

cooperative interaction between two elements in separate control regions of each *var* gene (the 5'-flanking region and the intron). This finding should help to clarify the mechanisms by which parasites coordinate the silencing and activation of *var* genes that are responsible for antigenic variation in malaria.

The proteins (PfEMP1) encoded by the *var* genes enable red blood cells infected with *P. falciparum* to adhere within the circulatory system, thereby avoiding destruction by the spleen. Different PfEMP1 forms can attach to different host molecules,

leading to patterns of sequestration that produce disease complications such as cerebral malaria or the severe malaria of pregnancy<sup>6,7</sup>. Because the exposed PfEMP1 molecules are subject to antibody attack during infection, *P. falciparum* parasites produce subpopulations with antigenically diverse PfEMP1 forms which must be continually chased by the immune response. The underlying switches in *var*-gene expression that result in this process of antigenic variation have yet to be understood.

Silent *var* promoters become transcriptionally active when removed from their chromosomal context<sup>8</sup>, suggesting that further control elements in the intact *var* gene are required to control or silence expression. Possible locations for such control elements are in the conserved *var* introns, which separate the two exons of all *var* genes and have sequences that are found in many heterogeneous sterile transcripts in erythrocyte-stage parasites<sup>9</sup>.

To test whether *var* introns function in gene control, we inserted a representative intron sequence (*int*) into two different plasmids containing a luciferase (*luc*) reporter driven either by a *var* promoter sequence or by a promoter sequence from the unrelated gene *hrp3*, which encodes histidine-rich protein 3 (pVLH and pHLH, respectively; Fig. 1a). Transfection experiments with pVLH and pVLH/*int* indicated that the presence of *int* downstream of *luc* strongly repressed the luciferase signal (Fig. 1b, left), irrespective of *int* orientation. In contrast, the presence of *int* in the pHLH/*int* plasmid caused no detectable change in the reporter activity (Fig. 1b, right). The fact that the *var*, but not the *hrp3*, promoter was affected indicates that *int* repression is specific and occurs by cooperative action with the upstream *var* 5'-flanking region.

These initial experiments revealed strong repression, but not complete silencing, of *luc* expression from pVLH/*int* (Fig. 1b). Transition through S phase of the cell cycle is known to be required for the assembly of silent chromatin structures in other organisms<sup>9</sup>. Because parasites continually take up DNA during their growth in plasmid-loaded erythrocytes<sup>10</sup>, our experiments may have included heterogeneous populations of plasmids acquired before and after S phase, leading to incomplete silencing of the *var* promoter.

To test this possibility, we measured *luc* expression from homogeneous plasmid populations before and after transition through S phase. Assays done 18 h after invasion of plasmid-loaded erythrocytes

(before the onset of S phase) confirmed that *luc* was expressed without repression (Fig. 1c, left). After their maturation to mature schizont stages, we separated transfected parasites from plasmid-loaded erythrocytes using Percoll/sorbitol gradients. Returning these parasites to fresh cultures with plasmid-free erythrocytes eliminated further plasmid uptake after re-invasion and ensured that all plasmid DNA in the parasites had been through S phase. Complete reporter silencing from pVLH/*int* was then evident (Fig. 1c, right). We detected no silencing in control transfections with the original pVLH, or with a pVLH/*hsp* construct in which the *int* sequence was replaced with a *P. falciparum hsp86* intron of similar size (Fig. 1c, right).

The regulatory elements and S-phase-dependent silencing we identify here implicate cooperative DNA-binding complexes and modifications of chromatin structure in the control of *var*-gene transcription. Experimentally manipulable plasmid systems that incorporate mechanisms for *var* control may offer a useful approach by which to identify and characterize these complexes.

