Neanderthals in western Europe probably existed at the same date as much more modern-looking populations in south-west Asia (as at Skhūl and Qafzeh) and perhaps in Europe (as at Velika Pećina, Brno, Mladeč (*contra* ApSimon) and Hahnöfersand)[10–16]. No well preserved fossils which are demonstrably intermediate in significant characters between Neanderthals and anatomically modern humans have been described from either of these areas. The fact that some of the earliest anatomically modern hominids in these areas display characters such as robust brow-bridges and large teeth does not necessarily imply that they evolved from Neanderthal ancestors, as such characters are probably merely plesiomorphous (primitive) for *Homo sapiens* generally, and therefore have no phylogenetic relevance in these comparisons. As European and south-west Asian Neanderthals share suites of characters which are apparently autapomorphous (uniquely derived), it is these traits which are significant in any analysis of relationship between Neanderthal and early anatomically modern hominids, as is the presence or absence of traits considered autapomorphous for anatomically modern hominids. With very few exceptions such characters do not cross the morphological division between the Neanderthal and early anatomically modern groups[10–13,17].

The many characters shared between the European and south-west Asian Neanderthals and the many different characters shared between the early anatomically modern fossils of the same two areas mitigates against any evolutionary scheme which posits only *in situ* evolution between Neanderthals and anatomically modern humans in each area[10–13,17]. Evidence now suggests that Eurasian Neanderthals were temperate or cold-adapted forms, whereas the early anatomically modern humans of the same area were not. This implies that a model involving at least some gene flow from outside this area at the time of the first appearance of anatomically modern humans is more appropriate[18].

Thus we agree with ApSimon that, pending further description, the Saint-Césaire Neanderthal disproves the idea of an *in situ* hominid transformation in Europe at a Mousterian/Upper Palaeolithic interface. Instead, the polyphyletic origins of the Upper Palaeolithic in Europe may be matched by a dichotomy, at least, in the morphology of the hominids that produced it. The wealth of new evidence that is now accumulating, together with the promise of a more reliable chronological framework, will allow us to monitor more precisely the events of this key period in prehistory. We would also argue that more sophisticated models are needed than those which posit either mass extinction, hybridization or rapid *in situ* evolution of Neanderthal hominids at the time of the appearance of anatomically modern humans in Europe.

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APSIMON REPLIES TO STRINGER *ET AL.*—Concerning Bacho Kiro: If the industry corresponds to accepted definitions of 'Aurignacian', 43,000 BP would be a surprising date, as it would be ~10,000 yr older than dates obtained elsewhere.

We can agree that Velika Pécina, Brno and Mladeč may be of the same order of age as Saint-Césaire, subject to the uncertainties of present chronologies, but not that they might be substantially older, as was implied by the traditional interpretation of Würm I-II-III in central Europe.

I do not believe that the case has yet been made for the previous evolution of the Aurignacian. Interstratification of Aurignacian and Châtelperronian raises the possibility that they are functionally differentiated variants of the same tradition. Blade technology is not substantially more important in these early European 'Upper Palaeolithic' industries than in some Mousterian industries and development from the Mousterian lithic tradition seems to be their most likely origin.

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Why do jackals help their parents?

BLACK-BACKED jackals (*Canis mesomelas*) sometimes stay with their parents and help them raise subsequent litters. Based on a positive correlation between the number of pups surviving in a litter and the number of adults (parents plus helpers) in the family unit, Moehlman[1] concluded that pup survivorship is enhanced by the presence of helpers. Unfortunately, her analysis contains errors of calculation and interpretation that seriously weaken this conclusion. Here I correct those errors and present an alternative explanation for her results.

First, an error in the calculation of the correlation coefficient (between 'pups surviving' and 'number of helpers') markedly inflates the statistical significance of the result. From the data shown in Moehlman's Fig. 1, I calculate $R_s = 0.58$ (Spearman rank correlation coefficient; $P < 0.05$) and not $R_s = 0.967$ ($P < 0.01$) as reported. Although the correlation coefficient is still statistically significant, factors other than the number of jackal helpers in a family unit obviously contribute substantially to the observed variation in the number of pups that are raised from a litter.

Second, it is stated[1] that "an adult helper gains more (yield 1 pup per adult) by being a helper of its parents than by finding a mate and raising its own pups aided only by its mate (yield $\frac{1}{2}$ pup per adult)." For both parents and helpers, however, the relevant measure of reproductive success is the total number of pups that survive from a litter, and not the number that survive per adult. As long as a helper's parents stay mated, the coefficients of relatedness between the helper and its siblings in subsequent litters, and between the parents and their new offspring, are the same (that is, $r = \frac{1}{2}$). Therefore, a helper realizes the same 'reproductive success' whether helping its parents increase their litter size by n pups or raising n pups itself (with its own mate). The calculation of 'yield per adult' always underestimates the benefit that accrues to helpers when they contribute to the increased reproductive success of their parents. For example, in terms of yield per adult, a jackal seems to increase its reproductive success by only $n/3$ when helping its parents raise an additional n pups, but it increases its reproductive success by $n/2$ by raising its own n pups. In fact, both of these increases in reproductive success should be the same.

Data shown in Moehlman's Fig. 1 can now be used to assess the reproductive consequences of becoming a helper instead of mating. The slope of the geometric mean regression[2] of 'pups surviving' over 'number of helpers' ($y = 0.9 + 1.67x$; $n = 15$) is an estimate of the

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