

the Y. Likewise, X chromosomes spend 2/3 of their time in females, and should be selected to produce female-biased sex ratios. Hamilton marshaled the evidence supporting biased sex ratios caused by genes on the sex chromosome. Because autosomes continue to favor a balanced sex ratio, the important implication is that individuals do not always have indivisible interests — instead there can be conflict between contending sets of selfish genes.

This particular bias will not occur in the haplodiploid Hymenoptera because sex is determined by ploidy rather than by special chromosomes, although maternally transmitted parasites can cause their preferred expected female biased sex ratios. But there is a spectacular example of a selfish sex ratio distorter in the parasitoid *Nasonia vitripennis* studied by Jack Werren. Called PSR for paternal sex ratio, it causes fathers to have excess sons, which ought to be puzzling because haplodiploid males cannot normally have sons (if the egg is fertilized, it becomes diploid and hence a daughter). It works because PSR is inherited on a B chromosome. B chromosomes are small inessential chromosomes that exist in one or more copies in some cells. They do not segregate neatly like autosomes (or A chromosomes) but copies do get transmitted in less regular fashion to offspring. When one or more copies of this B chromosome are transmitted via sperm, they cause the father's A chromosomes to condense into chromatin and be lost. What remains then, are the maternal autosomes, whose haploid state directs the development of a male, along with the successfully transmitted B chromosome. Models that incorporate the details of PSR's effects into sex ratio theory show that PSR can spread only when sex ratios are otherwise female-biased, but that it can spread at all is remarkable. It is an ultimate selfish element; in each generation, the B chromosome succeeds only by completely destroying its fellow

traveler A chromosomes and joining a new set.

Conclusion

Düsing's basic insight into how sex ratios evolve has been developed into a wide-ranging and successful theory that predicts both the conventional 1:1 sex ratios and numerous extraordinary ones. A surprising amount of the evidence has come from haplodiploid Hymenopteran insects, though many of these effects can also be found in other organisms, even where chromosomal sex determination mechanisms would seem to lock them into 1:1 sex ratios. Most important, this seemingly arcane topic has played very prominent roles in the development of game theory, in the debate over group selection, in supporting kin selection and parent-offspring conflict, and in the field of within-organism conflict. Many biological advances will require high tech instrumentation and deeper probing into molecular mechanisms of model organisms. But there remains room for a good theory, for adroit choice of non-standard organisms, and even for simple counting.

Further reading

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Road crossing in chimpanzees: A risky business

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During group movements, monkeys may cooperate to reduce the risk of predatory attacks through adaptive spatial patterning. For example, adult males move toward the front of the group when travelling towards potentially unsafe areas such as waterholes, and bring up the rear when retreating [1–4]. Comparable data on progression orders in moving groups of great apes are lacking.

We hypothesised that chimpanzees evaluate risk when crossing roads, and draw on a phylogenetically-old principle of protective socio-spatial organization to produce flexible, adaptive and cooperative responses to risk. Progression orders were studied in the small community of chimpanzees (*Pan troglodytes verus*) at Bossou, Guinea, as they crossed two roads, one large and busy with traffic, the other smaller and frequented mostly by pedestrians. We found evidence that the degree of risk, estimated in terms of the width of roads and the amount and type of traffic they carried, influenced the waiting time before crossing the roads and the order in which the chimpanzees crossed.

The home range of the 12-strong chimpanzee community at Bossou (7° 39' N; 8° 30' W), covers about 15 km² of mixed forests surrounded by abandoned and cultivated fields. It is dissected by a narrow road (3 m wide) which is used by pedestrians, and a recently widened larger road (12 m wide at the crossing point), which carries trucks, cars, motorbikes and pedestrians. The Bossou chimpanzees have to cross

both roads regularly to reach foraging sites in their fragmented home-range and typically cross at specific points that the group has used for decades. There is forest up to the edge of the roads, the latter being separated by secondary forest and plantations. Two observers recorded progression orders in both directions (Figure 1 and Supplemental data); the first chimpanzee to scan the road was termed first individual to scan. The latency between arrival of the first individual to scan and the last group-member to cross the forest-road edge was termed the waiting time. During the study (January–April 2005), the group contained three adult males, five adult females, three juveniles and one infant [5]. The social rank of the Bossou males has varied over the years, but during this study the relative statuses of the alpha male (Yolo), the second male (Foaf) and the third male (Tua) were stable [5].

Waiting time was analysed for 19 combined road-crossings in which the same group members crossed the two roads. The analysis of road-crossing progressions used data from 28 mixed-group progressions (17 small and 11 large road crossings), with mean group size 10.6 individuals (SD 2.1). Chimpanzees waited longer before crossing the large road than the small road (means: 180 versus 24 seconds; Wilcoxon test: $T = 5$, $N = 19$, $p < 0.01$). Presence or absence (either auditory or visual) of people had no effect on waiting time on the small road (Mann-Whitney test: $Z = -0.168$, $N = 19$, $p = 0.905$), but people ($Z = -2.059$, $N = 19$, $p = 0.043$) and vehicles ($Z = -2.043$, $N = 19$, $p < 0.01$) increased waiting time on the large road. A significant effect of direction of travel emerged concerning the large road ($Z = -2.083$, $N = 19$, $p = 0.041$); the same effect for the small road approached significance ($Z = -1.915$, $N = 19$, $p = 0.062$): the chimpanzees took longer to move from forest to more open areas than vice-versa.

When all three adult males were present, one led more



Figure 1. How do chimpanzees cross roads?

