

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

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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 $(X_n^\theta - f(n\theta))/\theta^{1/2}$ is asymptotically normally distributed, with mean 0 and variance $g(t)$, as $\theta \rightarrow 0$ and $n\theta \rightarrow t < \infty$. 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 $n \rightarrow \infty$ and $\theta \rightarrow 0$.

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

$$(1.1) \quad E(\Delta X_n^\theta | X_n^\theta = x) = \theta w(x) + O(\theta^2)$$

$$(1.2) \quad \text{Var}(\Delta X_n^\theta | X_n^\theta = x) = \theta^2 s(x) + o(\theta^2)$$

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

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

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

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

$$(1.4) \quad \inf_{y \in I_\theta} |y - x| \rightarrow 0$$

as $\theta \rightarrow 0$. 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

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

Received June 25, 1973; revised November 10, 1973.

AMS 1970 subject classifications. Primary 60F05, 60J05; Secondary 92A10.

Key words and phrases. Central limit theorem, Markov process, step-size parameter.

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

$$(1.5) \quad \mathcal{L}(Z_n^\theta) \rightarrow \mathcal{N}(0, g(t, x))$$

as $\theta \rightarrow 0$, $x_\theta \rightarrow x$, and $n\theta \rightarrow t < \infty$. 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 $\mathcal{L}(Z_n^\theta)$ as $\theta \rightarrow 0$ and $n\theta \rightarrow \infty$ 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*

$$(1.6) \quad \mathcal{L}(Z_n^\theta) \rightarrow \mathcal{N}(0, g(\infty))$$

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

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

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 $d(\mathcal{L}_n, \mathcal{L}) \rightarrow 0$ whenever $\mathcal{L}_n \rightarrow \mathcal{L}$ weakly. Then

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

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

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

as $\theta \rightarrow 0$, where

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

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 $\theta_k \rightarrow 0$ as $k \rightarrow \infty$, but

$$(1.8) \quad D(n_k, \theta_k, x_k) \geq c$$

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

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

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

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

$$(1.9) \quad \mathcal{L}(\theta) \rightarrow \mathcal{N}(0, g(\infty))$$

as $\theta \rightarrow 0$. 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 $\mathcal{L}(\theta)$ 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 $n \geq 0$.*

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 $\alpha > 0$,

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

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

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

and

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

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.

$$(2.3) \quad E(\Delta Z_n | Z_n) = \theta w'(\nu_n) Z_n + o(\theta)$$

$$(2.4) \quad E((\Delta Z_n)^2 | Z_n) = \theta s(\nu_n) + o(\theta)$$

$$(2.5) \quad E(|\Delta Z_n|^3 | Z_n) = o(\theta),$$

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

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

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

Since w' is Lipschitz, this yields

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

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

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

$$(2.7) \quad E((\Delta Z_n)^2 | Z_n) = \theta^{-1} \text{Var}(\Delta X_n | X_n) + E(\Delta Z_n | Z_n)^2.$$

As a consequence of (2.6),

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

so that

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

and

$$(2.9) \quad E(\Delta Z_n | Z_n)^2 = o(\theta)$$

by Lemma 1. Next, (1.2) yields

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

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

Finally,

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

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 $Z_n^\theta, n \geq 0, \theta \in J$, is a family of real-valued stochastic processes such that*

$$(3.1) \quad E(\Delta Z_n^\theta | Z_n^\theta) = \theta a(n, \theta) Z_n^\theta + o(\theta)$$

$$(3.2) \quad E((\Delta Z_n^\theta)^2 | Z_n^\theta) = \theta b(n, \theta) + o(\theta)$$

$$(3.3) \quad E(|\Delta Z_n^\theta|^3 | Z_n^\theta) = o(\theta),$$

where

$$\sup_{n \geq 0} E(|o(\theta)|)/\theta \rightarrow 0$$

as $\theta \rightarrow 0$,

$$(3.4) \quad a(n, \theta) \rightarrow a \quad \text{and} \quad b(n, \theta) \rightarrow b$$

