Fixation probabilities and hitting times
for low levels of frequency-dependent selection

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Abstract

In population genetics, diffusions on the unit interval are often used to model the frequency path of an allele. In this setting we derive approximations for fixation probabilities, expected hitting times and the expected frequency spectrum for low levels of frequency-dependent selection. Specifically, we rederive and extend the one-third rule of evolutionary game theory (Nowak et al., 2004) and effects of stochastic slowdown (Altröck and Traulsen, 2009). Since similar effects are of interest in other application areas, we formulate our results for general one-dimensional diffusions.

1 Introduction

Our motivation for this note came from the desire to find a both intuitive and generalizable explanation for the so-called one-third rule in evolutionary game theory [Nowak et al., 2004]. Phrased in the language of population genetics, the one-third rule says: Assume that $X$ is a Wright-Fisher diffusion with selection coefficient $\alpha > 0$ and linear frequency-dependent selection

$$
\psi(y) = \beta - \gamma y, \quad 0 \leq y \leq 1,
$$

(1.1)

with $\beta, \gamma \in \mathbb{R}$, i.e. $X$ is a $[0,1]$-valued process $X$ satisfying the stochastic differential equation

$$
dX_t = \alpha \psi(X_t) X_t (1 - X_t) + \sqrt{X_t (1 - X_t)} dW_t
$$

(1.2)

with $W$ being a standard Brownian motion. Then the probability of fixation in 1 is, for small positive $\alpha$ and a small initial frequency $x$, larger than $x$ (which is the fixation probability in the neutral case $\alpha = 0$; see e.g. (5.17) in Ewens, 2004) if and only if $\psi(1/3) > 0$.

We write $T_0$ and $T_1$ for the first times at which $X$ hits the boundaries 0 and 1, respectively, and $T := T_0 \wedge T_1$ for the first time at which $X$ hits the boundary $\{0,1\}$. We ask the following questions: Under which conditions on the frequency dependent selection $\psi$ – which may then as well be more general than given in (1.1) – is for small positive $\alpha$, but not necessarily small $x$,

- the fixation probability $P^x_\alpha(X_T = 1)$ larger than $x$ (which is the fixation probability in the neutral case, $\alpha = 0$)

- the expected time to fixation (either unconditional or conditional on fixation) or extinction larger than that in the neutral case?

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Hitting probabilities. To illustrate our findings, let us come back to $\psi$ as given in (1.1). We will show (see Corollary 2.1) that

$$P_x^\alpha(T = 1) = x + \alpha x (1 - x) (\beta - \frac{2\beta}{3} (1 + x)) + O(\alpha^2)$$

(1.3)
as $\alpha \to 0$. This gives the following generalization of the one-third rule:

For the Wright-Fisher diffusion (1.2) with frequency dependent selection $\psi$ given by (1.1), the fixation probability in 1 is, for small positive $\alpha$ and fixed initial frequency $x$, larger than $x$ (which is the fixation probability in the neutral case $\alpha = 0$) if and only if $\psi(\frac{1+x}{2}) > 0$.

Fixation times. In a series of papers (Altrock and Traulsen, 2009; Altrock et al., 2010, 2012) have reported the following – at first sight maybe counter-intuitive – result on what they call a stochastic slowdown effect: Conditioned on fixation, a selective allele can have a longer expected fixation time than a neutral one. This effect was analyzed in the just quoted papers for a finite population. Some structural insights, however, arise in the appropriate diffusion limit. Thus, in Theorem 2 we will analyze the expected hitting time of the boundary $\{0, 1\}$ as $\alpha \to 0$. In a similar way, in Theorems 3 and 4 we will obtain the approximate expected conditional hitting times of boundary points 1 and 0 as $\alpha \to 0$ when starting near 0. For the Wright-Fisher diffusion (1.2), Corollaries 2.2, 2.3 and 2.4 specialize to

$$E^\alpha_x[T_h] = 2x - 2x \log x + 2\alpha \beta x + o(x, \alpha) \quad \text{as } x, \alpha \to 0,$$

(1.4)

$$E^\alpha_{x^+}[T_1] = 2 + \alpha \frac{\gamma}{9} + o(x, \alpha) \quad \text{as } \alpha \to 0,$$

(1.5)

$$E^\alpha_{x^+}[T_0] = -2x \log x + \alpha x \frac{5\gamma}{9} + o(x, \alpha) \quad \text{as } x, \alpha \to 0,$$

(1.6)

where $E^\alpha_{x^+}$ and $E^\alpha_{x^+}$ denote the conditional expectation $E^\alpha_{x^+}[T_1 < T_0]$ and $E^\alpha_{x^+}[T_0 < T_1]$, respectively. Notably, (1.4) does not depend on $\gamma$, whereas (1.5) and (1.6) do not depend on $\beta$, and, while $\beta$ and $\gamma$ enter with different signs in (1.1), all signs in (1.4) – (1.6) are positive. Intuitive interpretations / explanations of these facts will be given in Section 4.

Frequency spectrum. Consider a population whose allele frequencies follow (1.2); see e.g. Bustamante et al. (2001) for such a model. Assume that $\psi$ satisfies (1.1). Let $f^\alpha(x)dx$ be the expected number of alleles at frequency $x$ in a model with constant immigration of new alleles. (For details, see Theorem 4). We obtain from Corollary 2.4

$$f^\alpha(x) = \frac{1}{x} + \alpha (\beta + \gamma (1 - 2x)) + o(\alpha) \quad \text{as } \alpha \to 0,$$

(1.7)
i.e. for low levels of selection there are more alleles in low frequencies than there are in the neutral case.

Diploid populations. Classically, linear frequency dependent selection as given above also arises in diploid populations undergoing selection, which lead to $\psi(x) = h + x(1 - 2h)$, and $h$ is called the dominance coefficient. If $h = 0$, the diffusion models the frequency path of a selected recessive allele, whereas the allele is dominant for $h = 1$. In the case $h \in (0, 1)$, we speak of incomplete dominance. Overdominance refers to $h > 1$, and means (if $\alpha > 0$) that the heterozygote is fitter than any homozygote. Finally, underdominance refers to $h < 0$, and implies that the homozygote is less fit (if $\alpha > 0$) than any homozygote.

By setting $\beta = h$ and $\gamma = 2h - 1$, (1.4) then implies the (somewhat counter-intuitive) result that fixation or extinction of a positively (i.e. $\alpha > 0$) selected allele takes longer than under neutrality for $h > 1/2$. Moreover, (1.5) gives that – conditional on fixation – the positively selected allele takes longer to fix than under neutrality if $h > 1/2$. The latter result was shown already by Mafessoni and Lachmann (2015). In addition, they report that mildly deleterious (i.e. $\alpha < 0$)
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recessive (i.e. \( h = 0 \)) alleles on average survive in a population slightly longer than neutral ones, before getting lost. This is a direct consequence of (1.6).

