TABLE I: Fits to the cumulative probability distributions.

Force (fN)	60 ± 5	78 ± 6	121 ± 9	183 ± 15
Looped				
$\tau(s)$	20.8 ± 0.3	22.5 ± 0.2	24.1 ± 0.3	24.8 ± 0.7
Unlooped				
$\tau_1(s)$	3.0 ± 0.2	4.0 ± 0.42	9.7 ± 0.4	14.5 ± 1
$\tau_2(s)$	31 ± 8	54 ± 10	91 ± 10	101 ± 6
c	0.77 ± 0.03	0.77 ± 0.02	0.74 ± 0.02	0.38 ± 0.03

of 10^{-19} J [11] and an operator region that spans $\sim$ 20 bp, the minimum force needed to remove the protein from the operator is $\sim$ 10 pN, which is several orders of magnitude greater than the tension we applied. It is clear then why the looped state is relatively insensitive to mechanical tension. On the other hand, the sensitivity of the looping rate to such small forces is quite striking and potentially rich in implications. Since the characteristic force that results from thermal fluctuations of ds-DNA is approximately 80 fN, and since DNA looping is a result of thermal fluctuations, femtonewton forces can clearly impact the loop formation process.

Quantitatively useful models of loop formation must explicitly consider the orientation of the operators along the DNA in the looped state, as the exact geometry of the loop matters significantly. Such theories were developed by Blumberg *et al.*[6] and, independently, by Yan *et al.* [7]. In this paper, we use the model developed by Blumberg *et al.* so begin by finding the difference in the force dependent contributions to the free energy between a looped and a stretched length of DNA: $\Delta F = F_L(f, \theta) - F_S(f)$. The kink angle θ is defined as the angle between the tangent vectors of the DNA at the operator sites of the protein-DNA complex. A relation for the excess contribution to the free energy as a function of kink angle, imposed on the DNA by the loop, is given by:

$$F_L = \frac{4f^{1/2}(1 - \cos(\theta/4))}{1 + 12f^{-3/2}(1 - \cos(\theta/4))/(1 + \cos(\pi - \theta))}, \tag{7}$$

where the free energy is in units of $k_B T$ and the force f is in units of the characteristic force for thermal fluctuations, $f_c = k_B T/l_p \approx 80$ fN.

An analytic relation for the free energy of a stretched segment of DNA is given by the