Writhe distribution of stiff biopolymers

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Motivated by the interest in the role of stiff polymers like actin in cellular processes and as components of biopolymer networks like the cytoskeleton, we present a statistical mechanical study of the twist elasticity of stiff polymers. We obtain simple, approximate analytical forms for the writhe distribution at zero applied force. We also derive simple analytical expressions for the torque-twist relation and discuss buckling of stiff polymers due to the applied torques. The theoretical predictions presented here can be tested against single-molecule experiments on neurofilaments and cytoskeletal filaments like actin and microtubules.

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I. INTRODUCTION

In recent years, statistical mechanics of semiflexible polymers has emerged as an area of active theoretical and experimental investigation. Interest in this direction has been triggered by single-molecule experiments designed to understand the role of elasticity of these polymers. Polymers abound in biological systems, for example the cytoskeleton which controls cell mechanics [1,2] is a biopolymer network; study of polymer elasticity is consequently of substantial relevance to biological research. The stiffness of a polymer is determined by a parameter β, the ratio of its contour length L to the persistence length L_P. In this paper we focus attention on rigid filaments; examples of such filaments are actin and microtubules which constitute the cytoskeletal structure and serve as tracks for motor proteins like myosin and kinesin [2,3]. Recently, filaments of intermediate rigidity like neurofilaments have also been studied in some detail [4]. It has been shown that the elastic properties of a single stiff filament are relevant to a study of the elasticity of cross-linked biofilament networks [2]. To understand the elastic response of the network, we need to understand the elastic properties of its constituent filaments. Twist elasticity of biopolymers has important relevance to biological processes; for example packaging of DNA in a cell nucleus a few micrometers across involves DNA-histone association which makes use of DNA supercoiling.

Experiments on single molecules can broadly be of two types—one can experimentally study the response of a semiflexible polymer molecule to forces and torques by measuring its extension as a function of applied forces and torques [5] or one can tag the ends with fluorescent dye [6,7] to determine the distribution of end-to-end distance. Such experiments furnish valuable information on the mechanical properties of single molecules and a theoretical model that can capture the essential features of the experimental results is needed; one such model is the wormlike chain model [8].

In this paper, we derive a simple analytical expression for the writhe distribution at zero forces. We study the elastic response of a stiff polymer to forces and torques applied at one of its ends and discuss the buckling of stiff polymers under applied torques. We also derive simple analytical expressions for the torque-twist relations. We consider boundary conditions in which both the ends of the polymer are *clamped*. The tangent vectors at the clamped ends are kept in a fixed direction. In an earlier study [9] a pure bend model for stiff polymers was developed. In a stiff polymer, the tangent vector never wanders too far away from the north pole of the unit sphere of directions. We refer to this approximation as the paraxial approximation. This approximation has been previously used to study the elasticity of twist-storing flexible stretched polymers [10–13] in the paraxial wormlike chain (PWLC) model. For stiff polymers, a convenient and accurate analytical approximation is well motivated because a numerical scheme that had been developed earlier in Ref. [14] to study semiflexible polymers has a limitation in describing stiff polymers due to convergence problems.

The mean values of the experimentally measurable physical quantities depend on the choice of ensemble [15], an effect of the finite-size fluctuations, which are entirely absent in the elasticity of a classical rod. For example, the qualitative features of the force-extension curves in the constant force ensemble differ distinctly from those in the constant extension ensemble [16–18]. In this paper, we remain throughout in the Gibbs ensemble, where the applied forces and torques are held fixed, and we measure the mean extension and writhe, respectively.

The organization of this paper is as follows. We first derive simple analytical forms for the partition function with the tangent vector at both the ends fixed in the direction of the applied force. We develop simple analytical expressions for the writhe distribution at zero pulling force; this is the central result of our paper (Fig. 1). We also study the mean

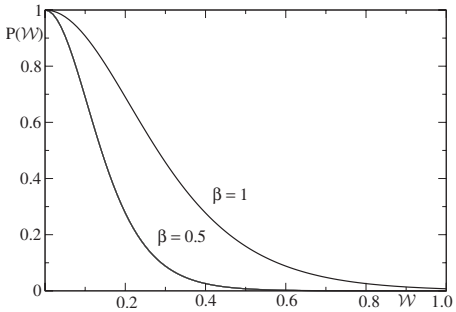

FIG. 1. Normalized writhe distribution for the boundary condition in which the tangent vectors at both the ends of the polymer are held fixed for $f=0$ and $\beta=0.5,1$. Larger values of the average link (or writhe) are suppressed for the smaller value of β.