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

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

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

PROOF. Let

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

Then

$$(3.6) \quad h_{n+1}(\gamma) = E(\exp(i\gamma Z_n))E(\exp(i\gamma \Delta Z_n | Z_n)).$$

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

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

where

$$(3.8) \quad |d_n(\gamma)| \leq \theta \varepsilon_\theta |\gamma|$$

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 $n \geq 0$ as long as γ is bounded, $|\gamma| \leq \Gamma$. From (3.7) it follows that

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

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

$$(3.10) \quad |e_n(\gamma)| \leq \theta c(n, \theta)|\gamma|,$$

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

Let

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

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

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

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

$$(3.12) \quad |D_n(\gamma)| \leq \theta\varepsilon_\theta|\gamma|$$

and

$$(3.13) \quad |E_n(\gamma)| \leq \theta c(n, \theta)|\gamma|$$

for $|\gamma| \leq \Gamma$.

Let

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

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

$$(3.14) \quad |\gamma_j| \leq e^{a\theta j}|\xi|.$$

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

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

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

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

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

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

It may assist the reader in understanding the proof that $\mathcal{H}_M - \mathcal{H}_k \rightarrow 0$ 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 $\mathcal{H}_m = H_m(\gamma_{M-m})$ to approximate $H(m\theta, \gamma_M e^{-am\theta})$. Thus \mathcal{H}_m should vary little with m .

Clearly

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

for $m \geq 1$, 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

$$(3.15) \quad |\mathcal{H}_M - \mathcal{H}_k| \leq \sum_{m=k+1}^M |A_m - B_m|.$$

Now

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

where

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

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

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

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

Note, finally, that

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

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

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

as $\theta(M-k) \rightarrow \infty$. 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

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

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 $\bar{u}, \bar{v} \geq 0.$ 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

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

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 $\bar{s}_1 \leq 2\bar{s}_2.$ (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 $\bar{s}_1 \leq 2\bar{s}_2$ 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 $x_\theta,$ the conclusion of Theorem 1 can be expressed as follows:

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

as $N \rightarrow \infty$ and $n/N^{\frac{1}{2}} \rightarrow \infty.$ 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 $\epsilon > 0,$ i.e., $s_i = \bar{s}_i\epsilon, u = \bar{u}\epsilon,$ and $v = \bar{v}\epsilon.$ Theorem 1 pertains directly to $\epsilon = (2N)^{-\frac{1}{2}},$ but it turns out that this result is typical of those obtained when $\epsilon \rightarrow 0$ sufficiently slowly that $N\epsilon \rightarrow \infty.$ If the function w given in (4.1) satisfies the hypotheses of Theorem 1, then $(\epsilon N)^{\frac{1}{2}}X_n,$ suitably centered, is asymptotically normally distributed as $\epsilon \rightarrow 0, N\epsilon \rightarrow \infty,$ and $n\epsilon \rightarrow \infty.$ 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 $\epsilon \rightarrow 0$ and $N\epsilon \rightarrow \infty,$ see Section 9 of [3].

Suppose now that $\epsilon = (2N)^{-1}.$ In this case, $\mathcal{L}(X_n^N) \rightarrow \mathcal{P}(t, x)$ as $x^N \rightarrow x, N \rightarrow \infty,$ and $n\epsilon \rightarrow t < \infty,$ where $\mathcal{P}(t, x)$ 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 $\mathcal{L}(X_n^N)$ converges to $\lim_{t \rightarrow \infty} \mathcal{P}(t, x)$ as $x^N \rightarrow x$, $N \rightarrow \infty$, and $n\epsilon \rightarrow \infty$.

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*

$$(5.1) \quad [x - \lambda, w(x)] < 0$$

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

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

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

$$\mathcal{L}(Z_n^\theta) \rightarrow \mathcal{N}(0, g(\infty))$$

as $\theta \rightarrow 0$ and $n\theta \rightarrow \infty$, 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, $\varphi_1, \varphi_2, \varphi_3, \varphi_4, \theta_1, \theta_2$, 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., $\varphi_i = \theta\hat{\varphi}_i$ and $\theta_j = \theta\hat{\theta}_j$, where $\hat{\varphi}_i$ and $\hat{\theta}_j$ 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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