Fig. 2 Frequency of sapwood numbers in oaks from: *a*, England[12,28]; *b*, West Germany[29]; *c*, Finland.

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patterns and the use dates for 'known age' paintings is shortened by 4 yr. In one of the examples used by Fletcher *et al.*[4] (Thomas, second Baron Wentworth, painted 1568), the '1550' chronology placement leaves only 20 yr between its last heartwood ring and 1568. This period has to account for both sapwood and seasoning factors. In the case of the First-Viscount-Montague panel (painted 1569) only 15 yr are left to account for possible missing heartwood, missing sapwood and seasoning. Such intervals would be unacceptably short for English panels given the numbers of sapwood rings observed on modern English oaks[12,28] and it may have been the erroneous belief in an English origin for the panels which made the possible '1550' dating unacceptable.

If our revised dating is accepted, it suggests that the number of oak sapwood rings in the area from which the panels derived must have been less than the numbers normally accepted in England. Sapwood on mature oaks tends to be shorter in Western Germany[29] and substantially shorter for Roman (mean 18, range 11–27) and Dark Age (mean 17, range 11–21) oaks in South Germany[20,30]. We now have evidence for oaks from the eastern Baltic as the result of field work by members of the University of East Anglia Climatic Research Unit in 1984. The samples are 60 cores from 49 trees from two sites in southwestern Finland— Ruissalo and Solbole (all trees were *Q. robur*). The mean number of sapwood rings is 13.9 with a standard deviation of 3.2 and values range from 7 to 24. All trees were >120 yr in age. The mean number of sapwood rings from the Finnish sites is significantly smaller than the English sapwood values at the $P < 0.0001$ level (Fig. 2).

These results suggest that: (1) an eastern Baltic origin for the art-historical chronologies as suggested on historical grounds; (2) a movement of the art-historical chronologies forward to a '1550' placement; and (3) a very short sapwood interval are all compatible. When vindicated by subsequent work on Polish or Lithuanian timbers, these results make it inevitable that all of the art-historical datings derived using the '1545' or '1546' chronology placements, and the specifically tailored sapwood estimates favoured by some workers[15,31], will have to be revised. If the German art-historical dendrochronologists favour a '1548' chronology placement for their equivalent Netherlands II chronology[3], then all their dates will move forward in time by 2 yr. However, their estimated felling dates may have to be additionally revised in the light of the very short Baltic sapwood observations above.

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Patterns of mortality and age at first reproduction in natural populations of mammals

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There is great variation in the age at which females of different mammalian species first breed. Recent comparative analyses have focused on the relationship between age at first reproduction and body size[1-9], but differences in patterns of mortality experienced by natural populations are expected to have major effects on selection for age at first reproduction[10-14]. Here we show that the age at which females first reproduce is strongly correlated with expectation of life at birth, after the effects of body size have been removed, within and among species of mammals living in natural populations.

Some shrews give birth when they are only 7 weeks old[15], whereas female African elephants produce their first offspring at an age of some 15 years[16]; such differences in age at first reproduction are highly correlated with the species' differences in body size[1,2,8,9], suggesting that the time required to grow to adult size determines the age at which mammals become sexually mature[2,4]. Consistent with this idea, the timing of many physiological and reproductive processes (for example, cardiac cycle time and maximum recorded lifespan) scale in similar ways with body size, approximately to the 0.25 power[4,8].

However, body size might be a confounding factor in the sense that it influences one variable which in turn influences some other variable; both variables would then be correlated with body size. For example, species with high rates of mortality in the wild might be selected to mature earlier than those which are long-lived, but rates of mortality might be influenced by body size (larger species can defend themselves against predators more effectively and they can survive for longer periods without food[6]). Data are now available on mortality patterns,

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body sizes and age at first reproduction of females for 29 mammal species (representing 25 genera and 6 orders) from natural populations with stable age distributions[17]. The species range in weight from 20 g to 4,000 kg. In addition, equivalent data are available from six populations of a further species, the Columbian ground squirrel, *Spermophilus columbianus*[18,19]. These data can be used to test the hypothesis that differences in patterns of mortality are correlated with the ages of the females at first reproduction.