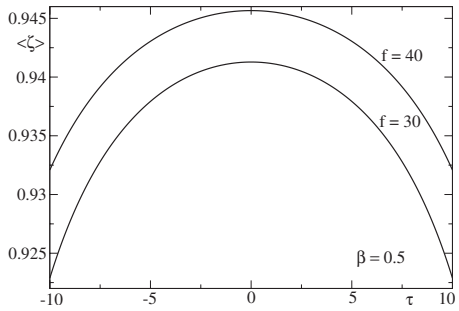

FIG. 2. Mean extension vs torque τ for β=0.5 and f=30,40 for a setup with both ends clamped.

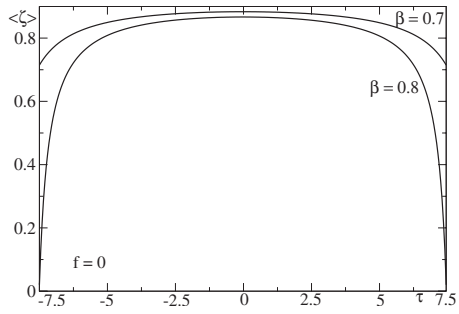

FIG. 4. Buckling of the stiff polymer for f=0 and β=0.7,0.8 with the tangent vectors at both ends of the polymer held fixed.

extension of the polymer in response to applied forces and torques and display the hat-shaped curves (Figs. 2 and 3); we study the buckling phenomenon in analogy with the classical Euler buckling phenomenon in thin rods and the consequent breakdown of the paraxial approximation (Fig. 4). Finally, we conclude the paper with derivation of simple analytical expressions for the torque-twist relation (Fig. 5).

II. THE PARAXIAL HAMILTONIAN AND THE PARTITION FUNCTION

Our starting point is the wormlike chain (WLC) model in which the polymer is modeled as a framed space curve $\mathcal{C}=\{\vec{x}(s),\hat{e}_i(s)\}$, $i=1,2,3$, where $0\leq s\leq L$ is the arc-length parameter along the curve. The unit tangent vector $\hat{e}_3=d\vec{x}/ds$ to the curve describes the bending of the polymer while the twisting is captured by a unit vector $\hat{e}_1$ normal to $\hat{e}_3$; $\hat{e}_2$ is then fixed by $\hat{e}_2=\hat{e}_3\times\hat{e}_1$ to complete the right-handed moving frame $\hat{e}_i(s)$, $i=1,2,3$.

The evloution of the moving frame is described with respect to a reference frame $\{e_i^0\}$ $(i=1,2,3)$ where $\{e_3^0\}$ points along a constant direction which we choose to call the z axis. The moving frame is obtained from the reference frame by the application of an element of the rotation group $\mathcal{R}(s)$ that is parametrized by the Euler angles $\{\phi,\theta,\psi\}$. The rate of change of the moving frame along the curve can be measured by its "angular velocity vector" $\mathbf{\Omega}$, whose components are given by $\Omega_i=\mathbf{\Omega}\cdot\hat{e}_i$. The components of the angular momentum can be expressed in terms of the Euler angles [10]. The statistical physics of such twist-storing polymers has been studied in detail [10,11,19]. Here we briefly outline the derivation of the relevant Hamiltonian for the sake of completeness; the details can be found in the above references. The energy $\mathcal{E}[\mathcal{C}]/k_BT$ of a configuration of the polymer is a sum of contributions coming from its bending and twisting modes. In units of k_BT, the bending and twist energies are given by

$$E_{\text{bend}}=A/2\int_0^L(\Omega_1^2+\Omega_2^2)ds=A/2\int_0^L(d\hat{t}/ds)^2 \qquad (1)$$

and

$$E_{\text{twist}}=C/2\int_0^L\Omega_3^2ds, \qquad (2)$$

respectively. The potential energy associated with stretching is

$$E_{\text{stretch}}=-\hat{e}_3\cdot\vec{F}/k_BT=-\int_0^L ds\cos[\theta(s)]F/k_BT \qquad (3)$$

and that due to the torsional constraint is

$$E_{\text{torsion}}=-2\pi\tau\mathcal{L}. \qquad (4)$$

The last two terms appear as Lagrange multipliers to ensure the constant force f and the constant torque τ ensemble. $\mathcal{L}$ is the total link, which can be split, using Fuller's theorem [20], into two parts—$\mathcal{L}=\mathcal{T}+\mathcal{W}$. Twist $(\mathcal{T})$ involves rotation of the normal vector about the tangent vector to the curve,