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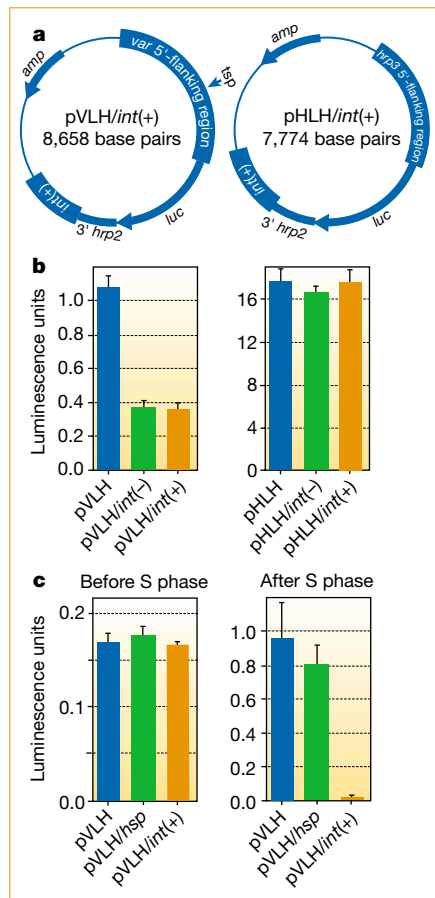
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**An unusual social display in gorillas**

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Our claim that the manipulation of water for communicative means by western lowland gorillas had not previously been described in any wild primate was incorrect: we were unaware of observations of a small number of male chimpanzees in a community in Tanzania throwing stones into streams<sup>1</sup>, apparently for the purpose of intimidation.

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**Figure 1** The role of cooperative control elements in S-phase-dependent silencing of *var* expression. **a**, Maps of pVLH/*int*(+) and pHLH/*int*(+). Plasmids pVLH/*int*(+), pVLH/*int*(-), pHLH/*int*(+) and pHLH/*int*(-) were constructed from the pVLH (pVLH-1) and pHLH (pHLH-1) plasmids<sup>8</sup> by inserting a *var* intron (*int*) in the (+) or (-) orientation downstream of the 3'-flanking region of the *hrp2* gene. Plasmid pVLH/*hsp* was obtained by inserting the intron sequence from the unrelated *P. falciparum hsp86* gene into pVLH at the same position. GenBank accession numbers for pVLH/*int*(+), pVLH/*hsp* and pHLH/*int*(+) sequences are AF338824, AF379854 and AF338825, respectively. The transcription start point (tsp) for *var* is indicated. **b**, Luciferase activity from *P. falciparum* parasites after spontaneous transformation with original and modified pVLH and pHLH plasmids. Assays were carried out after cultivation of parasites for 72 h in the presence of plasmid-loaded erythrocytes<sup>10</sup>. **c**, Luciferase activity from homogeneous plasmid populations before and after S phase in synchronized transfected parasites. Experiments were carried out in triplicate and repeated on at least three separate occasions. Error bars indicate calculated standard deviations.

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tions. The submergence must therefore have involved processes other than a progressive rising of sea level and isostatic lowering of land (which together account for less than 3 m of vertical offset since AD 700).

Although wave damage is known to have occurred on the Levantine margin in AD 746 (possibly in AD 743 or 745)<sup>9</sup>, no earthquake activity is recorded in Egypt during this period<sup>10</sup>. We attribute Canopic riverbank failure to local weighting by turbulent, sediment-rich Nile waters being suddenly added upon the soft, organic-rich, physically unstable muds. Sudden failure of the low-elevation margins (less than 1 m) of the river banks probably allowed water to flow over them, leading to an eastward lateral shift of the river channel.

Similar processes have occurred at the mouth of the modern Mississippi river in the United States<sup>11</sup>. Like the Canopic branch of the Nile, this is in a relatively stable area; sediment failure during Mississippi flooding includes liquefaction, slumping on slopes of less than one degree, and diapirism near the river mouths.

