherms, which they interpreted as due to a periodical, irregular growth rate (a "slow life"). Subsequently, Köhler et al. (2012) found that LAG presence is actually the common pattern in ruminants of all body sizes, to which *Myotragus* therefore forms no exception. Interestingly, the latter's eruption and wear rate appears to have been almost twice as fast as that of similar-sized *Ovis aries*, based on analysis of incremental structures in enamel (Jordana and Köhler, 2011). However, as Clauss et al. (2014) demonstrated, life history properties are strongly correlated to ancestral size, not to acquired size.

All in all, the issue of fast versus slow life is complicated and unresolved, especially as it applies to extinct species, and we restrict ourselves here to mortality patterns. In the case of *Candiacervus*, significant deviation from the ancestral condition is unlikely, because the deciduous premolars were still functional at the time that the third molar started to erupt. According to Schultz's Rule, replacement premolars erupt before or simultaneously with the molars in mammals with slower life histories (Smith, 2000).

Excessive tooth wear and loss of function in molar teeth are frequently cited as being strongly related to decreased late-life fitness in general and reduced reproductive fitness in particular (e.g., Skogland, 1988; Gaillard et al., 1993; Kojola et al., 1998). The relatively large number of adults with heavily worn molars in the *Candiacervus* age profiles might therefore indicate a low reproduction rate in the Gerani 4 and Liko populations. However, as Nussey et al. (2007) showed for *Cervus elaphus* on the Isle of Rum, this need not have been the case: these authors found no evidence that their index for estimating stage of tooth wear (first molar height) was associated with reproductive senescence. Absence of correlation may be due to the fact that, although molar height lessens over the years, molar surface area changes little, or may perhaps even increase somewhat as the tooth loses loph relief. Thus, the total effect of vertical wear on digestive efficiency may be limited (Nussey et al., 2007). Making an analogy between *Cer. elaphus* and *Candiacervus* in this regard seems highly justifiable, because the Cretan deer sample is marked by the total absence of lost (i.e., evulsed) mandibular teeth. Apart from postmortem loss, all teeth were consistently present in senile individuals, even if worn down to the roots, which implies that the teeth were still functional during mastication. The time needed for efficient mastication in such individuals might have been significantly increased compared to younger animals, but this would have little effect on overall digestive efficiency since ruminants of all postweaning age stages chew cud.

A more significant factor for interpreting the *Candiacervus* data may be the effects of population density. In living ruminants, adult mortality is highly density dependent, in contrast to juvenile mortality, with loss attributed at least partly to malnutrition (Hutchinson, 1978; Tremblay et al., 2005, Simard et al., 2008). Interestingly, in less productive environments supporting fewer animals, death rates may actually be lower and the percentage of long-lived individuals higher than in more productive locales (as suggested by Veiberg et al. [2007] for roe deer in France). Taber and Dasmann (1958) have shown this to be the case for populations of black-tailed mule deer (*Odocoileus hemionus columbianus*) living in two dissimilar habitats in California, one poor in nutrients and the other rich. The first population had a lower density (10 vs. 34 deer/km$^2$) and lower reproduction (0.77 vs. 1.65 fawn per adult doe/yr) than the second population, but the survivorship curve had a much gentler slope. In this case, for any given adult age class the percentage of survivors was higher in the first population than the second. In juvenile age classes, on the other hand, percentages were identical. Interestingly, this may imply that the adult mortality patterns in zebra and elephant detected by Klein (1982: fig. 3; see also above) may actually be driven mainly by density factors.

With regard to the Cretan context, in the absence of any detailed understanding of the environments that previously existed around Gerani 4 and Liko, the most that can be said at present is that our profiles do not suggest a high-density scenario but indicate rather a nutrient-poor environment. This perhaps applies more to Liko than to Gerani 4 as indicated by the gentler survivorship curve for the former.