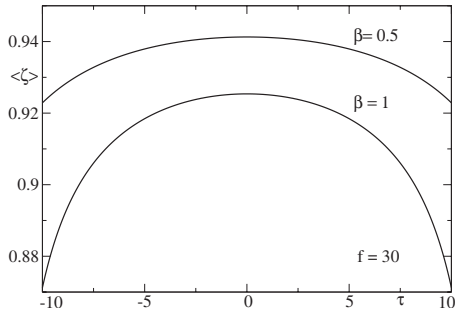

FIG. 3. Mean extension as a function of the torque τ for a pulling force f=30 for a stiff polymer with both the ends clamped for β=0.5 and 1.

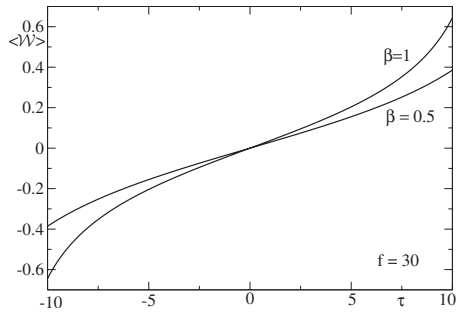

FIG. 5. Torque-link relation for f=30 and β=0.5,1. For the same applied torque, larger values of the average link (or writhe) are suppressed for the stiffer polymer.

$$\mathcal{T}=\int_0^L \Omega_3 ds \tag{5}$$

Writhe ($\mathcal{W}$), which involves one part of the polymer crossing another part, is expressed by a nonlocal formula due to Călugăreanu and White [21]. A simpler formula due to Fuller relates the difference between the writhes of two curves that can be deformed smoothly into each other without self-intersections and such that their tangent vectors never point in opposite directions [20]. Taking the e_3^0 axis to be the reference curve, the writhe of all conformations of the polymer that satisfy the above criteria can be written as $\mathcal{W}=\int_0^L \dot{\phi}(1-\cos\theta)ds$. This can be written as $\int_0^L ds[d\vec{r}/ds\cdot\vec{A}_m(\vec{r})]$. $\vec{A}_m(\vec{r})$, as obtained from Fuller's formula, is the vector potential produced by a magnetic monopole of unit charge; $A_\phi=(1-\cos\theta)$. This gets multiplied by a factor of τ when substituted in the energy term due to the torsional constraint. For reasons explained later, it is convenient to put $\tau=-iB$. We now express the partition function as a path integral,

$$Z[\mathcal{E}[\mathcal{C}]]=\int \mathcal{D}(\theta,\phi,\psi)\exp(-\mathcal{E}[\mathcal{C}]/k_BT). \tag{6}$$

The integral over ψ is just a Gaussian path integral that can be integrated out to be $\exp(-B^2L/2C)$ up to a trivial constant. We perform an analytic continuation toward the imaginary s axis; in the writhe integral, the factor i appearing with B disappears and we arrive at the action integral of a particle with unit charge moving on the unit sphere under the action of an electric field $-F/k_BT$ and a magnetic monopole of charge B [10]. To get the corresponding Hamiltonian, we replace $\vec{p}$ by $(\vec{p}-\vec{A})$; we introduce two dimensionless variables $f=FL_{\mathrm{BP}}/k_BT$ and $\alpha=L_{\mathrm{BP}}/L_{\mathrm{TP}}$ where L_{BP} is the bend persistence length and L_{TP} is the the twist persistence length. The form of the Hamiltonian obtained finally is

$$H=p_\theta^2/2+(p_\phi-A_\phi)^2/2\sin^2\theta-f\cos\theta+\alpha B^2/2. \tag{7}$$

For a stiff polymer with one end clamped along the $\hat{z}$ direction, we can approximate the sphere of directions by a tangent plane at the north pole of the sphere as the angular coordinate θ always remains small. In this limit where the tangent vector never wanders too far away from the north pole of the sphere of directions (the paraxial limit), the polymer Hamiltonian [10–12,19,22] reduces to

$$H_{\mathrm{PWLC}}=\frac{p_\theta^2}{2}+\frac{(p_\phi-A_\phi)^2}{2\theta^2}+\frac{B^2\alpha}{2}-f\left(1-\frac{\theta^2}{2}\right)$$
$$=H_P-f+\frac{B^2\alpha}{2},$$

