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A CENTRAL LIMIT THEOREM FOR MARKOV PROCESSES THAT MOVE BY SMALL STEPS

BY M. FRANK NORMAN

University of Pennsylvania

We consider a family X_n^θ of discrete-time Markov processes indexed by a positive "step-size" parameter θ. The conditional expectations of ΔX_n^θ, $(\Delta X_n^\theta)^2$, and $|\Delta X_n^\theta|^3$, given X_n^θ, are of the order of magnitude of θ, θ^2, and θ^3, respectively. Previous work has shown that there are functions f and g such that $(X_n^\theta - f(n\theta))/\theta^{\frac{1}{2}}$ is asymptotically normally distributed, with mean 0 and variance $g(t)$, as $\theta \to 0$ and $n\theta \to t < \infty$. The present paper extends this result to $t = \infty$. The theory is illustrated by an application to the Wright–Fisher model for changes in gene frequency.

1. Introduction and overview. Let J be a bounded set of positive numbers with infimum 0. For every $\theta \in J$, let $\{X_n^\theta\}_{n\geq 0}$ be a Markov process with stationary transition probabilities in a Borel subset I_θ of the real line R. The parameter θ is an index of the magnitude of $\Delta X_n^\theta = X_{n+1}^\theta - X_n^\theta$. We will be concerned with the asymptotic behavior of the distribution of X_n^θ as $n \to \infty$ and $\theta \to 0$.

The following assumptions, or their higher dimensional analogs, are in force throughout the paper:

$$E(\Delta X_n^\theta \,|\, X_n^\theta = x) = \theta w(x) + O(\theta^2) \tag{1.1}$$

$$\operatorname{Var}(\Delta X_n^\theta \,|\, X_n^\theta = x) = \theta^2 s(x) + o(\theta^2) \tag{1.2}$$

$$E(|\Delta X_n^\theta|^3 \,|\, X_n^\theta = x) = O(\theta^3)\,, \tag{1.3}$$

uniformly over $x \in I_\theta$. Thus the error terms in (1.1) and (1.2) satisfy

$$\sup_{\theta\in J, x\in I_\theta} |O(\theta^2)|/\theta^2 < \infty$$

and

$$\sup_{x\in I_\theta} |o(\theta^2)|/\theta^2 \to 0$$

as $\theta \to 0$. Let I be the closed convex hull of $\bigcup_{\theta\in J} I_\theta$. We assume that I_θ approximates I as $\theta \to 0$ in the sense that, for any $x \in I$,

$$\inf_{y\in I_\theta} |y - x| \to 0 \tag{1.4}$$

as $\theta \to 0$. The functions w and s are defined throughout I, s is Lipschitz, and w has a bounded Lipschitz derivative.

Under these assumptions the differential equations

$$f'(t) = w(f(t))$$

and

$$g'(t) = 2w'(f(t))g(t) + s(f(t))$$

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have unique solutions $f(t) = f(t, x)$ and $g(t) = g(t, x)$ with $f(0) = x$ and $g(0) = 0$, where x is an arbitrary point of I. Suppose that $x_\theta \in I_\theta$ and $X_0^\theta = x_\theta$ a.s., and let

$$Z_n^\theta = (X_n^\theta - f(n\theta, x_\theta))/\theta^{\frac{1}{2}} .$$

Let $\mathscr{L}(Z)$ be the distribution of a random variable Z, and let $\mathscr{N}(\mu, \sigma^2)$ be the normal distribution with mean μ and variance σ^2. It has been established previously ([6] Theorem 8.1.1) that

$$\mathscr{L}(Z_n^\theta) \to \mathscr{N}(0, g(t, x)) \tag{1.5}$$

as $\theta \to 0$, $x_\theta \to x$, and $n\theta \to t < \infty$. Moreover, it can be shown that the distribution over $C[0, T]$ of the random polygonal line Z^θ with vertices $Z^\theta(n\theta) = Z_n^\theta$ converges weakly to the distribution of the diffusion Z satisfying the stochastic differential equation

$$dZ(t) = w'(f(t))Z(t)\,dt + s(f(t))^{\frac{1}{2}}\,dB(t)$$

and the initial condition $Z(0) = 0$ a.s., where B is Brownian motion. Weak convergence theorems of this type have been established in similar contexts by Rosén [9] and Kurtz [4].