Six of the species in the sample belonged to two genera (*Spermophilus* and *Peromyscus*) and, to reduce taxonomic bias, analyses were performed at the generic level (that is, on the averages of logarithmically transformed congeneric species' values). All variables were logarithmically transformed before analysis. As a summary measure of mortality, we have used Millar and Zammuto's[17] estimates of mean life expectancy at birth in years (a comparison of the use of this versus other measures will be presented elsewhere). Genera with low mortality have a high expectation of life at birth. The correlation between age of females at first reproduction and life expectancy at birth is high and positive ($r = 0.976$, $n = 25$, $P < 0.001$). This correlation, however, might result from independent correlations of each variable with body size, but this seems not to be the case since the two variables are more highly correlated with each other ($r = 0.976$) than either is with body size ($r = 0.894$ and 0.873 respectively, $n = 25$ in both cases), and they remain highly correlated after the effects of body size have been removed by partial correlation ($r = 0.892$, $n = 25$, $P < 0.001$). The latter relationship means that mammals with an unexpectedly long lifespan (relative to body size) start reproducing relatively late (again relative to body size). The relationship is demonstrated graphically in Fig. 1—note the taxonomic spread. Genera from each of the two best-represented orders, the Artiodactyla and the Rodentia, cover most of the ranges of relative age at first reproduction and relative life expectancy. The removal of size effects is also evident: values for squirrels lie near that for the elephant, and the value for mice near that for the warthog. A positive partial correlation between age at first reproduction and life expectancy at birth, with the effects of body size removed, also holds among populations of the Columbian ground squirrel ($r = 0.874$, $n = 6$, $P = 0.05$).

Probably as a consequence of constraints imposed by seasonality, seven of the genera in the cross-species sample mature as 1-yr-olds (ranging in weight from the 0.1-kg *Tamias* to the 7.5-kg *Lynx*). When the analysis is repeated without these genera, the correlation between age at first reproduction and life expectancy (with body size effects removed) remains high and significant ($r = 0.836$, $n = 17$, $P < 0.001$). Of course, differences in body size may still influence age at first reproduction. Elephants could not mature and produce offspring in the few weeks that it takes shrews or mice to mature and, indeed, the partial correlation between age at first reproduction and body size with the effects of life expectancy removed is positive, though barely significant ($r = 0.390$, $n = 25$, $P < 0.1$).

To test for the possibility that gestation length, litter size, neonatal weight or litter weight was ultimately responsible for the correlation between age at first reproduction and life expectancy, data on these variables for the species in the sample were extracted from the literature[20-24], and the effect of each new variable was removed by partial correlation. With the effect of each variable removed, in no instance did the correlation between age at first reproduction and life expectancy fall below 0.9.

The positive relationship between age at first reproduction and expectation of life at birth, after removal of the effects of body size, calls for an explanation in terms of the costs and benefits of reproduction at different ages. Perhaps the most straightforward interpretation is that each bout of reproduction reduces subsequent reproductive success (either by further increasing mortality or by decreasing fecundity), and that older mothers produce larger litters (and/or more viable offspring) than do younger mothers[19]. As life expectancy at birth decreases
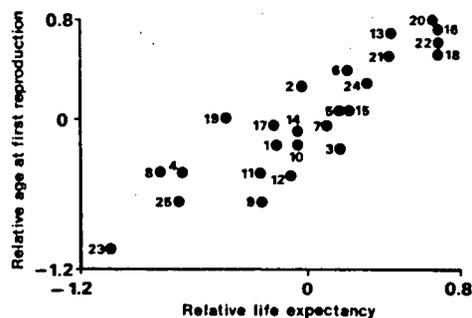
Fig. 1 Relative age at first reproduction plotted against relative life expectancy at birth for natural populations of mammals. Relative values refer to deviations from logarithmic regression lines of age at females' first breeding, or expectation of life at birth, on adult female body size. Numbers refer to different mammalian genera. Artiodactyla: 1, *Syncerus* (buffalo); 2, *Hippopotamus*; 3, *Aepyceros* (impala); 4, *Sus* (pig); 5, *Cervus* (deer); 6, *Ovis* (sheep); 7, *Hemitragus* (tahr); 8, *Phacochoerus* (warthog); 9, *Kobus* (kob); 10, *Connochaetes* (gnu). Carnivora: 11, *Taxidea* (American badger); 12, *Lynx*; 13, *Lutra* (river otter); 14, *Mephitis* (skunk). Lagomorpha: 15, *Sylvilagus* (cottontail rabbit); 16, *Ochotona* (pika). Perissodactyla: 17, *Equus* (zebra). Proboscidea: 18, *Loxodonta* (African elephant). Rodentia: 19, *Castor* (beaver); 20, *Tamias* (chipmunk); 21, *Spermophilus* (ground squirrel); 22, *Sciurus* (grey squirrel); 23, *Clethrionomys* (vole); 24, *Tamiasciurus* (red squirrel); 25, *Peromyscus* (mouse).

under such circumstances, selection will favour maturation at earlier ages. (This interpretation may also be consistent with an apparently similar relationship, pointed out by Lack[25], between age at first reproduction and patterns of mortality among families of birds.) At a more proximate level, nutrition levels may influence the correlations. High nutrition levels can result in early maturation[26,27] and decreased lifespan[28] within and among mammal species, for example, Columbian ground squirrel populations mature earlier and have shorter life expectancies when natural food resources are more abundant[18,19].

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