This paper is organized as follows: In Section 2, we derive an approximation for the fixation probability (Theorem 1) for small \( \alpha \). Unconditional hitting times (Theorem 2) as well as conditional hitting times (Theorems 3 and 4) are treated as well, also in the situation of a more general one-dimensional diffusion (2.1). Finally, we compute the effect of low levels of frequency-dependent selection on the frequency spectrum (Theorem 5). All our theorems come with corollaries which treat the special case, where \( X \) is a solution of (1.2) and \( \psi \) is a polynomial describing the frequency dependence. Such a polynomial frequency-dependence is the topic of Section 3, which starts by recalling how the Wright-Fisher dynamics (1.2) arises as a scaling limit of an evolutionary game. We will discuss evolutionary games in a haploid population, give the generalization of the one-third rule as described above, and connect our results to the effect of stochastic slowdown. In addition, we will review a diploid situation considered in Hashimoto and Aihara (2009), and show how this leads to a frequency dependence given by \( \psi \) being a polynomial of degree 3. Our Theorem will then directly render (and explain) the 2/5 and 3/10 rules discovered in Hashimoto and Aihara (2009).

Section 4 contains a discussion and some more implications of our findings. In Appendix A, we give the proofs to all our main results from Section 2.

2 Main results

In this section, we are concerned with the following situation. Let \( \sigma : [0,1] \to \mathbb{R}_+ \) have a continuous derivative, and let \( \psi : [0,1] \to \mathbb{R} \) be such that \( \mu := \psi \cdot \sigma^2 \) is bounded. For \( \alpha \in \mathbb{R} \), let \( X \) under the measure \( P^\alpha \) be the Itô diffusion started in \( X_0 = x \in (0,1) \) and solving

\[
dX = \alpha \mu(X)dt + \sigma(X)dW
\]  

(2.1)

up to the first hitting time \( T = T_0 \wedge T_1 \) of \( \{0,1\} \). A most important special case is that \( \sigma^2(y) = y(1-y) \), which brings us back to the Wright-Fisher diffusion with frequency dependent selection, and that \( \psi \) is a polynomial. However, we note that our results also apply to more general \( \sigma^2 \) and \( \psi \). We formulate our results for the state space \([0,1]\) (also because of notational convenience); versions for more general state spaces \([u,v]\) are easily obtained by scaling.

Our first result is on fixation probabilities for low levels of selection, and can be seen as a generalization of the 1/3-rule described after (1.3).

**Theorem 1** (Hitting probabilities). We have

\[
\frac{1}{2\alpha} \left( P^\alpha_x(T_1 < T_0) - x \right) \xrightarrow{\alpha \to 0} x \int_0^1 (1-y)\psi(y)dy - \int_0^x (x-y)\psi(y)dy.
\]  

(2.2)

Next we specialize this to monomial \( \psi \); by linearity of the r.h.s. of (2.2) in \( \psi \), this then immediately extends to polynomial \( \psi \).

**Corollary 2.1** (Hitting probabilities for polynomial \( \psi \)). Let \( k = 0,1,2,... \)

1. If \( \psi(x) = x^k \), then

\[
\frac{\partial}{\partial \alpha} P^\alpha_x(T_1 < T_0) = \frac{1}{(k+2)} x(1-x^{k+1}).
\]

In particular, for \( k = 0 \),

\[
\frac{\partial}{\partial \alpha} P^\alpha_x(T_1 < T_0) = x(1-x),
\]

while for \( k = 1 \),

\[
\frac{\partial}{\partial \alpha} P^\alpha_x(T_1 < T_0) = \frac{1}{3} x(1-x^2).
\]
2. If $\psi(x) = (1-x)^k$, then
\[
\frac{\partial}{\partial \alpha} \mathbb{E}_x^\alpha(T_1 < T_0) = \frac{1}{(k+2)^2} (1-x)(1-(1-x)^{k+1}).
\]

We now turn to the analysis of fixation times. First, we are dealing with the unconditional case, i.e. the the expectation of the hitting time $T$. Note that, for $\psi$ as in (1.1), Corollary 2.2 specializes to (1.3) in the introduction.

**Theorem 2** (Expected hitting time – unconditional case). Consider the same situation as in Theorem 1. Then, if all integrals exist,
\[
\lim_{\alpha \to 0} \frac{1}{4\alpha} \int_0^x \left( (1-y)^{k+1} - \frac{y(1-y^k)}{k+2(k+1)(k+2)} \right) dy + o(x) \quad \text{as } x \to 0.
\]

In particular, for $k = 0, 1, 2, \ldots$

1. If $\psi(x) = x^k$,
\[
\frac{\partial}{\partial \alpha} \mathbb{E}_x^\alpha(T)|_{\alpha = 0} = 4x \int_0^1 \frac{1}{\sigma^2(y)} \left( \frac{(1-y)^{k+1}}{k+2} - \frac{y(1-y^k)}{k+1(k+2)} \right) dy + o(x) \quad \text{as } x \to 0.
\]

2. If $\psi(x) = (1-x)^k$,
\[
\frac{\partial}{\partial \alpha} \mathbb{E}_x^\alpha(T)|_{\alpha = 0} = \frac{4x}{k+2} \int_0^1 \frac{1}{\sigma^2(y)} (1-y)(1-(1-y)^{k+1}) dy + o(x) \quad \text{as } x \to 0.
\]

We now study the conditional hitting times in two versions, which directly lead to (1.5) and (1.6) in the introduction. First, the process exits at the boundary point opposite to where it entered, and second the process exits at the same boundary point. Here $\mathbb{E}_x^\alpha[.] := \lim_{\alpha \to 0} \mathbb{E}_x^\alpha[|T_1 < T_0]$ denotes the expectation under the measure of the diffusion started in 0 and conditioned to reach 1, and $\mathbb{E}_x^\alpha[.] := \mathbb{E}_x^\alpha[|T_0 < T_1]$ denotes the expectation under the measure of the diffusion started in $x$ and conditioned to reach 0 before 1.

**Theorem 3** (Expected hitting time - conditional case I). In the situation of Theorem 1, if all integrals exist,
\[
\lim_{\alpha \to 0} \frac{1}{4\alpha} \left( \mathbb{E}_x^\alpha[|T_1] - 2 \int_0^1 \frac{(1-y)y}{\sigma^2(y)} dy \right)
= \int_0^1 \frac{1}{\sigma^2(y)} \left( (1-y)^2 \int_y^1 z\psi(z)dz - y^2 \int_y^1 (1-z)\psi(z)dz \right) dy.
\]
Corollary 2.3 (Expected hitting time – conditional case I – polynomial ψ). Let $k = 0, 1, 2, ...$

1. If $\psi(x) = x^k$,
   \[
   \frac{\partial}{\partial \alpha} \mathbb{E}^*_{0+}[T_1]|_{\alpha=0} = 4 \int_0^1 \frac{1}{\sigma^2(y)} \cdot \frac{(1-y)y^{k+2}}{k+2} - \frac{y^2(1-y^{k+1})}{(k+1)(k+2)} dy. \tag{2.8}
   \]
   In particular, for $k = 0$,
   \[
   \frac{\partial}{\partial \alpha} \mathbb{E}^*_{0+}[T_1]|_{\alpha=0} = 0. \tag{2.9}
   \]
   and for $k = 1$
   \[
   \frac{\partial}{\partial \alpha} \mathbb{E}^*_{0+}[T_1]|_{\alpha=0} = -\frac{2}{3} \int_0^1 \frac{y^2(1-y)^2}{\sigma^2(y)} dy. \tag{2.10}
   \]

2. If $\psi(x) = (1-x)^k$,
   \[
   \frac{\partial}{\partial \alpha} \mathbb{E}^*_{0+}[T_1]|_{\alpha=0} = -4 \int_0^1 \frac{1}{\sigma^2(y)} \cdot \frac{(1-y)y^{k+2}}{k+2} - \frac{(1-y)^2(1-(1-y)^{k+1})}{(k+1)(k+2)} dy.
   \]

We note that – according to (11) in Griffiths (2003) – the expected age of an allele which is at frequency $x$ is given by $a(x) = \mathbb{E}^*_{x+}[T_0]$. Therefore, our next result is also a statement on average ages of alleles for low levels of selection.