## Gender-related Patterns

In sexually dimorphic species, juvenile males generally have a lower survival rate than females of the same age (Clutton-Brock, 1991), perhaps because of faster growth rates in the former and thus higher susceptibility to nutrient deficiency (Clutton-Brock et al., 1985). The opposite trend, however, seems to apply to adults. This was first demonstrated by Caughley (1966) for Dall sheep (*Ovis dalli*) in Alaska, on the basis of raw data collected by Murie (1944). From the 4th year onward, rams have a higher survival rate than ewes and live about two years longer. No gender effect at all was found in the African buffalo (*Syncerus caffer*) living in the Serengeti region until the end of the 18th year (Sinclair, 1974). By then all cows had died, but bulls showed a pronounced drop in mortality and survived up to 19–20 years of age. In contrast, in cases of extreme male dominance combined with polygyny, male death rates increase enormously when they reach maturity. This results in conspicuously divergent survivorship curves for the two sexes, as is illustrated by the gray seal (*Halichoerus grypus*) on the coasts of Britain (Hewer, 1964).

Although there is, of course, no observational information on the reproductive behavior of *Candiacervus*, it is unlikely it differed dramatically from that of other gregarious deer (for details see Type of Profile). Most likely, in *Candiacervus* gender-specific patterns would have resembled those for medium-sized ruminants like *O. dalli*. Unfortunately, the effect of gender cannot be rigorously evaluated for Cretan deer because the sex of individual specimens is almost always unknown. Males did not retain the upper canine (the ancestral condition for deer), leaving the presence of antler pedicles in bucks as the only unequivocal gender-specific trait in *Candiacervus* (pedicles are entirely missing in does). Regrettably, the number of skulls preserving presence/absence evidence of the pedicle and sufficient dental elements to estimate degree of wear is too limited for good statistical interpretation of the sex ratio relative to age stage. Nonetheless, in the studied populations the number of adult males cannot have been excessively low per age stage, for the simple reason that the number of mature shed antlers is large while that of unshed yearling antlers is low. In *Candiacervus* antlers were simplified but not small, especially in the case of typical *Can. ropalophorus* in which they were remarkably elongate. Marked male dominance is unlikely given the shallowness of the preorbital fossae (implying weak development of preorbital glands) and, again, the large number of shed antlers (implying low mortality of yearling stags). Under conditions of marked male dominance, the survival of young males into adulthood is low. In a thanatacoenose, this pattern would be consistent with the occurrence of a relatively high number of unshed yearling antlers and a relatively low number of shed adult antlers.

## Relation to Selective Pressure

Apart from body size decrease (less pronounced in *Candiacervus* sp. II at Liko than in *Can. ropalophorus* at Gerani 4; de Vos, 1979), the smaller species/ecomorphs of Cretan deer display certain morphological features that are not shared with mainland deer. But since they occur in other insular ruminants, such as *Myotragus balearicus*, these features may be plausibly interpreted as adaptations to insular environments. These features include: (1) greatly increased robusticity of the limb bones (de Vos, 1979, 1984), (2) slightly increased incidence of partial fusion of the tarsometatarsal joint (~10% of adult individuals; de Vos, 1979) relative to average frequencies in mainland populations (van der Geer, 2014); (3) lacrimal fossa weak or even absent; (4) relatively short lower limbs in relation to thoracolumbar length (van der Geer et al., 2006b), likely related to topography (see Terada et al., 2012); and (5) a slight increase in molar hypsodonty (de Vos, 1979). The trend in body proportions (4) is already in evidence at birth and becomes more apparent during ontogeny (van der Geer et al., 2006a). The presence of these characters, which substantially differ from any plausible plesiomorphous conditions in the ancestor, indicate the action of strong selective pressures. Moreover, there is increasingly persuasive evidence that certain morphological changes (especially changes in body size) characteristically occur in a relatively short time during the early stages of adaptation to novel insular environments (Lister, 1996; Millien, 2006), which also implies strong selection. It follows from this that, for selective pressures to be highly directional and to operate on very short schedules, at any one time a high percentage of individuals must be excluded from reproduction, either by dying before the reproductive age or by exclusion of most males for behavioral reasons (as in the gray seal; see Hewer, 1964).

