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A Comparison of Three Ageing Techniques for Feral Pigs from Subalpine and Semi-arid Habitats

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Abstract

Three ageing techniques were tested on samples of wild-caught feral pigs from subalpine ($n = 35$) and semi-arid ($n = 64$) areas in eastern Australia, and on a sample of known-age captive feral pigs reared from stock from semi-arid areas ($n = 15$). Techniques employed were based on morphometric relationships, patterns of tooth eruption and wear, and counts of cementum lines in permanent incisors. Cyclic seasonal conditions led to apparently annular cementum line deposition for pigs from the subalpine area. In contrast, stochastic variation in seasonal conditions led to irregular cementum line deposition in pigs from the semi-arid area and captive-reared pigs of semi-arid stock. On the assumption that cementum lines are annular in pigs from the subalpine site, patterns of tooth eruption and wear and morphometrics returned reasonably accurate age estimates, the former being more precise. Patterns of tooth eruption and wear returned reasonably accurate age estimates for known-age captive-reared pigs, whereas morphometrics gave increasing underestimates of age for progressively older pigs. On the assumption that patterns of tooth eruption and wear return similarly accurate age estimates for wild pigs from the semi-arid area, morphometrics again underestimated true age. A correction to the morphometric technique to improve its accuracy for semi-arid areas is given.

Introduction

Studies of the population biology of animals often involve collection of age-specific data on size (growth), body condition, mortality, and/or fecundity. Collection of such data requires the age of individual animals to be estimated. The ages of feral and wild pigs (*Sus scrofa*) have been estimated using patterns of tooth eruption and replacement (Matschke 1967; Clarke *et al.* 1992), cementum lines (Quere and Pascal 1984; Saez-Royuela *et al.* 1989; Clarke *et al.* 1992), width of incisor pulpar cavity (Saez-Royuela *et al.* 1989), eye-lens weight (Sweeney *et al.* 1970), epiphysial fusion (Wijngaarden-Baker and Maliepard 1982) and morphometric relationships (Boreham 1981).

This study applied techniques based on morphometric relationships, tooth eruption and wear, and counts of cementum lines to determine the age of feral pigs from a subalpine habitat and a semi-arid riverine habitat, and known-age captive feral pigs reared from stock from semi-arid areas. Counts of cementum lines require pigs to be killed. Of the two non-fatal techniques, morphometric-based age estimates are less stressful to pigs and safer for researchers than are estimates derived from patterns of tooth eruption and wear. The accuracy and precision of the three techniques in subalpine and semi-arid areas are assessed.

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Methods

Study Sites and Animals

Wild pigs were trapped and shot in two areas of New South Wales. Only pigs old enough to have lower primary incisors (I_1) were included in the study. The ages of 35 pigs from Kosciusko National Park (KNP) in the south-eastern alpine region and of 64 from Nocoleche Nature Reserve (NNR) on the Paroo R. in the State's semi-arid north-west were estimated. In addition, 15 pigs born and raised on the Trangie Agricultural Research Centre (TARC) were killed and their ages estimated for the study.

Pigs sampled from KNP were trapped in the region of Long Plain (36°43′S.,148°32′E.). Details of the topography, vegetation and climate of the area are given in Costin *et al.* (1979). The area contains a complex of essentially treeless plains covered by sod tussock grasslands and rimmed by heavily timbered mountains, hills and ridges. The area has a cool temperate climate, modified by altitude and landscape. No month is frost free and although snow cover is rarely continuous, good falls may remain on the ground for a number of weeks. Precipitation is about 1400 mm annually with high reliability. Average monthly precipitation for Kiandra, adjacent to the study site, is summarised in Fig. 1*a*.

Pigs sampled from NNR were trapped along the Paroo R. (29°50′S.,144°10′E.). Details of the topography, vegetation and climate of the area are given in Beadle (1948) and Cunningham *et al.* (1981). The area contains a complex of lignum- and canegrass-dominated black soil flats along and adjacent to the river, with shrub- and grass-covered red soil areas on higher ground. The area is characterised by often extreme summer temperatures (>40°C), and low annual precipitation (average of 267 mm). Rainfall has little seasonality and is highly unpredictable. Average monthly rainfall for Wanaaring, 18 km north of the study site, is summarised in Fig. 1*b*.