**Theorem 4** (Expected hitting time – conditional case II). In the situation of Theorem II and if all integrals exist

\[
\lim_{x \to 0} \frac{1}{\alpha} \left( \frac{1}{x} \mathbb{E}^*_{x+}[T_0] \right) - \frac{2}{x} \int_0^x \frac{y}{\sigma^2(y)} dy - 2 \int_0^1 \frac{(1-y)^2}{\sigma^2(y)} dy
= \int_0^1 \frac{1}{\sigma^2(y)} \left( (1-y)^2 \int_0^y (1-2z)\psi(z) dz - 2y(1-y) \int_y^1 (1-z)\psi(z) dz \right) dy. \tag{2.11}
\]

Corollary 2.4 (Expected hitting time – conditional case II – polynomial ψ). Let $k = 0, 1, 2, ...$

1. If $\psi(x) = x^k$,
   \[
   \frac{\partial}{\partial \alpha} \mathbb{E}^*_{x+}[T_0]|_{\alpha=0} = 4x \int_0^1 \frac{y}{\sigma^2(y)} \left( \frac{k(1-y^{k+1})}{(k+1)(k+2)} - \frac{1-y^k}{k+1} \right) dy + o(x) \quad \text{as } x \to 0.
   \tag{2.12}
   \]
   In particular, for $k = 0$,
   \[
   \frac{\partial}{\partial \alpha} \mathbb{E}^*_{x+}[T_0]|_{\alpha=0} = o(x) \quad \text{as } x \to 0 \tag{2.13}
   \]
   and for $k = 1$
   \[
   \frac{\partial}{\partial \alpha} \mathbb{E}^*_{x+}[T_0]|_{\alpha=0} = -\frac{2}{3} x \int_0^1 \frac{(1-y)^2(1-(1-y)^2)}{\sigma^2(y)} dy + o(x) \quad \text{as } x \to 0. \tag{2.14}
   \]

2. If $\psi(x) = (1-x)^k$,
   \[
   \frac{\partial}{\partial \alpha} \mathbb{E}^*_{x+}[T_0]|_{\alpha=0} = 4x \int_0^1 \frac{(1-y)^2(1-(1-y)^{k+1})}{\sigma^2(y)} \frac{k}{(k+1)(k+2)} dy + o(x) \quad \text{as } x \to 0.
   \]
Another classical application of diffusion theory in population genetics is the frequency spectrum. The underlying idea is that new mutations arise with an intensity \( \theta \) (more precisely, in the limit \( \varepsilon \downarrow 0 \), a Poisson stream of immigrants of frequency \( \varepsilon \) comes in with immigration intensity \( \theta \varepsilon \)). The frequency path of each mutation follows the diffusion \( X \). Then, let \( \theta f^\alpha(x) dx \) be the expected number of diffusion paths in frequency \( x \). According to Theorem 7.20 of Durrett (2008), in our situation this is given by

\[
f^\alpha(x) := e^{2\alpha \int_0^x \psi(y) dy} \sigma^2(x) P^\alpha_x(T_0 < T_1).
\]

This function we study next.

**Theorem 5 (Frequency spectrum).** The function \( f^\alpha \) defined above satisfies

\[
\lim_{\alpha \to 0} \frac{1}{2\alpha} \left( f^\alpha(x) - \frac{1-x}{\sigma^2(x)} \right) = \frac{x}{\sigma^2(x)} \int_0^x (1-y)\psi(y)dy - \int_0^1 (1-y)\psi(y)dy.
\]

**Corollary 2.5 (Frequency spectrum – polynomial \( \psi \)).** Let \( k = 0, 1, 2, \ldots \)

1. If \( \psi(x) = x^k \),

\[
\left. \frac{\partial}{\partial \alpha} f^\alpha(x) \right|_{\alpha = 0} = -\frac{2x}{\sigma^2(x)} \left( 1 - x^k (1 - (1-x)(k+1)) \right).
\]

In particular, for \( k = 0 \),

\[
\left. \frac{\partial}{\partial \alpha} f^\alpha(x) \right|_{\alpha = 0} = \frac{x(1-x)}{\sigma^2(x)}
\]

and for \( k = 1 \)

\[
\left. \frac{\partial}{\partial \alpha} f^\alpha(x) \right|_{\alpha = 0} = -\frac{x(1-x)(1-2x)}{3\sigma^2(x)}
\]

2. If \( \psi(x) = (1-x)^k \),

\[
\left. \frac{\partial}{\partial \alpha} f^\alpha(x) \right|_{\alpha = 0} = -\frac{2x}{\sigma^2(x)} \left( 1 - \frac{1}{x} (1 - (1-x)^{k+2}) \right)
\]

### 3 Applications in Evolutionary Game Theory

Limits of weak selection and large population size have been studied also in evolutionary game theory; see e.g. [Sample and Allen (2017)] for a recent discussion on this topic. These limit arises as follows: Each individual in the population has a certain genotype. At some high rate, pairs of individuals are chosen at random, and the first individual imposes its genotype upon the second. In addition to these neutral events, which in the limit of large populations would give rise to a Wright-Fisher diffusion, also selective events happen at a lower rate. For this, consider two different strategies \( S_1 \) and \( S_2 \) such that genotype \( g \) has a probability \( p_g \) to play strategy \( S_1 \) and \( 1 - p_g \) to play strategy \( S_2 \).

In order to determine the fitness of a genotype, consider the payoff matrix

\[
\begin{array}{c|cc}
  & S_1 & S_2 \\
 S_1 & a & b \\
 S_2 & c & d \\
\end{array}
\]

The absolute fitness of genotype \( g \) is then proportional to the average payoff it receives upon playing against a random individual from the population.
3.1 Evolutionary games in haploid populations

In haploid populations, assume that there are two genotypes, $A$ and $B$, and $A$ always plays strategy $S_1$ whereas $B$-individuals play $S_2$. Then, if $x$ is the frequency of $A$-alleles, the fitness of any $A$-individual is $1 + \alpha(xa + (1-x)b)$, since this individual receives payoff $a$ if it plays against $S_1$ and $b$ if it plays against $S_2$. By the same argument, the fitness of a $B$-individual is $1 + \alpha(xc + (1-x)d)$.

