Additional evidence for our hypothesis comes from an examination of morphology and behaviour of the living species. In social structure and craniofacial morphology, the orang-utan is an odd animal. The sex difference in the body size of orang-utans is among the greatest of all primates[21,22]. This is usually explained on the basis of aggressive competition between adult males[20,21,23-27], even though sexual selection is not clearly indicated by field observations. For example, Horr[24] admits that "direct evidence for male competition in the form of dominance or aggressive encounters is limited" and Leutenegger and Kelley[21] observe that their acceptance of intrasexual selection is "partly based on negative evidence for other selective factors". While allometry[28], bioenergetic and reproductive constraints on female size[29] or a maximisation of food resources by niche separation due to body size[22] remain possible factors, it is also plausible that the sex difference and large body size of orang-utans are remnants ('heritage' characters) of a more terrestrial pattern[30] (accompanied perhaps by a different type of social structure, of which we can know nothing).

Several aspects of dental and craniofacial morphology differ from those seen in most primate arboreal herbivores. Orang-utans have high crowned, low cusped (bunodont) cheek teeth with marked occlusal wrinkling, different from those of other catarrhine primates which exhibit well-defined cusps and shearing facets[31,32]. The enamel on the occlusal surfaces of their cheek teeth is relatively and absolutely thicker than in any other species of living primate yet examined[33]. Enamel thickness is relatively thicker on the occlusal surfaces of species of *Macaca, Papio, Theropithecus* and *Cercopithecus (C. aethiops)* than of species of *Colobus, Presbytis, Alouatta, Ateles, Pan* or *Gorilla*[34]. This appears to separate species with potentially more abrasive (omnivorous) diets from those with less abrasive (folivorous, frugivorous) diets. *Pongo* is the apparent exception[33,34].

The mandibular condyle of the orang-utan is high above the occlusal plane and the ramus forms a relatively acute angle with the mandibular corpus. The dental arches are relatively forward in position and tilted up[35]. Although Biegert[35] suggests that these changes parallel those seen in *Alouatta* and can be explained by hyolaryngeal specialisations, Hershkovitz[36] argues that *Alouatta* craniofacial morphology has nothing to do with hyoidal hypertrophy, but rather with masticatory adaptations to herbivorous browsing, and Zingeser[37] confirms that several of these features are characteristic of folivory in New World monkeys.

Living orang-utans therefore have unusual (for an arboreal frugivore) dental and craniofacial adaptations. This suggests either that we do not yet have a clear understanding of the relationships between diet and anatomy in living arboreal or frugivorous primates (which is a distinct possiblity), or that ancestral orangs were not arboreal frugivores. What they were we cannot say, but that they have retained a number of characteristics from ancestors adapted to doing very different things seems a real possibility.

Consideration of a terrestrial phase in orang-utan evolution goes hand-in-hand with a growing awareness within the past 5 yr that Miocene hominoid evolution is much more complex than envisioned 15 yr ago[38]. Typical Neogene hominoids (including our hypothetical Pliocene orang-utan) were probably neither forest nor savannah dwellers, but woodland creatures. Most of these species did not resemble living hominoids. Whether some of them are ancestral to living hominoids, or whether they all became extinct without issue, it seems to us that an even wider range of possible evolutionary scenarios must be considered by students of hominoid evolution than was the case a few years ago. Selecting the correct one is probably not possible given the still poor state of the hominoid fossil record. It will not be made easier unless we realise that past hominoid morphologies, distribution and habitats were probably rather different from those of today; that we should not cling too tenaciously to principles of irreversibility or parsimony; that parallelism in hominoid evolution may have been much more widespread than some of us have thought; and that we should intentionally begin searching for more heterodox explanations.

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Dispersal and the sex ratio

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It has been shown by Fisher that a 1:1 sex ratio should be evolutionarily stable as there would otherwise be a frequency-dependent advantage to the rarer sex[1]. Hamilton pointed out that Fisher's argument depends on the assumption of population-wide random mating, and showed that a female-biased sex ratio was expected in a model in which mating occurred within small local subgroups before population-wide dispersal of mated females. We consider here the sex ratio under some other models of dispersal in a geographically structured population.

For simplicity we consider one-dimensional models, and we suppose that the habitat consists of $2M + 1$ discrete patches placed round a circle and labelled $-M, \ldots, -1, 0, 1, \ldots, M$. In our first model we suppose that there is one mated pair in each patch, which produces k offspring and then dies. Male and female offspring disperse a distance j with probabilities p_j and q_j, respectively ($-M \le j \le M$). After dispersal, one pair establishes itself in each patch in the next generation, the male and female partners being chosen at random from the individuals in the patch.

To find the sex ratio which is evolutionarily stable, suppose that the pair in patch 0 has sex ratio s (producing sk sons and $(1-s)k$ daughters), while all other pairs have sex ratio r. To see whether the pair in patch 0 is at a selective advantage to other pairs, let the genes of this pair at a typical autosomal locus be coloured red. We shall now calculate then expected number of red genes in mated pairs in the next generation.