These results are the background for the present study. We shall consider the limit of $\mathscr{L}(Z_n^\theta)$ as $\theta \to 0$ and $n\theta \to \infty$ under certain additional assumptions. Our main project is to prove the following theorem, which was announced in ([8] Theorem 3.2(ii)).

THEOREM 1. *Suppose that I is bounded, w has a unique zero λ, and $w'(\lambda) < 0$. Then*

$$\mathscr{L}(Z_n^\theta) \to \mathscr{N}(0, g(\infty)) \tag{1.6}$$

as $\theta \to 0$ and $n\theta \to \infty$, where

$$g(\infty) = \lim_{t\to\infty} g(t, x) = s(\lambda)/2|w'(\lambda)| .$$

The limiting process in Theorem 1 places no constraint on x_θ. This implies that (1.6) holds uniformly over x_θ in the following sense. Let d be a metric (or pseudometric) on probability distributions over R, such that $d(\mathscr{L}_n, \mathscr{L}) \to 0$ whenever $\mathscr{L}_n \to \mathscr{L}$ weakly. Then

$$\sup_{x_\theta \in I_\theta} d(\mathscr{L}(Z_n^\theta), \mathscr{N}(0, g(\infty))) \to 0$$

as $\theta \to 0$ and $n\theta \to \infty$. Proceeding further in this direction, we may combine (1.5) with Theorem 1 to obtain the rather striking conclusion that

$$\sup_{n\geq 0, x_\theta \in I_\theta} D(n, \theta, x_\theta) \to 0 \tag{1.7}$$

as $\theta \to 0$, where

$$D(n, \theta, x_\theta) = d(\mathscr{L}(Z_n^\theta), \mathscr{N}(0, g(n\theta, x_\theta))) .$$

For if (1.7) were not true, there would be a $c > 0$ and sequences θ_k, n_k, and

$x_k \in I_{\theta_k}$ such that $\theta_k \to 0$ as $k \to \infty$, but

$$D(n_k, \theta_k, x_k) \geqq c \tag{1.8}$$

for all $k \geqq 1$. We could, moreover, choose these sequences in such a way that $n_k \theta_k \to t \leqq \infty$ and $x_k \to x$. It follows from (1.5) and (1.6) that $\mathscr{L}(Z_n^\theta) \to \mathscr{N}(0, g(t, x))$ as $k \to \infty$, where $\theta = \theta_k$, $n = n_k$, and $g(\infty, x) = \lim_{t\to\infty} g(t, x)$. Furthermore, it can be shown that g is continuous over $[0, \infty] \times I$, so $\mathscr{N}(0, g(n_k \theta_k, x_k)) \to \mathscr{N}(0, g(t, x))$. Therefore, by the triangle inequality, $D(n_k, \theta_k, x_k) \to 0$ as $k \to \infty$, contradicting (1.8).

Another corollary of Theorem 1 is obtained by permitting θ to approach 0 after $n \to \infty$. Suppose that $\mathscr{L}(X_n^\theta)$ converges weakly as $n \to \infty$, for every fixed θ. Let $\mathscr{L}(\theta)$ be the corresponding limit of $\mathscr{L}(Z_n^\theta)$, or, equivalently, of $\mathscr{L}(z_n^\theta)$, where

$$z_n^\theta = (X_n^\theta - \lambda)/\theta^{\frac{1}{2}}$$

($f(t) \to \lambda$ as $t \to \infty$). It follows easily from (1.6) that

$$\mathscr{L}(\theta) \to \mathscr{N}(0, g(\infty)) \tag{1.9}$$

as $\theta \to 0$. Some special results of this type were established in [5]. It is also a consequence of Theorem 1 that (1.9) holds for an arbitrary family $\mathscr{L}(\theta)$ of stationary distributions of z_n^θ. This implies Part B of Theorem 10.1.1 (i) of [6].