Pigs from TARC (31°59′S.,147°57′E.) were of known-age, all being born in captivity from wild-caught stock. Parent stock were obtained from a variety of sites in semi-arid western New South Wales. Pigs were kept amongst a group of 30–70 pigs in large outdoor yards. Throughout their lives, pigs were supplied with water *ad libitum*, and enough pelleted ration to keep them visibly fat. The climate at TARC is qualitatively similar to that at NNR (Fig. 1*c*).

Age from Morphometrics

Head length (minimum curved distance from the tip of the nose to the posterior edge of the cranium) (H), and total body length (minimum curved distance from the tip of the nose to the base of the tail) (B), of each pig was measured in centimetres using a flexible fibreglass tape. Boreham (1981) used these measures to estimate age in days from an age index (I) related to body measurements by:

$$I = (H + B)/2\ .$$

Boreham (1981) related this index to age estimated from tooth eruption and wear using a visual plot. We reanalysed Boreham's data and derived polynomial regressions relating age to the age index separately for males and females. Separate equations were used to account for the different growth rates of male and female pigs (Saunders 1988). The age (A) of males was related to Boreham's age index by

$$A\,(\text{days}) = -5\cdot019I + 0\cdot140I^2$$

and the age of females by

$$A\,(\text{days}) = -5\cdot707I + 0\cdot158I^2\ .$$

We used this approach to derive age indices and to estimate age in days for all pigs examined in this study. The technique can only be used to estimate the age of pigs less than 1000 days old (33 months), equivalent to an age index of approximately 96. Pigs estimated to be more than 1000 days old by this method were excluded from analyses that involved age estimated from morphometrics.

Age from Tooth Eruption and Wear

The ages of pigs were estimated in months using patterns of tooth eruption and wear according to a scheme elaborated by Barrett (1971) from an earlier scheme developed by Matschke (1967). Matschke's (1967) scheme used tooth eruption and replacement to estimate the age of pigs to 25 months. Barrett's (1971) scheme used additional assessment of gradual eruption of the third permanent upper molars (M^3) to estimate the age of pigs to 36 months. Thereafter, wear on the third permanent molars (M^3 and M_3) was used to estimate the age of pigs in years to 72 months (6 years).

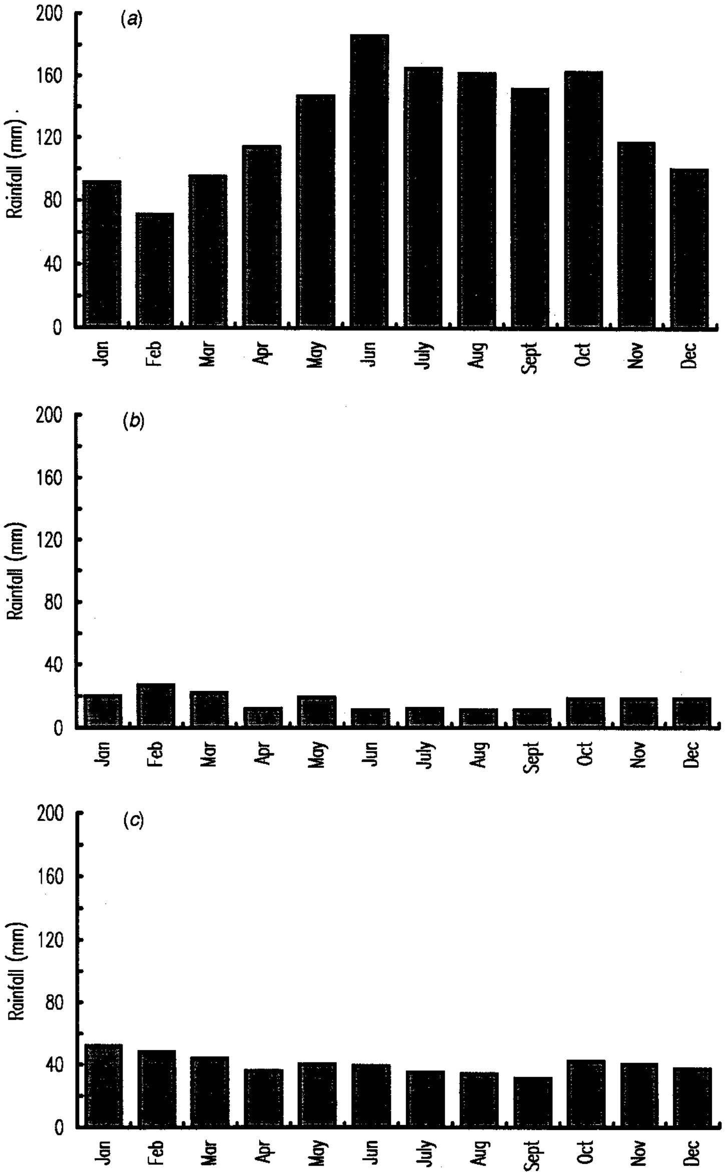

Fig. 1. Average monthly rainfall. *a*, Kiandra; *b*, Wanaaring; *c*, Trangie Agricultural Research Centre.