where H_P is the Hamiltonian of interest in the paraxial limit after we take out a constant piece. Without loss of generality, we can set $\alpha=0$ (see below), and we consider twist to be infinitely expensive energetically and all of the link resulting from the applied torque goes into the writhe. Thus the PWLC maps onto the problem of a particle moving on a plane in the presence of a magnetic field B and an oscillator confining potential, which stems from the small-θ approximation $-f\cos\theta\approx -f(1-\frac{\theta^2}{2})=-f+f\frac{\theta^2}{2}$ [10,11]. Notice that in the stiff limit ($\beta\sim 1$), because of the paraxial approximation, the configurations in which the polymer folds back onto itself are suppressed; consequently self-avoidance effects are unimportant. The polymer cannot release an imposed twist by passing through itself and so, in contrast to the WLC model [19], the free energy is *not* a periodic function of the imposed twist in the PWLC model. We introduce Cartesian coordinates $\xi_1=\theta\cos\phi$ and $\xi_2=\theta\sin\phi$ on the tangent plane R^2 at the north pole.

In terms of the Cartesian coordinates we can express the small-θ Hamiltonian H as $H=H_P-f$ where H_P is

$$H_P=\frac{1}{2}(p_{\xi_1}-A_{\xi_1})^2+\frac{1}{2}(p_{\xi_2}-A_{\xi_2})^2+\frac{f}{2}(\xi_1^2+\xi_2^2) \tag{8}$$

where $A_{\xi_1}=-B\xi_2/2$ and $A_{\xi_2}=B\xi_1/2$. In an azimuthally symmetric situation, the above Hamiltonian becomes

$$H_P=\frac{1}{2}p_{\xi_1}^2+\frac{1}{2}p_{\xi_2}^2+\frac{(f-\tau^2/4)}{2}(\xi_1^2+\xi_2^2). \tag{9}$$

We immediately notice that H_P is the Hamiltonian of a two-dimensional harmonic oscillator with a frequency $\omega=\sqrt{(f+B^2/4)}=\sqrt{(f-\tau^2/4)}$. For a single oscillator in real time the propagator is given by [23]

$$K(\xi_i,\xi_f,T)=F(T)\exp\frac{i\omega}{2\sin\omega T}[(\xi_i^2+\xi_f^2)\cos\omega T-2\xi_i\xi_f] \tag{10}$$

where $F(T)=\sqrt{\frac{\omega}{2\pi i\sin(\omega T)}}$.

Setting $\xi_i=\xi_f=0$ in Eq. (10) and continuing the expression to imaginary time, we find that the trigonometric functions are replaced by hyperbolic ones. We can express the partition function $Z(f)$ as $\exp(\beta f)$ times the product of the propagators of two independent harmonic oscillators:

$$Z(f,\tau)=\sqrt{f-\tau^2/4}\,\exp(\beta f)/[2\pi\sinh(\beta\sqrt{f-\tau^2/4})] \tag{11}$$

in Euclidean time β.

III. WRITHE DISTRIBUTION

In this section, we obtain explicit analytical expressions for the writhe distribution at zero pulling force for the tangent vectors at both the ends of the polymer held fixed. Consider the link distribution

$$\tilde{Z}(f,Lk)=\int Z(f,B)e^{iB\mathcal{L}}dB, \tag{12}$$

where we have used $Z(f,B)$ instead of $Z(f,\tau)$. We recall that we have assumed twist to be energetically infinitely expensive and so the link goes completely into the writhe; in this limit, the link distribution reduces to the writhe distribution. Setting $\alpha=0$ does not result in any loss of generality; on obtaining the writhe distribution in this limit, the full link distribution $P(f,\mathcal{L})$ can be obtained by convolving the writhe distribution with the twist distribution for *all* values of α; in the generating function space, the writhe partition function

$Z_{\mathcal{W}}(f,B)$ needs to be multiplied by the factor $\exp(-\alpha B^2/2)$ which pertains to the pure twist distribution at finite α [10,12]. We shall now derive simple analytical expressions for the writhe distribution.

Consider the expression for $Z(f,\tau)$ derived earlier in Eq. (11); replacing τ^2 by $-B^2$, we derive, for $f=0$, the scaled writhe distribution function as

$$P(f,\mathcal{W}) = 1/\cosh(\pi\mathcal{W}/\beta)^2. \tag{13}$$

The integration in Eq. (12) can be done by going to the complex-B plane and using a semicircular contour closed in the upper half plane. The integrand has simple poles at $B = i2n\pi/\beta$ at which the residues are evaluated. Finally the sum over residues turns out to be the derivative of a simple geometric series that can be easily evaluated.