The likeliest selective mechanism in *Candiacervus* would have been one that preferentially affected juveniles. High juvenile mortality may increase the pace of morphological change in a species (e.g., Stearns and Koella, 1986). Any trait that enhances survivorship at an early stage of life has a greater overall impact than a similar trait acting at a later stage. Theoretically, selection could have been accelerated during years of nutrient surplus, perhaps by the mechanism that controls longevity and turnover rate via population-density effects. We speculate that in the early phases of adaptation to insularity, change is accelerated (as during the boom period of a boom/bust cycle) but later becomes more gradual after the establishment of stable, relatively stationary populations with intermittent periods of higher density (as is perhaps indicated at Gerani 4).

## CONCLUSION

Two age profiles obtained for the Cretan Late Pleistocene deer *Candiacervus* show high juvenile mortality and longevity trends comparable to mainland deer. The absence of ecologically relevant predators seems to have had no measurable effect on juvenile mortality in this insular deer as compared to mainland relatives, in which high juvenile mortality is also very pronounced. This leaves accidents, diseases, and genetic defects as major causes of mortality. The profiles obtained here for *Candiacervus* are attritional in nature and thus reflect the average age distribution of the population, which consisted mainly of fawns and (very) old individuals and only a small portion of individuals in their prime. Our profiles indicate a nutrient-poor environment supporting relatively few individuals, which is in agreement with the hypothesis that islands tend to be resource limited. In view of evidence from other island taxa that morphological change (e.g., body size decrease, metapodial shortening) may take place within geologically short time spans, we conclude that selective pressure for morphological change must be both substantial and directional. We argue that the likeliest means for forcing such change is high juvenile mortality.

## ACKNOWLEDGMENTS

We would like to thank Reinier van Zelst (Naturalis Biodiversity Center, Leiden, the Netherlands) and George Theodorou (Museum of Palaeontology and Geology, National and Kapodistrian University of Athens, Greece) for granting us access to the collections in their care. The authors are also grateful to Gertrud Rössner and Mugino Kubo for constructive comments and critical review of the manuscript. G. Lyras received support from the SYNTHESYS Project (http:://www.synthesys.info/) financed by European Community Research Infrastructure Action under the FP6 "Structuring the European Research Area" Programme.

The research of A. van der Geer, R. MacPhee, and H. Drinia was cofinanced by the European Union (European Social Fund) and Greek national funds through the Operational Program "Education and Lifelong Learning" of the National Strategic Reference Framework (NSRF)—Research Funding Program: THALIS—UOA "Island biodiversity and cultural evolution: Examples from the Eastern Mediterranean, Madagascar, Mauritius and Philippines during the past 800,000 years" (MIS375910, KA:70/3/11669).

## REFERENCES

Bachmayer, F., J.P. Brinkerink, and N. Symeonidis. 1976. Pleistozäne Schildkröten aus Höhlen der Insel Kreta. Annales Géologiques des Pays Helléniques 27: 100–120.

Biskop, A. 1978. Relatieve groei van de pootelementen van *Candiacervus cretensis*. Master's thesis, Universiteit van Utrecht.

Boekschoten, G.J., and P.Y. Sondaar. 1966. The Pleistocene of the Katharo basin (Crete) and its hippopotamus. Bijdragen tot de Dierkune 36: 17–44.

Bover, P. 2004. Noves aportacions al coneixement del gènere *Myotragus* Bate, 1909 (Artiodactyla, Caprinae) de les illes Balears. Ph.D. dissertation, Universitat de les Illes Balears, Palma de Mallorca.

Caloi, L., and M.R. Palombo. 1996. Functional aspects and ecological implications in hippopotamus and cervids of Crete. *In* D.S. Reese (editor), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in World Archaeology 28: 125–151. Madison, WI: Prehistory Press.

Capasso Barbato, L. 1992. Observations on the biostratigraphy of Cretan Pleistocene vertebrates. Il Quaternario 5: 67–76.