The proof of Theorem 1 is given in Sections 2 and 3. Section 4 presents an application to the Wright–Fisher model for the evolution of gene frequency under the influence of mutation, selection, and random drift. In that context, $\theta = (2N)^{-\frac{1}{2}}$, where N is the population size, and the function f is the classical deterministic approximation to gene frequency for very large populations (see [2] Section 2.3). The results (1.6) and (1.7), which relate to the distribution of the error of this approximation, appear to be new even for this much studied model.

Section 5 gives a multidimensional analog of Theorem 1, and an illustrative application to a mathematical learning model.

2. Conditional moments of ΔZ_n^θ. A basic component of the proof of Theorem 1 is Lemma 1.

LEMMA 1. *Under the hypotheses of Theorem* 1, $E((Z_n^\theta)^2)$ *is bounded over all* $\theta \in J$, $x_\theta \in I_\theta$, *and* $n \geqq 0$.

This result follows immediately from Theorem 3.2 (i) of [8]. The latter theorem assumes that J is an interval and $I_\theta = I$ for all θ, but these assumptions are not used in the proof. It emerges in the course of the proof that, for some $K < \infty$ and $\alpha > 0$,

$$|f(t, x) - \lambda| \leqq Ke^{-\alpha t}$$

for all $x \in I$ and $t \geqq 0$. Since w' and s satisfy Lipschitz conditions, we have

$$|w'(f(t, x)) - w'(\lambda)| \leqq Ke^{-\alpha t} \tag{2.1}$$

and

$$|s(f(t,x)) - s(\lambda)| \leqq Ke^{-\alpha t} \tag{2.2}$$

for suitable new constants K.

Henceforth we suppress the θ superscript on Z_n^θ, and let $\nu_n = f(n\theta, x_\theta)$. The purpose of this section is to establish Lemma 2.

LEMMA 2.

$$E(\Delta Z_n \mid Z_n) = \theta w'(\nu_n) Z_n + o(\theta) \tag{2.3}$$

$$E((\Delta Z_n)^2 \mid Z_n) = \theta s(\nu_n) + o(\theta) \tag{2.4}$$

$$E(|\Delta Z_n|^3 \mid Z_n) = o(\theta)\,, \tag{2.5}$$

where the quantities $o(\theta)$ satisfy $E(|o(\theta)|)/\theta \to 0$ as $\theta \to 0$, uniformly over $x_\theta \in I_\theta$ and $n \geqq 0$.

PROOF. Since w and w' are bounded,

$$f''(t) = w'(f(t))w(f(t))$$

is too. Thus

$$\Delta\nu_n = \theta w(\nu_n) + O(\theta^2)$$

uniformly over x_θ and n. This expression and (1.1) imply that

$$\begin{aligned} E(\Delta Z_n \mid Z_n) &= \theta^{-\frac{1}{2}}(E(\Delta X_n \mid X_n) - \Delta\nu_n) \\ &= \theta^{\frac{1}{2}}(w(X_n) - w(\nu_n)) + O(\theta^{\frac{3}{2}})\,. \end{aligned} \tag{2.6}$$

Since w' is Lipschitz, this yields

$$E(\Delta Z_n \mid Z_n) = \theta w'(\nu_n) Z_n + \theta^{\frac{3}{2}} O(|Z_n|^2) + O(\theta^{\frac{3}{2}})\,,$$

which, in view of Lemma 1, is of the form (2.3).