Age from Cementum Lines

A lower primary incisor (I_1) was removed from each pig. The crown of each incisor was removed, and the root decalcified in nitric acid (3%) for 48–96 h, sectioned across the labiolingual plane on a freezing microtome (30 μm), immersed in Ehrlich's haematoxylin for 24 h, and mounted on a slide for microscopic examination (Klevezal and Kleinenberg 1967). Cementum lines, where present, were counted for each pig and interpreted in relation to seasonal breeding patterns.

Pigs in KNP bred seasonally, the peak of births occurring in February (mean = 23 February, s.d. = 78·4 days), and undergo a winter food shortage during which their average body condition falls significantly (Saunders 1988). Spinage (1973) concluded that cementum deposition in mammals corresponds with periods of slow or interrupted growth related to times of food shortage. If, as seems likely, cementum lines in the primary incisors of KNP pigs form during periods of winter food shortage, the first cementum line would be deposited during a pig's second winter at an age of approximately 18 months [primary incisors of wild pigs erupt at 12 months of age in North America (Matschke 1967) and 13 months of age in the South I. of New Zealand (Clarke *et al.* 1992)]. On the assumption that all pigs from KNP are born in February and all cementum lines are deposited in July, age in months was calculated by taking the month of sampling (March 1988) as 0, adding 8 months for the difference between July (when the most recent cementum line was deposited) and the following March, adding 12 months for each cementum line present, and adding 18 months for the age of the pig when the first cementum line was probably deposited. Young pigs with no sign of obvious cementum deposition were most likely born during the breeding season centred on February 1987. They were assigned an age of 13 months.

Analyses

All age estimates were converted to months. Age estimates derived from tooth eruption and wear that were beyond 36 months were rounded to the nearest 12-month total (i.e. 48, 60 or ⩾72 months).

Interpretation of linear regressions between ages of individual pigs returned by the different techniques was used to assess accuracy and precision. Age estimates for individual pigs derived from the different techniques were non-independent, precluding direct statistical comparison of techniques. Where slopes of regressions between techniques did not differ significantly from 1, interpretation of failures to reject null hypotheses became necessary. The limitations of such interpretations are acknowledged.

Results

Regular cementum lines were evident in the incisors of all older pigs sampled from KNP, but not in pigs sampled at either NNR or TARC. The incisors of pigs from NNR all contained cementum lines, but these were irregularly spaced, and they often bifurcated and overlapped. The incisors of pigs from TARC contained few irregularly spaced cementum lines, many of which were bifurcated. The irregular nature and the high frequency of overlap of cementum lines evident in incisors of pigs from NNR and TARC suggest that it is unlikely that these lines reflect annular patterns of cementum deposition, and preclude accurate counts.

Regressions of age estimates for the KNP sample using morphometrics and patterns of tooth eruption and wear are shown in Fig. 2*a* and *b*, respectively, on age estimates using counts of cementum lines. Forcing each regression through its origin improved the fit of least-squares lines of best fit: r^2_{adj} (coefficient of determination adjusted for the number of parameters in the model) increased from 0·89 to 0·98 for morphometric age estimates, and from 0·93 to 0·99 for age estimates derived from tooth eruption and wear. Slopes of regressions through the origin were not significantly different from 1 for either morphometric age estimates ($F = 1 \cdot 180$, d.f. = 1, 13) or age estimates derived from tooth eruption and wear ($F = 2 \cdot 262$, d.f. = 1, 27). On the assumption that ages estimated from counts of cementum lines are accurate, both morphometrics and patterns of tooth eruption and wear provided reasonable estimates of age. Patterns of tooth eruption and wear lost some precision beyond 25 months of age when subjective judgment of the degree of eruption and wear of M^3 and M_3 became necessary. However, age estimates derived from tooth eruption and wear were generally more precise than those derived from morphometrics.