Dominant individuals act cooperatively with a high degree of flexibility to maximise group protection.

often than expected (18 of 28 progressions; binomial test: $p < 0.001$) and was more likely to scan the road prior to crossing (binomial: $p < 0.001$). In contrast, an adult male did not occupy the rearmost position more frequently than expected. As the

second- and third-ranking males frequently led, the frequency of the alpha male being last was tested; this was highly significant (Bonferroni correction included; binomial: $p < 0.01$).

Figure 2 summarizes the progression order data. The

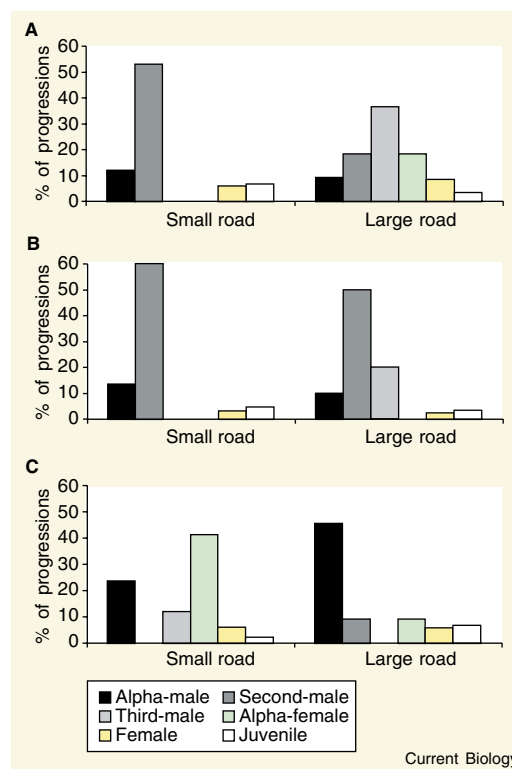


Figure 2. Summary of progression order data.

The percentages of progressions in which the three males, the alpha female and the average non-alpha female and juvenile were: (A) first to cross; (B) first to scan the road; and (C) last in the progression on the two roads (infant excluded from analysis).

first individual to scan was the first to cross the small road in 100% of cases, compared to 70% for the large road. On the large road the second-ranking male sometimes continued scanning while the elderly third male and alpha female took up the lead on the large-road progressions. The alpha male increased his rearward presence on the large road, whereas the alpha female showed a dramatic reduction in frequency of being last; in other words when the degree of risk increased she took up a more forward position. Additionally, when the alpha male was present in mixed-group progressions containing one other adult male ($N = 6$, mean group size: 6.7), he was first to scan and cross in 50% of large road-crossings and last in only 33%. This suggests that his rearward position at other times was not due to fear.

Modern Bossou chimpanzees encounter predators infrequently [6], and although humans themselves are not 'predators' of these chimpanzees, we propose that road-crossing, a human-created challenge, presents a new situation that calls for flexibility of responses by chimpanzees to variations in perceived risk.

Crossing the large road and leaving forest for open areas are potentially risky situations for chimpanzees, reflected in increased waiting time. During dangerous excursions certain positions may be more advantageous than others, depending upon age and sex [4]. Adult males, less fearful and more physically imposing than other group members, take up forward and rearward positions, with adult females and young occupying the more protected middle positions.

As hypothesised, the Bossou chimpanzees employ a phylogenetically-old mechanism to adapt to a more recent dangerous situation. However, the positioning of dominant and bolder individuals, in particular the alpha male, changed depending on both the degree of risk and number of

adult males present; dominant individuals act cooperatively with a high level of flexibility to maximise group protection. At a proximate level each individual may have preferred and recognised positions; however, it is unknown whether positioning is individual- or rank-specific. Data on progression orders of other great ape populations are required, and would help shape hypotheses about emergence of this aspect of hominoid social organisation.

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Supplemental data

Supplemental data, with a video-clip of the Bossou chimpanzees crossing the large road, are available at <http://www.current-biology.com/cgi/content/full/16/17/R668/DC1/>

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Minimal plastid genome evolution in the *Paulinella* endosymbiont

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It is an enduring mystery how organelles were first established in eukaryotes. A key player in this saga is the thecate amoeba *Paulinella chromatophora* which over 100 years ago [1] showed naturalists that once free-living cells could exist as endosymbionts [2]. This species has the honor of being the only known case of an independent primary (cyanobacterial) plastid acquisition [3,4] and is a model for understanding plastid establishment. The *Paulinella* plastid, often referred to as the cyanelle, retains typical cyanobacterial features such as peptidoglycan and phycobilisomes, but is considered to be a *bona fide* endosymbiont because it is no longer bound by a vacuolar membrane but lies free in the cytoplasm, its number is regulated, suggesting genetic integration, and it cannot be cultured outside the host [5–7]. *Paulinella* is, however, difficult to culture, and so it has resisted detailed molecular biological investigation. Here we took advantage of a Lambda DASH II phage library made from limited amounts of *Paulinella* total genomic DNA to reconstruct the evolutionary history of its recently established plastid [3]. Our data show the *Paulinella* plastid genome to have characteristics typical of cyanobacterial, not plastid genomes.

The *Paulinella* library was screened with the highly conserved *psbA*, *psbC* and 16S rDNA plastid genes from the glaucophyte *Glaucocystis nostochinearum*. Two plastid inserts of 9.4 kb and 4.3 kb were obtained by this approach; a third, 5 kb fragment has already been described [3]. Because the *P. chromatophora* culture is not axenic (see [3]), we