Turning to the proof of (2.4), we begin by writing

$$E((\Delta Z_n)^2 \mid Z_n) = \theta^{-1}\operatorname{Var}(\Delta X_n \mid X_n) + E(\Delta Z_n \mid Z_n)^2\,. \tag{2.7}$$

As a consequence of (2.6),

$$E(\Delta Z_n \mid Z_n) = \theta O(|Z_n|) + O(\theta^{\frac{3}{2}})\,, \tag{2.8}$$

so that

$$E(\Delta Z_n \mid Z_n)^2 \leqq K(\theta^2 |Z_n|^2 + \theta^3)$$

and

$$E(\Delta Z_n \mid Z_n)^2 = o(\theta) \tag{2.9}$$

by Lemma 1. Next, (1.2) yields

$$\begin{aligned} \theta^{-1}\operatorname{Var}(\Delta X_n \mid X_n) &= \theta s(X_n) + o(\theta) \\ &= \theta s(\nu_n) + \theta^{\frac{3}{2}} O(|Z_n|) + o(\theta) \\ &= \theta s(\nu_n) + o(\theta) \end{aligned} \tag{2.10}$$

by Lemma 1. Substituting (2.9) and (2.10) into (2.7), we obtain (2.4).

Finally,

$$E(|\Delta Z_n|^3 \mid Z_n) \leqq 4\theta^{-\frac{3}{2}}(E(|\Delta X_n|^3 \mid X_n) + |\nu_n|^3)$$
$$\leqq K\theta^{\frac{3}{2}}$$

as a consequence of (1.3) and the boundedness of w. This implies (2.5).

3. A general central limit theorem. In view of (2.1), (2.2), Lemma 1, and Lemma 2, Theorem 1 is a corollary of Theorem 2.

THEOREM 2. *Suppose that Z_n^θ, $n \geqq 0$, $\theta \in J$, is a family of real-valued stochastic processes such that*

$$E(\Delta Z_n^\theta \mid Z_n^\theta) = \theta a(n, \theta) Z_n^\theta + o(\theta) \tag{3.1}$$

$$E((\Delta Z_n^\theta)^2 \mid Z_n^\theta) = \theta b(n, \theta) + o(\theta) \tag{3.2}$$

$$E(|\Delta Z_n^\theta|^3 \mid Z_n^\theta) = o(\theta), \tag{3.3}$$

where

$$\sup_{n \geqq 0} E(|o(\theta)|)/\theta \to 0$$

as $\theta \to 0$,

$$a(n, \theta) \to a \qquad \text{and} \qquad b(n, \theta) \to b \tag{3.4}$$

as $\theta \to 0$ and $n\theta \to \infty$, and $a < 0$. Suppose also that

$$\sup_{n \geqq 0, \theta \in J} E((Z_n^\theta)^2) < \infty. \tag{3.5}$$

Then $\mathscr{L}(Z_n^\theta) \to \mathscr{N}(0, \sigma^2)$ as $\theta \to 0$ and $n\theta \to \infty$, where $\sigma^2 = b/2|a|$.

PROOF. Let

$$h_n(\gamma) = h_n^\theta(\gamma) = E(\exp(i\gamma Z_n)).$$

Then

$$h_{n+1}(\gamma) = E(\exp(i\gamma Z_n)) E(\exp(i\gamma\, \Delta Z_n \mid Z_n)). \tag{3.6}$$

Expanding $\exp(i\gamma\, \Delta Z_n)$ up to terms of third order in γ and using (3.1)—(3.3) we obtain

$$\Delta h_n(\gamma) = \theta\gamma a(n, \theta) h_n'(\gamma) - \theta 2^{-1}\gamma^2 b(n, \theta) h_n(\gamma) + d_n(\gamma), \tag{3.7}$$

where

$$|d_n(\gamma)| \leqq \theta \varepsilon_\theta |\gamma| \tag{3.8}$$

and ε_θ is our generic notation for a quantity that depends only on θ and approaches 0 as θ approaches 0. This estimate is valid for all $n \geqq 0$ as long as γ is bounded, $|\gamma| \leqq \Gamma$. From (3.7) it follows that