Figure 1 shows the plot of the scaled writhe distribution for two different values of β; we notice that, for a stiffer polymer, the higher values of writhe are suppressed. This is because, for higher rigidity, the bending freedom of the polymer is restricted and high writhe becomes extremely expensive energetically.

IV. TORQUE-EXTENSION RELATIONS AND EULER BUCKLING

From the expression of the partition function derived before [Eq. (11)], we calculate the free energy

$$G(f,\tau) = -\ln Z(f,\tau)/\beta = \frac{-1}{2\beta}\ln(f-\tau^2/4) - f + \frac{1}{\beta}\ln(2\pi) + \frac{1}{\beta}\ln[\sinh(\beta\sqrt{f-\tau^2/4})]. \tag{14}$$

The mean extension $\langle\zeta\rangle = \langle z\rangle/L = -\partial G(f)/\partial f$ is given by

$$\langle\zeta\rangle = 1 + 1/[2\beta(f-\tau^2/4)] - \coth(\beta\sqrt{f-\tau^2/4})/(2\sqrt{f-\tau^2/4}), \tag{15}$$

where $\langle\zeta\rangle$ is the $\hat{z}$ component of the extension (or the end-to-end distance vector).

For a stiff polymer even at a zero force, there is a nonzero extension, because of the boundary condition which fixes the tangent vector at the two ends of the polymer in the direction of the z axis and the stiffness of the polymer. The pure bend model has been studied in Ref. [9]; here we study the dependence of the mean extension on the applied torque τ. We find, as expected, that for the a certain applied pulling force, the extension decreases as the torque is increased. The mean extension is a symmetric function of τ, a feature that is reflected in the symmetry of the hat-shaped curve. Figure 2 shows that for a constant β the mean extension is larger for a larger value of the pulling force. In Fig. 3, we show the β dependence—the smaller the β (i.e., the stiffer the polymer), the larger is the extension for the same pulling force. These intuitively clear results follow from our simple analytical expressions.

For positive forces, the mean extension increases with increase in force for a fixed value of the torque and decreases with increase of torque when the force is kept fixed. There is a competition between the pulling force and the applied torque. If the force is compressive (negative), the mean extension decreases with increase in the magnitude of the compressive force until, at a critical value of the force, the extension sharply decreases [9]; this is a signature of the Euler buckling instability which is seen in thin rods [24]. Let $x = f - \tau^2/4$; for negative x, the hyperbolic functions appearing in Eq. (15) go over to circular functions. For instance, when both the end tangent vectors are clamped along the $\hat{z}$ direction, for negative x, the analytical form for the extension becomes

$$\langle\zeta\rangle = 1 + 1/(2\beta x) - \cot(\beta\sqrt{-x})/(2\sqrt{-x}), \tag{16}$$

which can be rewritten in the form

$$\langle\zeta\rangle = 1 + \beta u(y), \tag{17}$$

where $y = \beta\sqrt{-x}$ and

$$u(y) = \frac{\cot(y)}{2y} - \frac{1}{2y^2}.$$

The criterion for the onset of the buckling instability is the divergence of $\partial\langle\zeta\rangle/\partial\tau$. From Eq. (17) this is equivalent to the divergence of $\partial u/\partial y$, which takes place at a value of $y_c = \pi$. This gives us the following expression for the critical torque for buckling at a fixed value of the applied force [24]:

$$(\tau_c/2)^2 = f + \left(\frac{\pi}{\beta}\right)^2. \tag{18}$$

Figure 4 shows a plot of the mean extension vs the applied torque for the the tangent vectors when both the ends of the polymer are fixed. We notice that, beyond a certain magnitude of the torque, the extension decreases sharply with very small increase in the torque—this can be interpreted as a signature of buckling instability. From Eq. (18), we see that for $f=0$ the critical torque $\tau_c = 2\pi/\beta$; the approximate values of the critical torque for $\beta=0.7$ and 0.8 are 9 and 7.85 respectively. While the $\beta=0.8$ plot shows a distinct signature of buckling at $|\tau| \sim 7.5$, the plot for $\beta=0.7$ shows no buckling behavior at this range of the value of the torque. This agrees with our intuition that a stiffer polymer buckles at a higher value of the torque. A stiff polymer is energy dominated and its buckling is very similar to that of a classical rod subject to identical boundary conditions and a compressive force [9] and/or torques [24]. The effect of thermal fluctuations is to slightly smudge the transition point from the straight to the buckled configuration. This is due to thermally activated processes that permit the polymer to overcome the elastic energy barrier. As a result, the critical torque for a stiff polymer is slightly smaller in magnitude than that predicted by the expression for τ_c given above [Eq. (18)].