In the diffusion limit that is familiar from population genetics (see e.g. Ewens 2004), the relative frequency $X$ of type $A$-individuals then follows the dynamics

$$dX = \alpha X(1-X)(Xa + (1-X)b - Xc - (1-X)d)dt + \sqrt{X(1-X)}dW$$

for $\beta = b - d, \gamma = b - d + c - a$.

Alternatively, argue as follows: Each (ordered) pair of $A$ individuals plays “selective encounters” against each other at rate $\alpha a$, and the first individual has an offspring which replaces a randomly chosen individual from the population. At rate $\alpha b$, a pair $(A, B)$ does the same as well as at rate $\alpha c$ for $(B, A)$, and a pair $(B, B)$ does the same at rate $\alpha d$. Using this model we see that the frequency of $A$ increases if the first individual in the playing pair is $A$ and the replaced individual is $B$. Conversely, the frequency of $A$ decreases if the first individual in the pair is $B$ and the replaced is $A$. Again, in the appropriate scaling limit, this gives rise to (3.1).

In this situation, we can apply Theorems 1, 2, 3, 4, 5 and their corollaries to obtain (1.3), (1.4), (1.5), (1.6) and (1.7). Note that we have

$$\sigma^2(y) = y(1-y)$$

and

$$\psi(z) = \beta - \gamma z.$$ 

Since all right hand sides of Theorems 1–5 are linear in $\psi$, we can directly use Corollaries 2.1, 2.2, 2.3 and 2.4 and sum $\beta$ times the term for $\mu(x) = \sigma^2(x)$ and $-\gamma$ times the term for $\mu(x) = x\sigma^2(x)$. This directly shows our claims.

In the limit $x \to 0$, (1.3) is the classical one-third rule by Nowak et al. (2004). Moreover, note that the right hand side of the unconditioned expectation in (1.5) does not depend on $\gamma$ (compare with (22) in Altrock and Traulsen 2009), while the right hand side of (1.5) does not depend on $\beta$ (compare with (24) in Altrock and Traulsen 2009). In particular, for small $\alpha$, we see that in the unconditioned case the selected allele fixes slower than a neutral allele iff $\beta > 0$, while conditional on fixation, fixation is slower iff $\gamma > 0$.

3.2 Evolutionary games in diploid populations

In Hashimoto and Aihara (2009), evolutionary games in a diploid population were studied. Here, genotypes $AA$, $AB$ and $BB$ are formed from the haploids using the Hardy-Weinberg equilibrium (i.e. genotype $AA$ has a frequency of $x^2$, if $A$ has frequency $x$, etc.) For computing the fitness, we consider two different cases. In the case of a dominant $A$ allele, we have that $AA$ as well as $AB$ play strategy $S_1$ and $BB$ plays strategy $S_2$.

For a dominant $A$-allele, the fitness advantage of $A$ is then computed by assuming that it forms a genotype by randomly choosing a mate and then having an average payoff $\alpha((1-x)^2b + (1-(1-x)^2)a)$. For $B$, the same argument leads to $\alpha(x((1-x)^2b + (1-(1-x)^2)a) + (1-x)((1-x)^2d + (1-(1-x)^2c))$. (The $B$ allele can form $AB$ with probability $x$ and play strategy $S_1$ or form $BB$ with probability $1-x$ and play strategy $S_2$.) In total, we find that in the diffusion limit the frequency of $A$ follows

$$dX = \alpha X(1-X)^2((1-X)^2b + (1-(1-X)^2)a - (1-X)^2d - (1-(1-X)^2)c)dt + \sqrt{X(1-X)}dW$$

for $\beta = a - c, \gamma = a - c + d - b$. Plugging $\psi(x) = (1-x)(\beta - \gamma(1-x)^2)$ into Corollaries 2.1-2.2.
straightforward calculations give
\[
\frac{\partial}{\partial \alpha} P^x(T_1 \leq T_0)|_{\alpha=0} = \frac{2}{3} x \left( \beta - \frac{3}{5} \right) + o(x) \quad \text{as } x \to 0, \tag{3.2}
\]
\[
\frac{\partial}{\partial \alpha} E^x[T]|_{\alpha=0} = \frac{1}{3} x (6 \beta - 5 \gamma) + o(x) \quad \text{as } x \to 0, \tag{3.3}
\]
\[
\frac{d}{d \alpha} E_0^{\alpha \ast}[T]|_{\alpha=0} = \frac{1}{3} \left( \frac{1}{3} \beta - \frac{29}{100} \gamma \right), \tag{3.4}
\]
\[
\frac{d}{d \alpha} \frac{1}{2} E_{x \ast}[T_0]|_{\alpha=0} = \frac{5}{9} \beta - \frac{77}{100} \gamma + o(x) \quad \text{as } x \to 0, \tag{3.5}
\]
\[
\frac{d}{d \alpha} f^\alpha(x)|_{\alpha=0} = \beta \left( \frac{4}{3} - \frac{2}{3} x \right) - \gamma \left( \frac{8}{5} - \frac{12}{5} x + \frac{8}{5} x^2 - \frac{2}{5} x^3 \right). \tag{3.6}
\]

In the case of a recessive A-allele, the heterozygote AB plays strategy $S_2$. In this case, the fitness advantage of A is then $\alpha(x (x^2a + (1-x^2)b) + (1-x)(x^2c + (1-x^2)d))$, whereas the fitness advantage of B is $\alpha(x^2c + (1-x^2)d)$. In total, X follows
\[
d X = \alpha X^2(1-x)(x^2a + (1-x^2)b - x^2c - (1-x^2)d)dt + \sqrt{X(1-X)}dW
\]
\[
= \alpha X^2(1-x)(\beta - \gamma X^2)dt + \sqrt{X(1-X)}dW
\]
for $\beta = b - d, \gamma = b - d + c - a$. From Corollaries 2.1, 2.2, 2.3, 2.4 and 2.5 used with $\psi(x) = x(\beta - \gamma x^2)$, we obtain,
\[
\frac{\partial}{\partial \alpha} P^x(T_1 \leq T_0)|_{\alpha=0} = \frac{1}{3} x \left( \beta - \frac{3}{10} \gamma \right) + o(x) \quad \text{as } x \to 0, \tag{3.7}
\]
\[
\frac{\partial}{\partial \alpha} E^x[T]|_{\alpha=0} = \frac{1}{6} x \gamma + o(x) \quad \text{as } x \to 0, \tag{3.8}
\]
\[
\frac{d}{d \alpha} E_0^{\alpha \ast}[T]|_{\alpha=0} = -\frac{1}{3} \left( \frac{1}{3} \beta - \frac{29}{100} \gamma \right), \tag{3.9}
\]
\[
\frac{d}{d \alpha} \frac{1}{2} E_{x \ast}[T_0]|_{\alpha=0} = -\frac{5}{9} \beta + \frac{27}{100} \gamma + o(x) \quad \text{as } x \to 0, \tag{3.10}
\]
\[
\frac{d}{d \alpha} f^\alpha(x)|_{\alpha=0} = -\frac{1}{3} \beta \left( 1 - \frac{1}{200} x \right) + \frac{1}{10} \gamma \left( 1 + \frac{1}{9} x + x^2 - 4x^3 \right). \tag{3.11}
\]

Equations (3.2) and (3.7) correspond to (and explain) the so-called 2/5 and 3/10 rules in Hashimoto and Aihara (2009).