$$\Delta h_n(\gamma) = \theta\gamma a h_n'(\gamma) - \theta 2^{-1}\gamma^2 b h_n(\gamma) + d_n(\gamma) + e_n(\gamma), \tag{3.9}$$

where, in view of (3.4) and (3.5),

$$|e_n(\gamma)| \leqq \theta c(n, \theta)|\gamma|, \tag{3.10}$$

and $c(n, \theta)$ is a quantity that approaches 0 as $\theta \to 0$ and $n\theta \to \infty$. The inequality (3.10) presupposes $|\gamma| \leqq \Gamma$.

Let

$$v(\gamma) = \exp(2^{-1}\gamma^2\sigma^2),$$
$$H_n(\gamma) = v(\gamma)h_n(\gamma),$$
$$D_n(\gamma) = v(\gamma)d_n(\gamma),$$
$$E_n(\gamma) = v(\gamma)e_n(\gamma),$$

and note that

$$v(\gamma)h_n'(\gamma) = H_n'(\gamma) - \sigma^2\gamma H_n(\gamma).$$

Thus multiplication of (3.9) by $v(\gamma)$ yields

$$\Delta H_n(\gamma) = \theta\gamma a H_n'(\gamma) + D_n(\gamma) + E_n(\gamma). \tag{3.11}$$

As a consequence of (3.8) and (3.10),

$$|D_n(\gamma)| \leqq \theta\varepsilon_\theta|\gamma| \tag{3.12}$$

and

$$|E_n(\gamma)| \leqq \theta c(n, \theta)|\gamma| \tag{3.13}$$

for $|\gamma| \leqq \Gamma$.

Let

$$\gamma_j = (1 + \theta a)^j \xi,$$

where ξ is fixed for the remainder of the proof. Assuming $\theta \leqq 1/|a|$,

$$|\gamma_j| \leqq e^{a\theta j}|\xi|. \tag{3.14}$$

In particular, γ_j is bounded by $|\xi| = \Gamma$ for all j and θ.

For any $0 \leqq m \leqq M$, define $\mathscr{H}_m = \mathscr{H}_m(M, \theta)$ by

$$\mathscr{H}_m = H_m(\gamma_{M-m}).$$

Then $\mathscr{H}_M = H_M(\xi)$. Suppose that $\mathscr{H}_M - \mathscr{H}_k \to 0$ as $\theta \to 0$ and $k\theta \to \infty$, while $\mathscr{H}_k \to 1$ as $\theta(M - k) \to \infty$. Then choosing $k = [M/2]$ we see that $H_M(\xi) \to 1$,

$$h_M(\xi) \to \exp(-2^{-1}\xi^2\sigma^2),$$

and $\mathscr{L}(Z_M) \to \mathscr{N}(0, \sigma^2)$ as $\theta \to 0$ and $M\theta \to \infty$, as the theorem asserts. Thus it remains only to show that $\mathscr{H}_M - \mathscr{H}_k \to 0$ and $\mathscr{H}_k \to 1$.

It may assist the reader in understanding the proof that $\mathscr{H}_M - \mathscr{H}_k \to 0$ to regard (3.11) as an approximation to the partial differential equation

$$\frac{\partial H(t, \gamma)}{\partial t} = \gamma a \frac{\partial H(t, \gamma)}{\partial \gamma}.$$

For any constant g, (t, ge^{-at}) is a characteristic base curve of this equation ([1] page 63), so

$$\frac{d}{dt} H(t, ge^{-at}) = 0.$$

Since γ_{M-m} approximates $\gamma_M e^{-am\theta}$, we expect $\mathscr{H}_m = H_m(\gamma_{M-m})$ to approximate $H(m\theta, \gamma_M e^{-am\theta})$. Thus $\mathscr{H}_m$ should vary little with m.