The regression of age for the NNR sample estimated from morphometrics, on age estimated from patterns of tooth eruption and wear, is shown in Fig. 3. Forcing the regression line through its origin improved the fit of the least-squares line of best fit: r^2_{adj} increased from 0·85 to 0·98. The slope of the regression forced through its origin was significantly lower than 1 ($F = 104 \cdot 3$, d.f. = 1, 46, $P < 0 \cdot 01$), demonstrating that morpho-

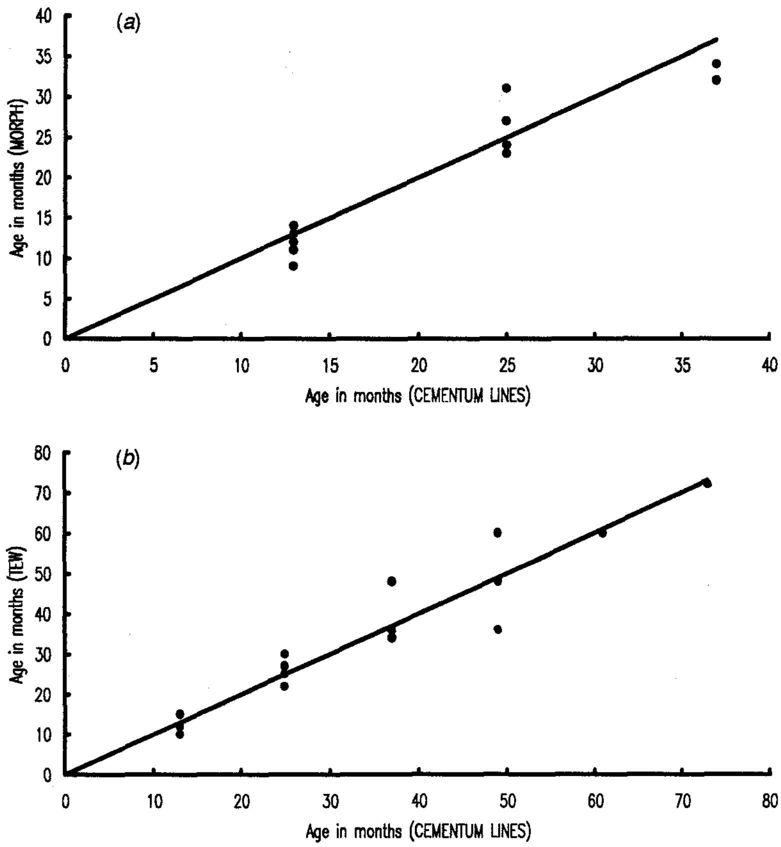

Fig. 2. Age estimated for individual pigs from KNP using (*a*) morphometrics (MORPH) ($n = 14$), and (*b*) patterns of tooth eruption and wear (TEW) ($n = 28$), plotted against age estimated from counts of cementum lines. Fitted regression lines are for $y = x$.

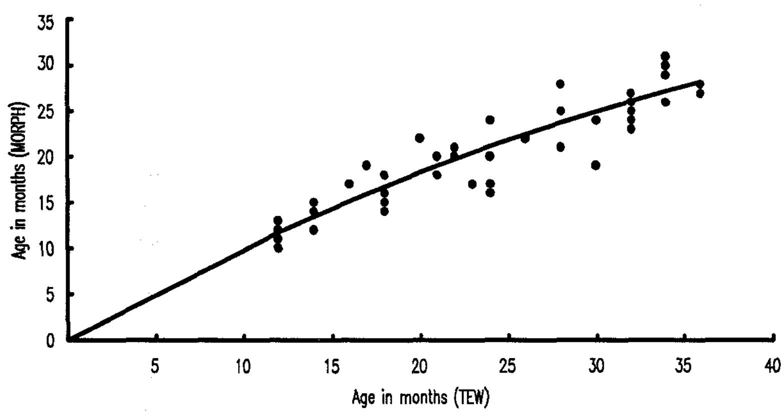

Fig. 3. Age estimated for individual pigs from NNR using morphometrics (MORPH) plotted on age estimated from patterns of tooth eruption and wear (TEW) ($n = 47$). The fitted regression line is $y = 1 \cdot 074x - 0 \cdot 008x^2$.

metrics returned lower average age estimates for pigs from NNR than did patterns of tooth eruption and wear. A polynomial term was added to the regression to examine the nature of differences between ages estimated from the two techniques in more detail. The term was significant ($t = -4 \cdot 148$, d.f. = 1, $P < 0 \cdot 01$) and negative, and its addition increased the relationship's linear term from 0·838 to 1·074, indicating that the morphometric technique returned lower age estimates than did patterns of tooth eruption and wear amongst older rather than younger pigs.