4 Discussion

As described in Sections 1 and 3, the results from Section 2 unify from the perspective of a diffusion approximation a number of recent findings, by Nowak et al. (2004) on the 1/3 rule, by Altrock and Traulsen (2009), Altrock et al. (2010, 2012) on stochastic slowdown, by Hashimoto and Aihara (2009) on the 2/5 and 3/10 rules in evolutionary games, and by Mafessoni and Lachmann (2015) on “selective strolls”. In addition, they lead to the approximate expected frequency spectrum (3.4) for low levels of selection.

A central tool for proving the results stated in Section 2 is the Green function $G^\alpha(x, y)$ of the process $X$ given by (2.1); see also (A.3) and (A.5) below. Recall that the occupation measure $G^\alpha(x, y)dy$ is the expected amount of time which $X$ (started in $x$) spends in $dy$ before time $T$.

Hitting probabilities. Here we describe how to quickly arrive at (1.3) and, more generally, at the assertion of Theorem 1 by using the Green function. This is based on ideas of Roussset (2003) and Ladret and Lessard (2007) for a time-discrete situation, and becomes even more elegant in
the diffusion setting. We first note that
\[
\mathbf{P}_x^\alpha(X_T = 1) = \mathbf{E}_x^\alpha[X_T]
= x + \int_0^\infty \frac{d}{dt} \mathbf{E}_x^\alpha[X_t] \, dt
= x + \int_0^\infty \mathbf{E}_x^\alpha[\alpha \mu(X_t)] \, dt
= x + \alpha \int_0^1 G^\alpha(x, y) \mu(y) \, dy
= x + \alpha \int_0^1 G^0(x, y) \mu(y) \, dy + \mathcal{O}(\alpha^2).
\]
(4.1)

For the last equality, we note (see the beginning of Appendix A) that \( G^\alpha = G^0 + \mathcal{O}(\alpha) \) and that
\[
G^0(x, y) = \begin{cases} 
2x(1-y) \frac{1}{\sigma^2(y)} & 0 \leq x \leq y \leq 1, \\
2(1-x)y \frac{1}{\sigma^2(y)} & 0 \leq y \leq x \leq 1. 
\end{cases}
\]
Hence we may continue (4.1) as
\[
= x + 2\alpha \left( 1 - x \right) \int_0^x y \psi(y) \, dy + x \int_x^1 (1-y) \psi(y) \, dy + \mathcal{O}(\alpha^2),
\]
which proves Theorem 1. Specializing to (1.1) (see also Corollary 2.1) gives (1.3) and thus the generalized $1/3$ rule.

**Unconditional hitting times.** Since \( \mathbf{E}_x^\alpha[T] = \int_0^1 G^\alpha(x, y) \, dy \), the Green function plays a central role for Theorem 2; indeed, the assertion there can be understood as a statement on the asymptotics of \( \frac{\partial}{\partial \alpha} \mathbf{E}_x^\alpha[T] \big|_{\alpha=0} = \int_0^1 \frac{\partial}{\partial \alpha} G^\alpha(x, y) \big|_{\alpha=0} \, dy \) as \( x \to 0 \). The proof of Theorem 2 (see the right hand side of (A.9)) tells the following refinement of (2.3):
\[
\frac{1}{x} \frac{\partial}{\partial \alpha} G^\alpha(x, y) \big|_{\alpha=0} \xrightarrow{x \to 0} \frac{4}{\sigma^2(y)} \left( 1 - y \right) \int_y^1 (1-z) \psi(z) \, dz - y \int_y^1 (1-z) \psi(z) \, dz.
\]
(4.2)

Setting \( \psi = 1 \), this gives (compare with (2.5))
\[
\frac{\partial}{\partial \alpha} G^\alpha(x, y) \big|_{\alpha=0} = 2x \frac{y(1-y)}{\sigma^2(y)} + o(x) \quad \text{as} \quad x \to 0.
\]

For an intuitive interpretation, note that as long as \( \alpha \) is positive there is a probability of escaping a quick hitting of 0, which for small \( \alpha \) contributes to the occupation measure \( G^\alpha(x, y) \, dy \) in a way that is asymptotically proportional to the neutral case. In particular, hitting the boundary on average takes longer for small positive \( \alpha \) than under neutrality, i.e. for \( \alpha = 0 \).

For the case \( \psi(x) = x^k \), the integrand in (2.4) can be written as
\[
\frac{1}{x} \frac{\partial}{\partial \alpha} G^\alpha(x, y) \big|_{\alpha=0} \xrightarrow{x \to 0} \frac{4y(1-y)}{\sigma^2(y)} \frac{1}{(k+1)(k+2)} \left( k+1 \right) y^k - \sum_{i=0}^{k-1} y^i.
\]
(with the convention that the sum over the empty set is 0).

Considering the case \( \sigma^2(x) = x(1-x) \) as in (1.2) and \( k = 1 \), we note that the right hand side is antsymmetric around 1/2. The leading term in this difference comes from the paths which, after starting near 0, escape a quick hitting of 0; the antisymmetry around 1/2 has to be attributed to
the linearity of $\psi$ and leads to a vanishing right hand side. For $k > 1$, we find by integrating the right hand side that

$$
\frac{1}{x} \frac{\partial}{\partial \alpha} E^0_x[T] \xrightarrow{x \to 0} - \frac{4}{(k+1)(k+2)} \sum_{i=2}^{k} \frac{1}{i}.
$$

In particular, the expected hitting time for small positive $\alpha$ is smaller than under neutrality.

**Conditional hitting times.** As for unconditional hitting times, the assertions of Theorems 3 and 4 are true even on the level of Green functions. Conditional under $T_1 < T_0$, and writing $G^*$ for the Green function in this case, we have (see formula (A.11) in the Appendix)

$$
\frac{\partial}{\partial \alpha} G^*(0+, y) \bigg|_{\alpha=0} = \frac{4}{\sigma^2(y)} \left( (1-y)^2 \int_0^y z\psi(z)dz - y^2 \int_y^1 (1-z)\psi(z)dz \right).
$$

Specializing to $\psi(x) = x^k$, this gives (as a reformulation of the integrand in (2.8))

$$
\frac{\partial}{\partial \alpha} G^*(0+, y) \bigg|_{\alpha=0} = \frac{4y^2(1-y)}{\sigma^2(y)} \frac{1}{(k+1)(k+2)} \left( (k+1)y^k - \sum_{i=0}^{k} y^i \right) \leq 0
$$

with equality if and only if $k = 0$. In particular, the expected hitting time of 1 decreases with $\alpha$ for small $\alpha$ and small initial value as long as $k \geq 1$. In Remark A.1 we will see a still finer result: again for small $\alpha$ and small $x$, conditional on $T_1 < T_0$, the additional infinitesimal mean displacement vanishes for $k = 0$ (cf. (2.9)) and is strictly positive and increases with $\alpha$ (which makes the expected hitting time shorter) for $k \geq 1$.