Our investigation in Abu Qir Bay indicates that structural failure of the cities that were once positioned on the river banks,

and their submergence to depths of more than 5 m at and near the Canopic mouth, are best explained by sediment failure triggered by flooding of the Nile as recently as 1,250 years ago.

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Animal behaviour

## An unusual social display by gorillas

We have observed wild western lowland gorillas (*Gorilla gorilla gorilla*) using water to generate spectacular 'splash displays'. Most of these displays were made by silverbacks in an agonistic context, and we propose that they are primarily linked to the intimidation of potential rivals for female acquisition. This unusual behaviour may have developed only in gorillas that visit open swampland, where visibility greatly exceeds that encountered in the forest and highly visual, long-distance displays are therefore of value.

Almost nothing is known about the social behaviour of western lowland gorillas because of poor observation conditions and

difficulties of habituation in dense forest. But the discovery that large numbers of gorillas feed in open, swampy clearings (bais) in the forest of northern Congo means that their social interaction can be investigated.

Display behaviour incorporating objects in the environment occurs in agonistic encounters in all ape species<sup>1</sup>, but manipulating water for communication has not been described in any wild primate and, with the possible exception of elephants, may be unique among terrestrial mammals.

We observed 124 gorillas over 32 months at the 12.9-hectare 'Mbeli Bai'. Gorillas were visible for 27% (1,681 h) of the time that we were present at the clearing. Ninety splash displays, representing 57 independent bouts of social interaction, were produced by 19 individuals (4 unaffiliated, 'solitary' silverback males and 15 individuals from 9 groups). Ten display styles were seen, of which three were used in 75% of all displays. These were the 'body splash' (35% of displays), in which a gorilla runs or leaps into standing water of up to 1.5 m in depth (Fig. 1), and one-handed and two-handed splashes (40%), in which one or both arms are raised and then brought down forcibly, the open palms striking the water surface at a slight angle. Each of these three techniques generates large plumes of spray.

Of all splash-display bouts, 67% were produced in an agonistic context, 17.5% were made in play and 5% were directed towards other species; in 10.5% of cases the context was not evident. Silverbacks dis-

played the most frequently (68%), and almost exclusively in an agonistic context.

When the observed frequencies of splash bouts were compared with the expected frequencies (calculated from the proportion of visits made to the bai by each age/sex class), group silverbacks displayed twice as often as expected, whereas solitary silverbacks displayed more than four times as often. Solitary silverbacks were also the most frequent recipients of the display (six times more often than expected). Adult females, although they were the most frequently seen age/sex class, never produced splash displays and were rarely targeted.

Directly attracting the attention of females is not considered the prime purpose of splash displays, because solitary males displayed almost as frequently to other solitary males as to groups, and in more than half of these cases no females were in sight. The more likely purpose is to intimidate potential competitors for acquiring females.

Splash displays are an example of object-mediated behavioural plasticity in response to unusual circumstances. Although the three primary display styles resemble the dry-land charges and ground-slap displays seen in many gorilla populations, differences in context, execution and intra-dyad distance confirm that splash displays represent a distinct behavioural element in gorillas' visual-display repertoire.

The bai offers visibility of up to 500 m, which is never encountered by gorillas in the forest, and so long-distance visual displays are clearly expedient. In the wild, the only other record of splash display comes from western lowland gorillas at Maya Bai, 180 km from Mbeli (F. Magliocca, personal communication).

The paucity of data on western lowland gorillas has led to generalizations about their behaviour based on that of mountain gorillas (*G. beringei beringei*). But their feeding ecology is different<sup>2</sup>, and our findings indicate that their social behaviour is too. We anticipate that gorillas, maligned as cognitively poor cousins to the other great apes, will emerge from further bai studies as adaptable, innovative and intelligent creatures that exploit a complex environment<sup>3</sup>.

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**Figure 1** A solitary silverback performing a 'body splash' display at Mbeli Bai, Nouabalé-Ndoki National Park, Congo (Brazzaville).