Clearly

$$\Delta\mathscr{H}_{m-1} = A_m - B_m$$

for $m \geqq 1$, where

$$A_m = H_m(\gamma_{M-m}) - H_{m-1}(\gamma_{M-m})$$

and

$$B_m = H_{m-1}(\gamma_{M+1-m}) - H_{m-1}(\gamma_{M-m}) .$$

Thus

$$|\mathscr{H}_M - \mathscr{H}_k| \leqq \sum_{m=k+1}^{M} |A_m - B_m| . \tag{3.15}$$

Now

$$\begin{aligned} B_m &= \Delta\gamma_{M-m} H'_{m-1}(\gamma_{M-m}) + F_{m-1} \\ &= \theta a\gamma_{M-m} H'_{m-1}(\gamma_{M-m}) + F_{m-1} , \end{aligned} \tag{3.16}$$

where

$$\begin{aligned} |F_{m-1}| &\leqq 2^{-1}|\Delta\gamma_{M-m}|^2 \max_{|\gamma|\leqq|\xi|} |H''_{m-1}(\gamma)| \\ &\leqq K\theta^2 e^{2a\theta(M-m)} \end{aligned} \tag{3.17}$$

by virtue of (3.14) and (3.5). When the expression (3.16) for B_m is subtracted from (3.11) for A_m, the leading terms cancel, so that

$$A_m - B_m = D_{m-1}(\gamma_{M-m}) + E_{m-1}(\gamma_{M-m}) - F_{m-1} .$$

Applying the estimates (3.12), (3.13), (3.14), and (3.17) to (3.15), we obtain

$$\begin{aligned} |\mathscr{H}_M - \mathscr{H}_k| &\leqq (\varepsilon_\theta + \sup_{n\geqq k} c(n, \theta))\theta \sum_{m=k+1}^{M} e^{a\theta(M-m)} \\ &\leqq (\varepsilon_\theta + \sup_{n\geqq k} c(n, \theta))\theta/(1 - e^{a\theta}) . \end{aligned}$$

Since $\varepsilon_\theta \to 0$ as $\theta \to 0$, and $c(n, \theta) \to 0$ as $\theta \to 0$ and $n\theta \to \infty$, it follows that $\mathscr{H}_M - \mathscr{H}_k \to 0$ as $\theta \to 0$ and $k\theta \to \infty$.

Note, finally, that

$$\begin{aligned} |h_k(\gamma_{M-k}) - 1| &\leqq |\gamma_{M-k}|E(|Z_k|) \\ &\leqq K|\gamma_{M-k}| \end{aligned}$$

by (3.5). Since $\gamma_{M-k} \to 0$ as $\theta(M - k) \to \infty$, we have $h_k(\gamma_{M-k}) \to 1$ and thus

$$\mathscr{H}_k = h_k(\gamma_{M-k})v(\gamma_{M-k}) \to 1$$

as $\theta(M - k) \to \infty$. This completes the proof.

4. The Wright-Fisher model. Suppose that there are two alleles, A_1 and A_2, at a certain chromosomal locus in a diploid population of N individuals. Let i be the number and $x = i/2N$ the proportion of A_1 genes in the population at any time. According to the model (see [2] Section 4.8), values X_n of x in successive generations form a finite Markov chain with transition probabilities

$$p_{ij} = \binom{2N}{j}\pi_i{}^j(1 - \pi_i)^{2N-j} ,$$

where

$$\pi_i = (1 - u)\pi_i{}^* + v(1 - \pi_i{}^*)$$

and

$$\pi_i{}^* = \frac{(1 + s_1)x^2 + (1 + s_2)x(1 - x)}{(1 + s_1)x^2 + 2(1 + s_2)x(1 - x) + (1 - x)^2} .$$

The constants s_1, s_2, u, and v control selection pressure and mutation rate. The fitnesses of the genotypes A_1A_1 and A_1A_2, relative to that of A_2A_2, are $1 + s_1$ and $1 + s_2$, respectively. The probability that an A_1 gene mutates to A_2 is u, while the probability that A_2 mutates to A_1 is v.