Conditional under $T_0 < T_1$, and writing $G_*$ for the Green function in this case, we see from formula (A.1) in the Appendix (see also the integrand in (2.11)) that

$$
\frac{1}{x} \frac{\partial}{\partial \alpha} G_*(x, y) \bigg|_{\alpha=0} \xrightarrow{x \to 0} \frac{4}{\sigma^2(y)} \left( (1-y)^2 \int_0^y (1-2z)\psi(z)dz - 2y(1-y) \int_y^1 (1-z)\psi(z)dz \right).
$$

For $\psi(x) = x^k$, straightforward calculations give that for small positive $\alpha$ the process $X$ stays in $dy$ longer than under neutrality, i.e. for $\alpha = 0$, if and only if $\frac{1}{2}ky^k > \sum_{i=0}^{k-1} y^i$. For $k = 0, 1$, such $y$'s do not exist.

**Frequency spectrum.** Changes in the frequency spectrum are often used to infer deviations from neutral evolution. From Theorem 3 frequencies at $x$ are higher for small positive $\alpha$ than for $\alpha = 0$ if and only if $h(x) > h(1)$ for $h(x) := \frac{1}{x} \int_0^x (1-y)\psi(y)dy$. For $\psi(x) = x^k$, we find that $h(x) = \frac{1}{x} x^k - \frac{1}{x+k} x^{k+1}$. Thus, $h(x) > h(1)$ if and only if $x^k((k+2) - (k+1)x) > 1$. For $k = 0$, this is the case for all $x$, whereas for $k = 1$, this is only the case for $x > 1/2$. In other words, high-frequency variants are more abundant under low levels of linear frequency dependent selection than under neutrality.

## A Proofs

In what follows, for notational convenience we will suppress the superscript $\alpha$ and simply write $P_x$, $E_x$, $G(x, y)$, $\ldots$, instead of $P^\alpha_x$, $E^\alpha_x$, $G^\alpha(x, y)$, $\ldots$.

We will express the hitting probability stated in Theorem 1 by the scale function of $X$ (see e.g. Karlin and Taylor 1981, p. 192ff)) given by

$$
S(x) := \int_0^x e^{-2\alpha \int_0^y \psi(z)dz}dy.
$$

(A.1)
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Then, we have

\[ P_x(T_1 < T_0) = \frac{S(x) - S(0)}{S(1) - S(0)}. \]  \hspace{1cm} (A.2)

Moreover, concerning Theorems 1-3, the expected amount of time which the diffusion started in \( x \) spends in \( dy \), is \( G(x,y)dy \), with the Green function

\[
G(x,y) = \begin{cases} 
2P_x(T_1 < T_0)\frac{S(1) - S(y)}{\sigma^2(y)S'(y)} = 2P_y(T_0 < T_1)\frac{S(x) - S(0)}{\sigma^2(y)S'(y)}, & x \leq y, \\
2P_x(T_0 < T_1)\frac{S(y) - S(0)}{\sigma^2(y)S'(y)} = 2P_y(T_1 < T_0)\frac{S(1) - S(x)}{\sigma^2(y)S'(y)}, & x \geq y.
\end{cases}
\]  \hspace{1cm} (A.3)

When conditioned on \( \{T_1 < T_0\} \), this changes to

\[
G^*(x,y) = G(x,y)\frac{P_y(T_1 < T_0)}{P_x(T_1 < T_0)},
\]  \hspace{1cm} (A.4)

whereas on \( \{T_0 < T_1\} \), the Green function is

\[
G^*(x,y) = G(x,y)\frac{P_y(T_0 < T_1)}{P_x(T_0 < T_1)}.
\]  \hspace{1cm} (A.5)

We already gave a proof of Theorem 1 in Section 4; here, we give another short proof using (A.1) and (A.2).

**Proof of Theorem 1** Linearizing (A.1) and using Fubini we obtain

\[
S(x) = x - 2\alpha \int_0^x \int_0^y \psi(z)\,dz\,dy + \mathcal{O}(\alpha^2) = x - 2\alpha \int_0^x \int_z^x \psi(z)\,dy\,dz + \mathcal{O}(\alpha^2)
\]  \hspace{1cm} (A.6)

Therefore,

\[
P_x(T_1 < T_0) = \frac{S(x) - S(0)}{S(1) - S(0)} = x - 2\alpha \int_0^x (x - y)\psi(y)\,dy + 2\alpha x \int_0^1 (1 - y)\psi(y)\,dy + \mathcal{O}(\alpha^2),
\]  \hspace{1cm} (A.7)

and the result follows.

**Proof of Corollary 2.1** 1. Here, \( \psi(x) = x^k \) and therefore, the right hand side of (2.2) becomes

\[
x \int_0^1 (1 - y)y^k\,dy - \int_0^x (x - y)y^k\,dy = (x - x^{k+2})\left(\frac{1}{k + 1} - \frac{1}{k + 2}\right) = x(1 - x^{k+1})\frac{1}{(k + 1)(k + 2)}.
\]

2. Here, we compute for the right hand side of (2.2)

\[
x \int_0^1 (1 - y)^{k+1}\,dy - \int_0^x (1 - y - (1 - x))(1 - y)^k\,dy
\]

\[
= \frac{x}{k + 2} - \frac{1}{k + 2}(1 - (1 - x)^{k+2}) + \frac{1}{k + 1}(1 - x)(1 - (1 - x)^{k+1})
\]

\[
= \frac{1}{(k + 1)(k + 2)}((1 - x) - (1 - x)^{k+2}).
\]
Proof of Theorem \(2\) Since \(E_x[T] = \int_0^1 G(x,y)dy\), we have to approximate the Green function, as given in (A.3). First,

\[
S(x) = x - 2\alpha \int_0^x (x-y)\psi(y)dy + O(\alpha^2),
\]

\[
S'(x) = 1 - 2\alpha \int_0^x \psi(y)dy + O(\alpha^2). \tag{A.8}
\]