Capasso Barbato, L. 1995. Un tentativo di analisi cladistica applicata ad un cervide endemico del Pleistocene di Creta. Geologica Romana 31: 243–248.

Capasso Barbato, L., and C. Petronio. 1986. *Cervus major* n. sp. of Bate Cave (Rethymnon, Crete). Atti della Accademia Nazionale dei Lincei, Memorie, Serie 8, 18: 59–103.

Caughley, G. 1966. Mortality patterns in mammals. Ecology 47: 906–918.

Caughley, G. 1971. Demography, fat reserves and body size of a population of red deer *Cervus elaphus* in New Zealand. Mammalia 35: 369–383.

Chapman, D.I., and N. Chapman. 1970. Development of the teeth and mandibles of fallow deer. Acta Theriologica 15: 11–131.

Clauss, M, M.T. Dittmann, D.W.H. Müller, P. Zerbe, and D. Codron. 2014. Low scaling of a life history variable: analysing eutherian gestation periods with and without phylogeny-informed statistics. Mammalian Biology/Zeitschrift für Säugetierkunde 79: 9–16.

Clutton-Brock, T.H. 1991. The evolution of parental care. Princeton: Princeton University Press.

Clutton-Brock, T.H., S.D. Albon, and F.E. Guinness. 1985. Parental investment and sex differences in juvenile mortality in birds and mammals. Nature 313: 131–133.

Croitor, R. 2006. Early Pleistocene small-sized deer of Europe. Hellenic Journal of Geosciences 41: 89–117.

Croitor, R., and M.-F. Bonifay. 2001. Étude préliminaire de cerfs du gisement Pleistocène inférieur de Ceyssaguet (Haute-Loire). Paleo 13: 129–144.

Damuth, J. 1982. Analysis of the preservation of community structure in assemblages of fossil mammals. Paleobiology 8: 434–446.

Dayan, T., and D. Simberloff. 1998. Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations. Mammal Review 28: 99–124.

Fosse, P. 1994. Taphonomie paléolithique: les grands mammifères de Soleilhac (Haute-Loire) et de Lunel-Viel 1 (Hérault). Ph.D. dissertation, Université de Provence-Aix-Marseille I.

Gaillard, J.-M., et al. 1993. Roe deer survival patterns: a comparative analysis of contrasting populations. Journal of Animal Ecology 62: 778–791.

Gaillard, J.-M., M. Festa-Bianche, and N.G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Tree 13: 58–63.

Geer, A.A.E. van der. 2014. Parallel patterns and trends in functional structures in extinct island mammals. Integrative Zoology 9: 167-182. [doi:10.1111/1749-4877.12066]

Geer, A.A.E. van der, M. Dermitzakis, and J. de Vos. 2006a. Relative growth of the metapodials in a juvenile island deer: *Candiacervus* (Mammalia, Cervidae) from the Pleistocene of Crete. Hellenic Journal of Geosciences 40: 119–125.

Geer, A.A.E. van der, J. de Vos, G.A. Lyras, and M. Dermitzakis. 2006b. New data on the Pleistocene Cretan deer *Candiacervus* sp. II (Mammalia, Cervinae). Courier Forschungsinstitut Senckenberg 256, 131–7.

Geer, A.A.E. van der, G.A. Lyras, M.V. Lomolino, M.R. Palombo, and D.F. Sax. 2013a. Body size evolution of palaeo-insular mammals: temporal variations and interspecific interactions. Journal of Biogeography 40: 1440–1450. [doi:10.1111/jbi.12119]

Geer, A.A.E. van der, G.A. Lyras, J. de Vos, and H. Drinia. 2013b. Morphology of articular surfaces can solve a phylogenetic issue: one instead of two ancestors for *Candiacervus* (Mammalia: Cervoidea). Zitteliana, Reihe B: Abhandlungen der Bayerischen Staatsammlung für Paläontologie und Geologie 31: 33–34.

Geist, V. 1998. Deer of the world: their evolution, behaviour and ecology. Mechanicsburg, PA: Stackpole Books.