Regressions of age for the TARC sample estimated from morphometrics and patterns of tooth eruption and wear are shown in Fig. 4*a* and *b*, respectively, on known age. Forcing each regression through its origin improved the fit of least-squares lines of best fit: r^2_{adj} increased from 0·81 to 0·98 for morphometric age estimates, and from 0·97 to 0·99 for age estimates derived from tooth eruption and wear. The slope of regressions through the origin was significantly lower than 1 for morphometric age estimates ($F = 14 \cdot 708$, d.f. = 1, 11, $P < 0 \cdot 01$), but not for age estimates derived from tooth eruption and wear ($F = 1 \cdot 415$, d.f. = 1, 14). Patterns of tooth eruption and wear returned good estimates of true age, but low sample size precluded assessment of the technique's precision for estimating the ages of pigs older than 25 months. Morphometrics returned underestimates of true age and, as with pigs from NNR, underestimates of age derived from patterns of tooth eruption and wear.

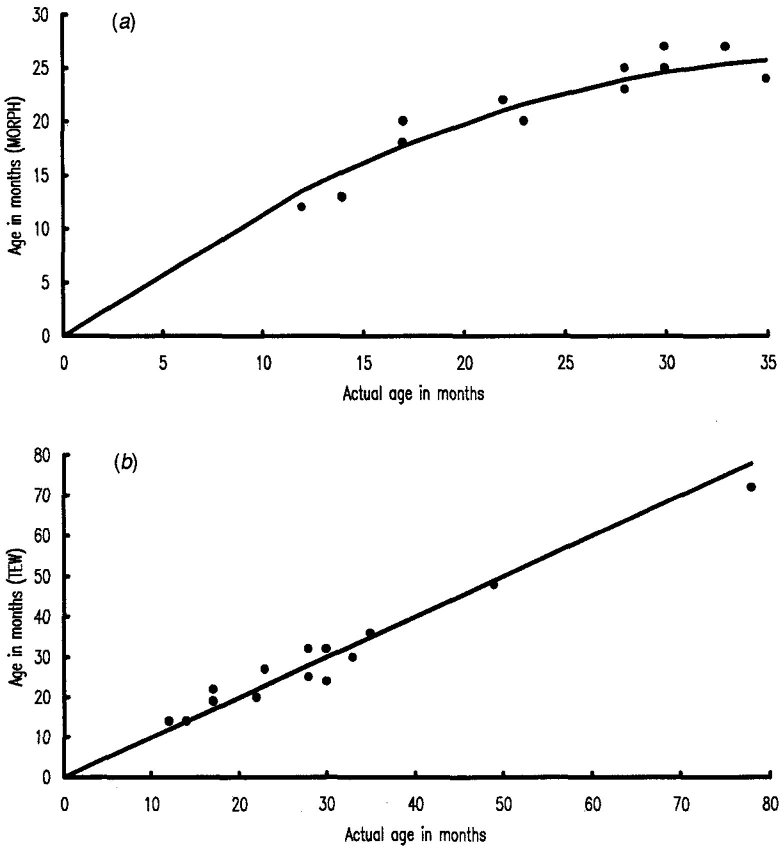

Fig. 4. Age estimated for individual pigs from TARC using (*a*) morphometrics (MORPH) ($n = 12$), and (*b*) patterns of tooth eruption and wear (TEW) ($n = 15$); plotted on actual age. Fitted regression lines: *a*, $y = 1 \cdot 324x - 0 \cdot 017x^2$; *b*, $y = x$.

A polynomial term was added to the regression of ages estimated from morphometrics on actual age to examine the nature of bias associated with the technique. The term was significant ($t = -5 \cdot 380$, d.f. = 1, $P < 0 \cdot 01$) and negative, and its addition increased the relationship's linear term from 0·867 to 1·32, indicating that the morphometric technique increasingly underestimated ages of progressively older pigs.