Then, for \(0 \leq x \leq y \leq 1\) (use (2.2) for the second equality)

\[
G(x, y) = 2P_x(T_1 < T_0) \frac{S(1) - S(y)}{\sigma^2(y)S'(y)}
\]

\[
= \frac{2}{\sigma^2(y)} \left( x + 2\alpha \left( \int_0^1 (1-z)\psi(z)dz - \frac{1}{x} \int_0^x (x-z)\psi(z)dz \right) \right)
\]

\[
\cdot \left( 1 - y - 2\alpha \left( \int_0^1 (1-z)\psi(z)dz - \int_0^y (y-z)\psi(z)dz \right) \left( 1 + 2\alpha \int_0^y \psi(z)dz \right) + O(\alpha^2) \right)
\]

\[
= \frac{2}{\sigma^2(y)} \left( x(1-y) + 2\alpha \left( (1-x)(1-y) \int_0^x z\psi(z)dz + x(1-y) \int_x^y (1-z)\psi(z)dz \right) \right.
\]

\[
- xy \int_0^1 (1-z)\psi(z)dz + x \int_0^y (y-z)\psi(z)dz \bigg) + O(\alpha^2) \tag{A.9}
\]

while for \(0 \leq y \leq x \leq 1\)

\[
G(x, y) = 2P_x(T_0 < T_1) \frac{S(y) - S(0)}{\sigma^2(y)S'(y)}dy
\]

\[
= \frac{2}{\sigma^2(y)} \left( 1 - x - 2\alpha \left( \int_0^1 (1-z)\psi(z)dz - \frac{1}{x} \int_0^x (x-z)\psi(z)dz \right) \right)
\]

\[
\cdot \left( y - 2\alpha \left( \int_0^y (y-z)\psi(z)dz \right) \left( 1 + 2\alpha \int_0^y \psi(z)dz \right) + O(\alpha^2) \right)
\]

\[
= \frac{2}{\sigma^2(y)} \left( (1-x)y + 2\alpha \left( (1-x)y \int_0^y \psi(z)dz - (1-x) \int_0^y (y-z)\psi(z)dz \right) \right.
\]

\[
- xy \int_0^1 (1-z)\psi(z)dz + y \int_0^x (x-z)\psi(z)dz \bigg) + O(\alpha^2) \tag{A.10}
\]

Dividing (A.9) and (A.10) by \(x\) and letting \(x \to 0\) gives the result. \qed
Proof of Corollary 2.2. 1. The right hand side of (2.3) becomes

\[
\int_0^1 \int_0^y \frac{1-y}{\sigma^2(y)} (1-z) z^k dz dy - \int_0^1 \int_y^1 \frac{y}{\sigma^2(y)} (1-z) z^k dz dy \\
= \int_0^1 \frac{1-y}{\sigma^2(y)} \left( \frac{1}{k+1} y^{k+1} - \frac{1}{k+2} y^{k+2} \right) - \frac{y}{\sigma^2(y)} \left( \frac{1}{k+1} (1-y^{k+1}) - \frac{1}{k+2} (1-y^{k+2}) \right) dy \\
= \int_0^1 \left( 1-y \right) \frac{y^{k+1}}{\sigma^2(y)} \left( \frac{1}{(k+1)(k+2)} + \frac{1}{k+2} (1-y) \right) \\
- \frac{y(1-y^{k+1})}{\sigma^2(y)} \left( \frac{1}{(k+1)(k+2)} + \frac{(1-y)y^{k+2}}{k+2} \right) dy \\
= \int_0^1 \frac{1}{\sigma^2(y)} \left( \frac{1-y}{k+2} y^{k+1} - \frac{y(1-y)}{k+1}(1-y^{k+1}) \right) dy.
\]

2. The right hand side of (2.3) becomes

\[
\int_0^1 \int_0^y \frac{1-y}{\sigma^2(y)} (1-z)^{k+1} dz dy - \int_0^1 \int_y^1 \frac{y}{\sigma^2(y)} (1-z)^{k+1} dz dy \\
= \int_0^1 \frac{1-y}{\sigma^2(y)} \left( \frac{1}{k+2} (1 - (1-y)^{k+2}) \right) - \frac{y}{\sigma^2(y)} \left( \frac{1}{(k+2)} (1 - y^{k+2}) \right) dy \\
= \frac{1}{k+2} \int_0^1 \frac{1}{\sigma^2(y)} (1-y)(1-(1-y)^{k+1}) dy. \quad \Box
\]

Proof of Theorem 3. Recall from (A.4) that for \( x \leq y \)

\[
G^*(x, y) = G(x, y) \frac{P_y(T_1 < T_0)}{P_x(T_1 < T_0)} = \frac{2}{\sigma^2(y)} P_y(T_0 < T_1) \frac{S(y) - S(0)}{S'(y)}.
\]

With \( S, S' \) as in (A.8), and with (A.7), we find that

\[
\lim_{x \to 0} E^{2*}[T_1] = \int_0^1 G^*(0, y) dy \\
= 2 \int_0^1 \frac{1}{\sigma^2(y)} (1-y) + 2\alpha \left( \int_0^y (y-z) \psi(z) dz - y \int_0^1 (1-z) \psi(z) dz \right) \\
\cdot \left( y - 2\alpha \int_0^y (y-z) \psi(z) dz \cdot \left( 1 + 2\alpha \int_0^y \psi(z) dz \right) \frac{1}{\sigma^2(y)} dy + O(\alpha^2) \right) \\
= 2 \int_0^1 \frac{1-y}{\sigma^2(y)} dy + 4\alpha \int_0^1 \frac{y(1-y)}{\sigma^2(y)} \int_0^y \psi(z) dz + \frac{y}{\sigma^2(y)} \int_0^y (y-z) \psi(z) dz \\
- \frac{y^2}{\sigma^2(y)} \int_0^1 (1-y + y - z) \psi(z) dz - \frac{1-y}{\sigma^2(y)} \int_0^y (y-z) \psi(z) dz dy + O(\alpha^2) \\
= 2 \int_0^1 \frac{1-y}{\sigma^2(y)} dy + 4\alpha \int_0^1 \frac{y(1-y)}{\sigma^2(y)} \int_0^y \psi(z) dz - \frac{(1-y)^2}{\sigma^2(y)} \int_0^y (y-z) \psi(z) dz \\
- \frac{y^2}{\sigma^2(y)} \int_0^1 (1-z) \psi(z) dz - \frac{y^2(1-y)}{\sigma^2(y)} \int_0^y \psi(z) dz dy + O(\alpha^2) \\
= 2 \int_0^1 \frac{1-y}{\sigma^2(y)} dy + 4\alpha \int_0^1 \frac{(1-y)^2}{\sigma^2(y)} \int_0^y z \psi(z) dz - \frac{y^2}{\sigma^2(y)} \int_0^1 (1-z) \psi(z) dz dy + O(\alpha^2)
\]

and we are done. \( \Box \)
Proof of Corollary 2.3. 1. For \( \psi(x) = x^k \), the right hand side of (2.7) becomes

\[
\int_0^1 \frac{1}{\sigma^2(y)} \left( (1-y)^2 \int_0^y z^{k+1}dz - y^2 \int_y^1 (1-z)z^kdz \right) dy \\
= \int_0^1 \frac{1}{\sigma^2(y)} \left( (1-y)^2 \frac{1}{k+2} y^{k+2} - y^2 \left( \frac{1}{k+1} (1-y^{k+1}) - \frac{1}{k+2} (1-y^{k+2}) \right) \right) dy \\
= \int_0^1 \frac{1}{\sigma^2(y)} \left( (1-y)^2 y^{k+2} \frac{1}{k+2} - y^2 \left( \frac{1}{k+1} (1-y^{k+1}) + y^{k+3} (1-y) \frac{1}{k+2} \right) \right) dy \\
= \int_0^1 \frac{1}{\sigma^2(y)} \left( \frac{(1-y)y^{k+2}}{k+2} - \frac{y^2 (1-y^{k+1})}{(k+1)(k+2)} \right) dy.
\]

where in the second equality we have used the display from part 1 of the proof.