Gompper, M.E. 2002. The ecology of northeast coyotes: current knowledge and priorities for future research. Wildlife Conservation Society Working Paper 17, July 2002. Bronx, NY: Wildlife Conservation Society.

Gonzáles, F.L. 2003. Paleontology and taphonomy of Pleistocene macromammals of Galicia (NW Iberian Peninsula). Ph.D. dissertation, Universidade de Coruña, Spain.

Harrington, J.L., and M.R. Conover. 2006. Characteristics of ungulate behavior and mortality associated with wire fences. Wildlife Society Bulletin 34: 1295–1305.

Hewer, H.R. 1964. The determination of age, sexual maturity, longevity and a life-table in the grey seal (*Halichoerus grypus*). Proceedings of the Zoological Society of London 142: 593–623.

Hinsbergen, D.J. van, and J.E. Meulenkamp. 2006. Neogene supradetachment basin development on Crete (Greece) during exhumation of the South Aegean core complex. Basin Research 18: 103–124.

Hutchinson, G.E. 1978. An introduction to population ecology. New Haven: Yale University Press.

Iliopoulos, G., H. Eikamp, and C. Fassoulas. 2010. A new Late Pleistocene mammal locality from western Crete. Bulletin of the Geological Society of Greece 43: 918–925.

Jackson, A.M. 2011. Survival estimates of white-tailed deer fawns at Fort Rucker, Alabama. Unpublished M.Sc. Thesis, Auburn University.

Jedrzejewski, W., B. Jedrzejewska, H. Okarma, and A.L. Ruprecht. 1992. Wolf predation and snow cover as mortality factors in the ungulate community of the Białowieza National Park, Poland. Oecologia 90: 27–36.

Jordana, X, and M. Köhler. 2011. Enamel microstructure in the fossil bovid *Myotragus balearicus* (Majorca, Spain): implications for life-history evolution of dwarf mammals in insular ecosystems. Palaeogeography, Palaeoclimatology, Palaeoecology 300: 59–66.

Jordana, X., N. Marín-Moratalla, D. DeMiguel, T.M. Kaiser, and M. Köhler. 2012. Evidence of correlated evolution of hypsodonty and exceptional longevity in endemic insular mammals. Proceedings of the Royal Society B 279 (1741): 3339–3346.

Klein, R.G. 1982. Patterns of ungulate mortality and ungulate mortality profiles from Langebaanweg (early Pliocene) and Elandsfontein (Middle Pleistocene), south-western Cape Province, South Africa. Annals of the South African Museum 90: 49–94.

Köhler, M., and S. Moyà-Solà. 2009. Physiological and life history strategies of a fossil large mammal in a resource-limited environment. Proceedings of the National Academy of Sciences of the United States of America 106 (48): 20354–20358.

Köhler, M., N. Marín-Moratalla, X. Jordana, and R. Aanes. 2012. Seasonal bone growth and physiology in endotherms shed light on dinosaur physiology. Nature 487 (7407): 358–361.

Koike, H., and N. Ohtaishi. 1987. Estimation of prehistoric hunting rates based on the age composition of sika deer. Journal of Archaeological Science 14: 251–269.

Kojola, I., T. Helle, E. Huhta, and A. Niva. 1998. Foraging conditions, tooth wear, and herbivore body reserves: a study of female reindeer. Oecologia 117: 2–30.

Kubo, M.O., M. Fujita, S. Matsu'ura, M. Kondo, G. Suwa. 2011. Mortality profiles of late Pleistocene deer remains of Okinawa island: evidence from the Hananda-Gama cave and Yamashita-cho cave I sites. Anthropological Science 119: 18–201.

Kurtén, B. 1953. On the variation and population dynamics of fossil and recent mammal populations. Acta Zoologica Fennica 76: 1–122.

Linnell, J.D.C., R. Aanes, R. Andersen. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildlife Biology 1: 209–223.

Lister, A.M. 1996. Dwarfing in island elephants and deer: processes in relation to time of isolation. Symposia of the Zoological Society of London 69: 277–292.