Buckling indicates the breakdown of the paraxial approximation because the small-θ condition does not hold good for a buckled conformation. This sets a limit on the applicability of the paraxial approximation.

V. TORQUE-TWIST RELATION

In this section, we present and discuss a simple analytical expression for the torque-twist relation. As mentioned earlier,

we restrict ourselves to the case of an infinite twist rigidity so that, from Fuller's relation link=twist+writhe [20], we see that all of the link resulting from the applied torque goes into the writhe, which pertains to the rotation of the axis curve of the polymer in space.

We differentiate the expression for the free energy [Eq. (14)] with respect to the applied torque τ to obtain the torque-twist or, in our case, the torque-writhe relation

$$\langle \mathcal{W} \rangle = \tau \coth(\beta\sqrt{f-\tau^2/4})/(4\sqrt{f-\tau^2/4}) - \pi/[4\beta(f-\tau^2/4)]. \tag{19}$$

For the same pulling force, large values of writhe are suppressed for a stiffer polymer (i.e., smaller β). Figure 5 shows a plot of the torque-twist relation. From Fig. 5 as well as from the analytical expression, we see that the torque-link relation is linear for small applied torques.

VI. DISCUSSIONS

Path integral techniques have proved to be very useful in polymer physics [9,14,25]. In this paper, standard results in path integrals (the propagator for the harmonic oscillator) have been used to study the physics of stiff biopolymers. Our main results are contained in the analytic forms displayed in Eqs. (11)–(19) and Figs. 1–5.

We have theoretically studied the twist elasticity of stiff biopolymers. We have treated a boundary condition that is realizable in single-molecule experiments. One can attach a magnetic bead at one end of a polymer and apply forces by magnetic field gradients and torques by magnetic fields. Such techniques allow a variety of boundary conditions to be realized. In Ref. [9], a second boundary condition, in which the tangent vector at one end of the polymer is fixed and that at the other end is free, was treated. In the context of studying twist elasticity, this boundary condition is untenable because the molecule can release links and relax by the process of "geometric untwisting" [26].

To understand the elasticity of the biopolymer networks, we have to understand the elastic properties of its constituent biopolymers at the single-molecule level [2]. An understanding of the bending and torsional elastic properties of actin is vitally important for understanding biological phenomena like muscle contraction, motion of motor proteins, and the role of the cytoskeleton in determining the shape of the cell [27]. A cytoskeleton is made up of a large number N of stiff polymers. A knowledge of the elastic properties of a single polymer constituting such a network will enable us to draw conclusions regarding the stability of the polymeric cytoskeletal structure. Here we have presented simple analytical expressions for the elastic response of a single stiff filament which can be tested against single-molecule experiments. These analytical results are expected to shed light on the structural stability of biopolymer networks.

We have derived an analytical expression for the writhe distribution for zero pulling forces. The writhe distribution has important implications in the context of transcription and gene regulation. Therefore, knowledge of writhing of a biopolymer backbone and its stabilization is crucial for understanding the cellular processes mentioned above. We have also derived simple analytical expressions for the torque-link relation. This result can be tested in single-molecule experiments.

In future it would be interesting to obtain a closed form expression for the writhe distribution for nonzero forces as well. For nonzero forces, all the moments of the writhe distribution $Z(f,\mathcal{W})$ can be obtained by differentiating the generating function $Z(f,B)$; thus effectively we have the information that can be obtained from the writhe distribution function itself. We would also like to investigate buckling of stiff filaments like actin in greater detail. This is an issue that is of relevance at the single-molecular level as well as at the level of a biopolymer network like the cytoskeletal structure and is expected to shed light on its structural stability [2,28] and collapse under stress. The stiffness and collapse of the cytoskeletal structure of a red blood cell [28] has a direct connection to its functional aspects and is used, for instance, as a diagnostic for detection of sickle cell anemia. In studying the cytoskeletal structure it would be useful to have a good understanding of the individual polymers that make up the structure.

We have restricted ourselves to the regime of the paraxial approximation, which breaks down for large values of the applied torque, in which case the polymer explores configurations that deviate considerably from the straight conformation. The present work will provide a limiting check on calculations done in the regime beyond the paraxial approximation. We expect our results to trigger interest in and efforts to explore the physics of stiff biopolymers at both the theoretical and experimental ends.

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