Discussion

Most indicators used to estimate the age of vertebrates interpret rates of cumulative change in some physical property. As such, the ability of an indicator to accurately predict age will depend upon the degree of variation or regularity in the probability and/or intensity of cumulative change over time. All three ageing techniques used in this study have the potential for some irregular variation in their rate of change. Morphometric measures rely on relative growth rates and maximum pig size, both subject to some degree of variation according to prevailing environmental conditions. Similarly, deposition of cementum lines in the teeth of mammals is related to food shortage, and its utility as an indicator of age to the cyclicity of periods of food shortage (Spinage 1973). While patterns of tooth eruption and replacement in mammals are developmentally set, rate of tooth wear can be affected by environmental factors that influence food quality (Skogland 1988). The following discussion focuses on the role of environmental variation on the performance of the ageing techniques used in this study in the two habitats sampled.

Environmental Cyclicity and Deposition of Cementum Lines

Presence of apparently annular cementum lines in KNP pigs but not in pigs from NNR or TARC conforms to hypotheses that relate cementum-line deposition to phases of interrupted or slower growth (Spinage 1973). An absolute demonstration that cementum lines are annular for pigs from KNP will require known-age material, or application of vital staining techniques. Pigs at KNP go through a regular period of under-nutrition during winter when forage production and quality falls, leading to a significant decline in body condition (Saunders 1988). A similar winter decline in condition related to an annual cycle in available nutrition and/or climate has been related to cyclic cementum-line deposition in wild boar from Spain (Saez-Royuela *et al.* 1989) and New Zealand (Clarke *et al.* 1992). In contrast, pigs from NNR deposit cementum lines that appear neither regular nor cyclic. Pigs at NNR go through aperiodic, often protracted intervals of under-nutrition during which condition declines markedly (D. Choquenot, unpublished data). It appears that cementum lines deposited by pigs in semi-arid areas like NNR reflect stochastic environmental variation, rather than any annual cycle of growth related to food availability.

Pigs raised at TARC were subject to no variation in food availability, and/or no extremes of low temperature over winter. Cementum lines were deposited in the incisors of these pigs, but these were the least distinct of any material examined. While alleviating pigs from periods of nutritional stress did not entirely suppress deposition of cementum lines, what deposition did occur was irregular and non-cyclic. Clarke *et al.* (1992) noted deposition of clear cementum lines in the molars of a sample of captive-reared feral pigs from the South I. of New Zealand that were subjected to more severe winter temperatures than pigs reared at TARC, suggesting an important climatic influence on cementum-line deposition.

Performance of Age Estimators

On the assumption that cementum lines in the incisors of pigs from KNP are annular, counts of these lines represent the most accurate technique for estimating the age of pigs from subalpine habitats. That these populations breed seasonally and cementum lines are probably laid down over winter suggests that the technique will also be precise. The marked seasonality of subalpine habitats becomes less pronounced at lower altitudes. At what point this will preclude the use of cementum lines for age estimation is unknown. Both the non-lethal techniques applied in this study gave reasonably accurate estimates of ages derived from cementum-line counts for pigs from KNP. Estimates derived from patterns of tooth eruption and wear were more precise than were estimates derived from morphometrics.

Cementum lines cannot be used to estimate the age of pigs from semi-arid habitats. Age estimates for pigs from TARC using patterns of tooth eruption and wear were, on average, accurate. In contrast, age estimates derived from morphometrics were biased, markedly underestimating the age of progressively older pigs. On the assumption that estimated ages of pigs from NNR derived from patterns of tooth eruption and wear were as accurate as those for the TARC sample, morphometrics again returned increasing underestimates of age amongst progressively older pigs. Boreham's (1981) morphometric method was derived from measures of pigs from Namadgi National Park, in mountains adjoining KNP. Pigs from these subalpine areas grow faster and attain larger adult sizes than do pigs from semi-arid habitats (Saunders 1988). Hence, it is not surprising that Boreham's method gave reasonably accurate age estimates for pigs from KNP, but underestimated the age of pigs from semi-arid areas. It appears that in the latter case, a different relationship between Boreham's age index and true age exists. On the basis of age estimates derived from patterns of tooth eruption and wear for pigs from NNR, the age (A) of male pigs from semi-arid habitats can be estimated in months from Boreham's age index (I) by

$$A\,(\text{days}) = -6\cdot540I + 0\cdot175I^2$$

and the age of females by

$$A\,(\text{days}) = -10\cdot240I + 0\cdot238I^2\,.$$

However, the technique is only useful for pigs up to 33 months of age and patterns of tooth eruption and wear provided more precise estimates of age than did morphometrics.

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