To apply Theorem 1 to this model, we assume that these parameters are proportional to $\theta = (2N)^{-\frac{1}{2}}$: $s_i = \bar{s}_i\theta$, $u = \bar{u}\theta$, and $v = \bar{v}\theta$, where $\bar{u}, \bar{v} \geqq 0$. The routine verification of the assumptions in the second paragraph of Section 1 is given in ([6] Section 18.1), where it is also shown that $s(x) = x(1 - x)$ and

$$w(x) = \bar{v} - (\bar{u} + \bar{v})x + x(1 - x)(\bar{s}_2 + (\bar{s}_1 - 2\bar{s}_2)x) \tag{4.1}$$

on $I = [0, 1]$. Thus Theorem 1 applies whenever w has a unique root λ and $w'(\lambda) < 0$ (i.e., λ is stable).

The following conditions are sufficient but by no means necessary for this: $\bar{u} > 0, \bar{v} > 0$, and $\bar{s}_1 \leqq 2\bar{s}_2$. (Proof. Since $w(0) = \bar{v} > 0$ and $w(1) = -\bar{u} < 0$, w has at least one zero in $(0, 1)$. If $\bar{s}_1 = 2\bar{s}_2$, w is quadratic or linear, and uniqueness and stability certainly obtain. If $\bar{s}_1 < 2\bar{s}_2$, the coefficient of x^3 is positive, so w has a root above 1 and a root below 0. Thus w has only one root λ in $(0, 1)$ and it must satisfy $w'(\lambda) < 0$.) The inequality $\bar{s}_1 \leqq 2\bar{s}_2$ admits a number of genetically significant special cases:

(i) no dominance, $\bar{s}_1 = 2\bar{s}_2$;
(ii) favored gene completely dominant, $\bar{s}_1 = \bar{s}_2 > 0$ or $\bar{s}_1 < \bar{s}_2 = 0$; and
(iii) heterozygote advantage, $\bar{s}_1 < \bar{s}_2 > 0$.

Writing X_n^N and x^N for X_n^θ and x_θ, the conclusion of Theorem 1 can be expressed as follows:

$$(2N)^{\frac{1}{4}}[X_n^N - f(n/(2N)^{\frac{1}{2}}, x^N)] \sim \mathscr{N}(0, g(\infty))$$

as $N \to \infty$ and $n/N^{\frac{1}{2}} \to \infty$. The occurrence of the fourth root on the left is noteworthy. (We observe that the related results in lines 13 and 22 on page 259 of [6] should have fourth roots instead of square roots.)

To see the relation of Theorem 1 to other diffusion approximations of the Wright–Fisher model, suppose that the mutation and selection parameters are proportional to a parameter $\varepsilon > 0$, i.e., $s_i = \bar{s}_i\varepsilon$, $u = \bar{u}\varepsilon$, and $v = \bar{v}\varepsilon$. Theorem 1 pertains directly to $\varepsilon = (2N)^{-\frac{1}{2}}$, but it turns out that this result is typical of those obtained when $\varepsilon \to 0$ sufficiently slowly that $N\varepsilon \to \infty$. If the function w given in (4.1) satisfies the hypotheses of Theorem 1, then $(\varepsilon N)^{\frac{1}{2}}X_n$, suitably centered, is asymptotically normally distributed as $\varepsilon \to 0$, $N\varepsilon \to \infty$, and $n\varepsilon \to \infty$. This generalization of Theorem 1 will be proved in a subsequent paper. For a clear heuristic analysis of the asymptotic behavior of X_n when $\varepsilon \to 0$ and $N\varepsilon \to \infty$, see Section 9 of [3].