2. For \( \psi(x) = (1-x)^k \), the right hand side of (2.7) becomes

\[
\int_0^1 \frac{1}{\sigma^2(y)} \left( (1-y)^2 \int_0^y z(1-z)^kdz - y^2 \int_y^1 (1-z)z^{k+1}dz \right) dy \\
y \to 1-y \to 1-z \\
= \int_0^1 \frac{1}{\sigma^2(1-y)} \left( y^2 \int_y^1 (1-z)z^kdz - (1-y)^2 \int_0^y z^{k+1}dz \right) dy \\
= - \int_0^1 \frac{1}{\sigma^2(1-y)} \left( \frac{(1-y)y^{k+2}}{k+2} - \frac{y^2 (1-y^{k+1})}{(k+1)(k+2)} \right) dy \\
= - \int_0^1 \frac{1}{\sigma^2(y)} \left( \frac{y(1-y)^{k+2}}{k+2} - \frac{(1-y)^2 (1-y(1)(1-y)^k)}{(k+1)(k+2)} \right) dy,
\]

Remark A.1. We append here the calculation (for small \( \alpha \)) of the infinitesimal mean displacement of the diffusion process \( X \) conditioned hit 1; this was announced in Section 4 as an additional explanation of the monotone increase of \( \mu^* \). Recall that for the solution of (2.4), conditioned to hit 1, \( \mu \) becomes (see e.g. Karlin and Taylor 1981, p. 263)

\[
\mu^*(x) = \alpha \mu(x) + \frac{S'(x)}{S(x) - S(0)} \sigma^2(x) = \alpha \mu(x) + \left( \frac{1}{x} - \frac{1}{x^2} \int_0^x \psi(y)dy \right) \sigma^2(x) + \mathcal{O}(\alpha^2) \\
= \alpha \mu(x) + \frac{1}{x} \int_0^x \psi(y)dy - \int_0^x \frac{x-y}{x} \psi(y)dy \right) \sigma^2(x) + \mathcal{O}(\alpha^2) \\
= \frac{1}{x} \sigma^2(x) + \alpha \left( \psi(x) - \frac{2}{x^2} \int_0^x \psi(y)dy \right) \sigma^2(x) + \mathcal{O}(\alpha^2).
\]

In particular, if \( \psi(x) = x^k \),

\[
\mu^*(x) = \frac{1}{x} \sigma^2(x) + \alpha \left( x^k - \frac{2}{k+2} x^k \right) \sigma^2(x) + \mathcal{O}(\alpha^2) = \frac{1}{x} \sigma^2(x) + \alpha \frac{k}{k+2} x^k \sigma^2(x) + \mathcal{O}(\alpha^2).
\]

This shows that the additional infinitesimal mean displacement increases with \( \alpha \). Moreover, the additional infinitesimal mean displacement vanishes for \( k = 0 \), which explains (2.9).

Proof of Theorem 4. We start by writing the Green function for the diffusion \( X \), conditional to hit 0, which is from \( \text{(A.5)} \)

\[
G_s(x, y) = G(x, y) \frac{P_y(T_0 < T_1)}{P_x(T_0 < T_1)}.
\]  

(A.12)
Note that for \( x \leq y \)

\[
\frac{P_y(T_0 < T_1)}{P_x(T_0 < T_1)} = \frac{1 - y - 2\alpha \left( \frac{1}{(1-x)^2} \int_0^1 (1-z)\psi(z)dz - \int_0^y (y-z)\psi(z)dz \right) + O(\alpha^2)}{1 - x - 2\alpha \left( \frac{1}{(1-x)^2} \int_0^1 (1-z)\psi(z)dz - \int_0^x (x-z)\psi(z)dz \right)}
\]

Combining the last equality with (A.12) and (A.9),

Proof of Corollary 2.4.

1. For \( \psi(x) = x^k \), the right hand side of (2.11) gives

\[
\int_0^1 \frac{1}{\sigma^2(y)} \left( (1-y)^2 \int_0^y (1-2z)z^kdz - 2y(1-y) \int_0^1 (1-z)z^kdz \right) dy
\]

\[
= \int_0^1 \frac{1 - y}{\sigma^2(y)} \left( (1-y) \left( \frac{k+1}{k+2} y^{k+1} - \frac{2}{k+2} y^{k+2} \right) - 2y \left( \frac{1}{k+1} (1-y^{k+1}) - \frac{1}{k+2} (1-y^{k+2}) \right) \right) dy
\]

\[
= \int_0^1 \frac{1 - y}{\sigma^2(y)} \left( (y(1-y^{k+2}) - (1-y)y^{k+2}) \frac{2}{k+2} + ((1-y)y^{k+1} - 2y(1-y^{k+1}) \frac{1}{k+1} \right) dy
\]

\[
= \int_0^1 \frac{y(1-y)}{\sigma^2(y)} \left( \frac{2(1-y^{k+1})}{k+2} - 2y - y^{k+1} \right) dy = \int_0^1 \frac{y(1-y)}{\sigma^2(y)} \left( \frac{k(1-y^{k+1})}{(k+1)(k+2)} - \frac{1}{k+1} \right) dy.
\]
2. For $\psi(x) = (1 - x)^k$, the right hand side of (2.11) becomes

$$
\int_0^1 \frac{1}{\sigma^2(y)} \left( (1-y)^2 \int_0^y (1-2z)(1-z)^k dz - 2y(1-y) \right) dy
$$

$$
y \to 1-y, z \to 1-z \\
= -\int_0^1 \frac{y}{\sigma^2(1-y)} \left( y(1-y)^{k+1} + \frac{2(1-y)y^{k+2} - 2y(1-y)^{k+2}}{k+2} \right) dy.
$$

Proof of Theorem 3.1. Because of (2.2), $f^\alpha$ satisfies

$$
f^\alpha(x) = \left\{ \begin{array}{ll}
\frac{1}{\sigma^2(x)} (1+2\alpha \int_0^x \psi(y) dy) & (1-x) - 2\alpha \left( \int_0^1 (1-y) \psi(y) dy - \int_0^x (x-y) \psi(y) dy \right) \\
= \frac{1-x}{\sigma^2(x)} + \frac{2\alpha}{\sigma^2(x)} \left( \int_0^x \psi(y) dy - \int_0^1 \psi(y) dy \right)
\end{array} \right. + O(\alpha^2)
$$

Proof of Corollary 3.2. 1. We compute

$$
\frac{1}{x} \int_0^x (1-y)y^k dy - \int_0^1 (1-y)y^k dy = \frac{1}{k+1} x^k - \frac{1}{k+2} x^{k+1} - \frac{1}{(k+1)(k+2)}
$$

$$
= -\frac{1-x^k(1+(1-x)(k+1))}{(k+1)(k+2)}.
$$

2. We compute

$$
\frac{1}{x} \int_0^x (1-y)^{k+1} dy - \int_0^1 (1-y)^{k+1} dy = \frac{1}{k+2} \left( \frac{1}{x} (1-(1-x)^{k+2}) - 1 \right).
$$

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