Lomolino, M.V. 1985. Body size of mammals on islands: the island rule re-examined. American Naturalist 125: 310–316.

Lomolino, M.V. 2005. Body size evolution in insular vertebrates: generality of the island rule. Journal of Biogeography 32: 1683–1699.

Lomolino, M.V., D.F. Sax, M.R. Palombo, and A.A. van der Geer. 2012. Of mice and mammoths: evaluations of causal explanations for body size evolution in insular mammals. Journal of Biogeography 39: 842–854.

Lomolino, M.V., et al. 2013. Of mice and mammoths: generality and antiquity of the island rule. Journal of Biogeography 40: 1427–1439.

Long, R.A., A.F. O'Connell, and D.J. Harrison. 1998. Mortality and survival of white-tailed deer *Odocoileus virginianus* fawns on a north Atlantic coastal island. Wildlife Biology 4: 237–247.

Louchart, A., C. Bedetti, and M. Pavia. 2005. A new species of eagle (Aves: Accipitridae) close to the Steppe Eagle, from the Pleistocene of Corsica and Sardinia, France and Italy. Palaeontographica A272: 121–148.

Marris, E. 2014. Rethinking predators: legend of the wolf. Predators are supposed to exert strong control over ecosystems, but nature doesn't always play by the rules. Nature 507 (7491): 158—160.

Michaux, J.R., J.G. de Bellocq, S. Maurizio, and S. Morand. 2002. Body size increase in insular rodent populations: a role for predators? Global Ecology 11: 427–436.

Mijares, A.S., et al. 2010. New evidence for a 67,000-year-old human presence at Callao Cave, Luzon, Philippines. Journal of Human Evolution 59 123–132.

Millien, V. 2006 Morphological evolution is accelerated among island mammals. PLOS Biology 4 (10): e321, 1863–1868.

Minami, M., N. Ohnishi, and S. Takatsuki. 2009. Survival patterns of male and female sika deer on Kinkazan Island, northern Japan. *In* D. R. McCullough, S. Takatsuki, and K. Kaji (editors), Sika deer: biology and management of native and introduced populations: 375–384. Tokyo: Springer.

Murie, A. 1944. The wolves of Mount McKinley. Fauna of the National Parks of the U.S., Fauna series 5, 20: 1–238 pp. Washington, DC: National Park Service.

Nussey, D.H., et al. 2007. The relationship between tooth wear, habitat quality and late-life reproduction in a wild red deer population. Journal of Animal Ecology 76: 402–412.

Parkes, J.P. 2005. Feral goat. *In* C.M. King (editor), The handbook of New Zealand mammals. 2nd ed.: 374–391. Victoria, NZ: Oxford University Press.

Pianka, E. 2000. Evolutionary ecology. San Francisco: Addison Wesley.

Raia, P., and S. Meiri. 2006. The island rule in large mammals: palaeontology meets ecology. Evolution 60: 1731–1742.

Raia, P., C. Barbera, and M. Conte. 2003. The fast life of a dwarfed giant. Evolutionary Ecology 17: 293–312.

Reese, D.S., G. Belluomini, and M. Ikeya. 1996. Absolute dates for the Pleistocene fauna of Crete. *In* D.S. Reese (editor), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in World Archaeology 28: 47–51. Madison WI: Prehistory Press.

Sarno, R.J., et al. 1999. Juvenile guanaco survival: management and conservation implications. Journal of Applied Ecology 36: 937–945.

Shipman, P. 1981. Life history of a fossil: an introduction to taphonomy and paleoecology. Cambridge, MA: Harvard University Press.

Simard, M.A., S. Côté, R.B. Weladji, and J. Huot. 2008. Feedback effects of chronic browsing on life-history traits of a large herbivore. Journal of Animal Ecology 77: 678–686.

Sinclair, A.R.E. 1974. The natural regulation of buffalo populations in East Africa: III. Population trends and mortality. East African Wildlife Journal 12: 185–200.