After dispersal there are $r(1-p_i)k$ males with no red genes and sp_ik with two red genes in patch j, with corresponding expressions for females. The expected number of red genes in the successful pair in patch j is

$$\alpha_i = \frac{2sp_i}{sp_i + r(1-p_i)} + \frac{2(1-s)q_i}{(1-s)q_i + (1-r)(1-q_i)} \qquad (1)$$

The total expected number of red genes in successful pairs in the next generation is $\alpha = \Sigma \alpha_i$. Writing $\varepsilon = (s-r)$ and then expanding α in a Taylor series we find that

$$\alpha = 4 + \varepsilon \left\{ \frac{2}{r}(1 - \Sigma p_i^2) - \frac{2}{(1-r)}(1 - \Sigma q_i^2) \right\} \qquad (2)$$

to order ε. The evolutionarily stable sex ratio is the value of r which makes the coefficient of ε zero, given by

$$\frac{(1-r)}{r} = \frac{1 - \Sigma q_i^2}{1 - \Sigma p_i^2} \qquad (3)$$

[The above argument is only approximate as it does not track the frequency of a gene determining sex ratio from one generation to the next and since we have only sought the value of r which is at a selective advantage over any mutant sex ratio s present in a single patch. We believe that the result is qualitatively correct, but a more exact analytical treatment of this problem would be valuable.]

Equation (3) can be interpreted as meaning that the evolutionarily stable sex ratio is biased in favour of the sex which disperses more widely and/or more evenly. The mechanism underlying this effect is the competition between siblings of the same sex which has been built into the model; siblings of the sex which disperses further (and/or more evenly) are less likely to be in the same patch after dispersal than siblings of the other sex. The equilibrium sex ratio in equation (3) is the point at which the advantage of producing offspring of the sex with less sibling competition is balanced by the disadvantage of producing offspring of the commoner sex. This mechanism also accounts for the female-biased sex ratio in Hamilton's model[2,3], as in this case there is competition between brothers for mates but no competition between sisters.

The above model assumes that mating occurs after dispersal (in contrast with Hamilton's model) and that individuals disperse independently of each other. The second assumption is more likely to be satisfied in animals dispersed passively by external physical forces (for example, marine plankton) than in animals which can control their own movement and can therefore mitigate the effect of competition for space by spacing themselves out. The assumption of independent, passive dispersal is also likely to be appropriate for plants; we shall now extend the model to the problem of resource allocation to male and female functions in hermaphrodite annual plants.

As before we suppose that the habitat consists of discrete patches round a circle. One plant grows in each patch, and each plant produces both pollen and seed. Pollen disperses a distance j with probability p_i, the seed in any patch is fertilised at random by the pollen arriving there, and then disperses a distance j with probability q_i. Of the seed arriving in a patch, exactly one is successful in establishing itself as a mature plant in the next generation.

We suppose that a plant can produce either N pollen grains or n ovules or any linear combination of rN pollen grains and $(1-r)n$ ovules $(0 \leqslant r \leqslant 1)$. The parameter r is the proportion of its resources allocated to male as opposed to female functions, and is the analogue of the sex ratio in dioecious organisms. To find the evolutionarily stable value of r, suppose that a plant in a single patch has a sex ratio s while all other plants have a sex ratio r. Using the argument invoked above, we find that the evolutionarily stable sex ratio is given by

$$\frac{1-r}{r} = \frac{1 + p_0 - \Sigma q_i^2 - \Sigma p_i q_{i-i} q_i}{1 - \Sigma p_i^2} \qquad (4)$$

This is a rather complicated expression, but it is clearly possible to obtain either a male-biased or a female-biased sex ratio, depending on the relative dispersal distance of seed and pollen. In general, we may suppose that pollen dispersal has a mode at zero, so that $p_0 \geqslant p_i$. In this case

$$\Sigma p_i q_{i-i} q_i \leqslant p_0 \Sigma q_{i-i} q_i = p_0$$

so that

$$\frac{1-r}{r} \geqslant \frac{1 - \Sigma q_i^2}{1 - \Sigma p_i^2} \qquad (5)$$

Comparing equations (3) and (5), we conclude that there is a tendency for the sex ratio to be biased towards male or female accordingly as pollen or seed disperses more, but that in addition there is some bias towards the female (seed production). This can be attributed to the fact that male (pollen) dispersal occurs in the gamete stage before fertilisation, while female (seed) dispersal occurs in the zygote stage after fertilisation.

The above argument places no restriction on selfing. If selfing is avoided, then effective pollen must come from a different plant. The argument goes through as before if we consider only effective pollen, and equation (4) remains valid if we replace p_i by the truncated distribution p_i', defined by

$$p_0' = 0$$
$$p_i' = p_i/(1-p_0), \quad j \neq 0$$

In general, the sex ratio will be slightly more male-biased with avoidance of selfing than if selfing is allowed.

We conclude that differential sibling competition is an important factor in determining the equilibrium sex ratio in a geographically structured population, and can lead to a bias in favour either of males or of females. It has been suggested[4] that sibling mating is a factor which determines departures from a 1 : 1 sex ratio in this situation, but in our view[5] sibling mating is only important as an indicator of the competition between brothers for mates. It is not possible to infer a general relationship between the amount of sibling mating or inbreeding and the sex ratio without considering the means by which inbreeding is caused.

Empirical evidence of the effect of sibling competition on the sex ratio has been found in the bushbaby *Galago crassicaudatus*[6]. There seems to be a male-biased sex ratio, which can be attributed to competition between female kin (sisters, and mothers and daughters) for local limiting resources of high quality food required by pregnant and nursing females.

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