Suppose now that $\varepsilon = (2N)^{-1}$. In this case, $\mathscr{L}(X_n^N) \to \mathscr{P}(t, x)$ as $x^N \to x$, $N \to \infty$, and $n\varepsilon \to t < \infty$, where $\mathscr{P}(t, x)$ is a nondegenerate distribution associated with a diffusion on I ([6] page 260). The standard diffusion approximations of population genetics are of this type ([2] Section 5.1). This result, like the analogous result (1.5), is valid whether or not the function w in (4.1) satisfies the hypotheses of Theorem 1. One would like to know what auxiliary conditions, if any, must be imposed to insure that $\mathscr{L}(X_n^N)$ converges to $\lim_{t\to\infty}\mathscr{P}(t, x)$ as $x^N \to x$, $N \to \infty$, and $n\varepsilon \to \infty$.

5. Multidimensional case. Suppose that the assumptions of the first two paragraphs of Section 1 are in force, except that X_n^θ is k dimensional, and the conditional variance in (1.2) is replaced by the conditional covariance matrix. Then (1.5) is valid, where the asymptotic covariance matrix $g(t) = g(t, x)$ satisfies

$$g'(t) = w'(f(t))g(t) + g(t)w'(f(t))^* + s(f(t)),$$

and * indicates transposition ([6] Theorem 8.1.1). Theorem 3 is the multidimensional analog of Theorem 1.

THEOREM 3. *Suppose that the following additional conditions obtain: I is bounded, there is a point λ such that $w(\lambda) = 0$, and there is an inner product $[x, y]$ on R^k such that*

$$[x - \lambda, w(x)] < 0 \tag{5.1}$$

for all $x \in I$, $x \neq \lambda$, and

$$[z, w'(\lambda)z] < 0$$

for all $z \in R^k$, $z \neq 0$. Then

$$\mathscr{L}(Z_n^\theta) \to \mathscr{N}(0, g(\infty))$$

as $\theta \to 0$ and $n\theta \to \infty$, where $g(\infty)$ is the unique solution of the system

$$w'(\lambda)g(\infty) + g(\infty)w'(\lambda)^* + s(\lambda) = 0$$

of linear equations.

Obviously (5.1) implies that λ is the only zero of w. The most general inner product on R^k is $[x, y] = (x, Py)$, where (x, y) is the Euclidean inner product and P is a positive definite matrix.

Theorem 3 can be established by a straightforward generalization of the proof of Theorem 1. This involves establishing the multidimensional generalizations of Lemmas 1 and 2 and Theorem 2. We omit details.

Theorem 3 is applicable to the Zeaman–House–Lovejoy learning model [7], which describes how a human or lower animal might learn to attend to a certain "relevant" dimension of a multidimensional stimulus. In this rather complex model, X_n is two dimensional and I is the closed unit square. There are six learning rate parameters, φ_1, φ_2, φ_3, φ_4, θ_1, θ_2, and two payoff probability parameters, π_B and π_W. To apply Theorem 3, we assume that the learning rate parameters are all proportional to a single parameter θ, i.e., $\varphi_i = \theta\bar{\varphi}_i$ and $\theta_j = \theta\bar{\theta}_j$, where $\bar{\varphi}_i$ and $\bar{\theta}_j$ are positive constants. It can be shown that the hypotheses of Theorem 3 are satisfied if and only if one of the following conditions holds: (i) $\pi_B < 1$ and $\pi_W < 1$, or (ii) $\max(\pi_B, \pi_W) = 1$, $\min(\pi_B, \pi_W) < 1$, and

$\bar{\varphi}_1 > \bar{\varphi}_3(\pi_B + \pi_W)/2$. In either case we can take $[x, x'] = x_1 x_1' + c x_2 x_2'$ for c sufficiently large. Under condition (i), λ is in the interior of I, while under condition (ii), it is one of the corners.

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DEPARTMENT OF PSYCHOLOGY
UNIVERSITY OF PENNSYLVANIA
3815 WALNUT STREET
PHILADELPHIA, PA. 19174