Skogland, T. 1988. Tooth wear by food limitation and its life history consequences in wild reindeer. Oikos 51: 23–242.

Smith, B.H. 2000. 'Schultz's Rule' and the evolution of tooth emergence and replacement patterns in primates and ungulates. *In* M.F. Teaford, M.M. Smith, and M. Ferguson (editors), Development, function and evolution of teeth: 212–227. New York: Cambridge University Press.

Smith, F.A. 1992. Evolution of body size among wood rats from Baja California, Mexico. Functional Ecology 6: 265–273.

Sondaar, P.Y. 1977. Insularity and its effects on mammal evolution. *In* M.K. Hecht, P.C. Goody, and B.M. Hecht (editors), Major patterns of vertebrate evolution: 671–707. New York, NY: Plenum.

Stearns, S.C., and J.C. Koella. 1986. The evolution of phenotypic plasticity in life-history traits: predictions of reaction norms for age and size at maturity. Evolution 40: 893–913.

Taber, R.D., and D.F. Dasmann. 1958. The dynamics of three natural populations of the deer *Odocoileus hemionus columbianus*. Ecology 38: 23–246.

Terada, C., Tatsuzawa, S., and S. Takashi. 2012. Ecological correlates and determinants in the geographical variation of deer morphology. Oecologia 169: 981–994.

Tremblay, J., I. Thibault, C. Dussault, J. Huot, and S. Côté. 2005. Long-term decline in white-tailed deer browse supply: can lichens and litterfall act as alternative food sources that preclude density-dependent feedbacks? Canadian Journal of Zoology 83: 1087–1096.

Veiberg, V., et al. 2007. Bigger teeth for longer life? Longevity and molar height in two roe deer populations. Biology Letters 3: 268–270.

Voorhies, M.R. 1969. Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. Contributions to Geology, Special Papers of the University of Wyoming 1: 1–69.

Vorreyer, F. 1957. Das Rotwild: Naturgeschichte, Hege und Jagd. Hamburg: Paul Parey.

Vos, J. de. 1979. The endemic Pleistocene deer of Crete. Proceedings of the Koninklijke Akademie van Wetenschappen B82: 59–90.

Vos, J. de. 1984. The endemic Pleistocene deer of Crete. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde 31: 1–100.

Vos, J. de. 1996. Taxonomy, ancestry and speciation of the endemic Pleistocene deer of Crete compared with the taxonomy, ancestry and speciation of Darwin's finches. *In* D.S. Reese (editor), Pleistocene and Holocene fauna of Crete and its first settlers. Monographs in World Archaeology 28: 111–124. Madison, WI: Prehistory Press.

Vos, J. de. 2006. Notes about parallels in the evolution of the Pleistocene cervids from Greece (Crete, Kassos and Karpathos), Japan (the Ryukyu-islands) and Philippines (Masbate). Hellenic Journal of Geosciences 41: 127–40.

Vos, J. de, and A.A.E. van der Geer. 2002. Major patterns and processes in biodiversity: taxonomic diversity on islands explained in terms of sympatric speciation. *In* W.H. Waldren and J.A. Ensenyat (editors), World islands in prehistory. British Archaeological Reports International Series 1095: 395–405.

Weesie, P.D.M. 1982. A Pleistocene endemic island form within the genus *Athene*, *Athene cretensis* n. sp. (Aves, Strigiformes) from Crete. Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B85: 323–336.

Weesie, P.D.M. 1988. The quaternary avifauna of Crete, Greece. Palaeovertebrata 18: 1–94.

Williams, G.R., and M.R. Rudge. 1969. A population study of feral goats (*Capra hircus* L.), from Macauley Island, New Zealand. Proceedings of the New Zealand Ecological Society 16: 17–28.

All issues of *Novitates* and *Bulletin* are available on the web (http://digitallibrary.amnh.org/dspace). Order printed copies on the web from:
http://shop.amnh.org/a701/shop-by-category/books/scientific-publications.html

or via standard mail from:
American Museum of Natural History—Scientific Publications
Central Park West at 79th Street
New York, NY 10024