

and a σ protein that assists only with initiation. Elongation synthesizes mRNA in the 5' to 3' direction at a rate of 40 nucleotides per second. Termination liberates the mRNA and occurs either by rho protein interaction or by the formation of an mRNA hairpin.

15.3 Eukaryotic Transcription

Transcription in eukaryotes involves one of three types of polymerases, depending on the gene being transcribed. RNA polymerase II transcribes all of the protein-coding genes, whereas RNA polymerase I transcribes rRNA genes, and RNA polymerase III transcribes rRNA, tRNA, and small nuclear RNA genes. The initiation of transcription in eukaryotes involves the binding of several transcription factors to complex promoter sequences that are usually located upstream of the gene being copied. The mRNA is synthesized in the 5' to 3' direction, and the FACT complex moves and reassembles nucleosomes as the polymerase passes by. Whereas RNA polymerases I and III terminate transcription by protein- or RNA hairpin-dependent methods, RNA polymerase II transcribes for 1,000 or more nucleotides beyond the gene template and cleaves the excess during pre-mRNA processing.

15.4 RNA Processing in Eukaryotes

Eukaryotic pre-mRNAs are modified with a 5' methylguanosine cap and a poly-A tail. These structures protect the mature mRNA from degradation and help export it from the nucleus. Pre-mRNAs also undergo splicing, in which introns are removed and exons are reconnected with single-nucleotide accuracy. Only finished mRNAs that have undergone 5' capping, 3' polyadenylation, and intron splicing are exported from the nucleus to the cytoplasm. Pre-rRNAs and pre-tRNAs may be processed by intramolecular cleavage, splicing, methylation, and chemical conversion of nucleotides. Rarely, RNA editing is also performed to insert missing bases after an mRNA has been synthesized.

15.5 Ribosomes and Protein Synthesis

The players in translation include the mRNA template, ribosomes, tRNAs, and various enzymatic factors. The small ribosomal subunit forms on the mRNA template either at the Shine-Dalgarno sequence (prokaryotes) or the 5' cap (eukaryotes). Translation begins at the initiating AUG on the mRNA, specifying methionine. The formation of peptide bonds occurs between sequential amino acids specified by the mRNA template according to the genetic code. Charged tRNAs enter the ribosomal A site, and their amino acid bonds with the amino acid at the P site. The entire mRNA is translated in three-nucleotide "steps" of the ribosome. When a nonsense codon is encountered, a release factor binds and dissociates the components and frees the new protein. Folding of the protein occurs during and after translation.

REVIEW QUESTIONS

- What is the flow of information for the synthesis of proteins according to the central dogma?
 - DNA to mRNA to protein
 - DNA to mRNA to tRNA to protein
 - DNA to protein to mRNA to protein
 - mRNA to DNA to mRNA to protein
- The DNA of virus A is inserted into the protein coat of virus B. The combination virus is used to infect *E. coli*. The virus particles produced by the infection are analyzed for DNA and protein contents. What results would you expect?
 - DNA and protein from B
 - DNA and protein from A
 - DNA from A and protein from B
 - DNA from B and protein from A
- The AUC and AUA codons in mRNA both specify isoleucine. What feature of the genetic code explains this?
 - Complementarity
 - Degeneracy
 - Nonsense codons
 - Universality
- How many nucleotides are in 12 mRNA codons?
 - 12
 - 24
 - 36
 - 48
- Which of the following molecules does not contain genetic information?
 - DNA
 - mRNA
 - Protein
 - RNA
- Which molecule in the central dogma can be compared to a disposable photocopy of a book kept on reserve in the

library?

- a. DNA
- b. mRNA
- c. Protein
- d. tRNA

7. Which subunit of the *E. coli* polymerase confers specificity to transcription?

- a. α
- b. β
- c. β'
- d. σ

8. Why are the -10 and -35 regions of prokaryotic promoters called consensus sequences?

- a. They are identical in all bacterial species.
- b. They are similar in all bacterial species.
- c. They exist in all organisms.
- d. They have the same function in all organisms.

9. The sequence that signals the end of transcription is called the:

- a. promoter
- b. stop codon
- c. TATA box
- d. terminator

10. If the ρ protein is missing, will a prokaryotic gene be terminated?

- a. It depends on the gene.
- b. No, the rho protein is essential.
- c. Transcription termination is not required.
- d. Yes, the rho protein is not involved in transcription.

11. Which feature of promoters can be found in both prokaryotes and eukaryotes?

- a. GC box
- b. octamer box
- c. TATA box
- d. -10 and -35 sequences

12. At what stage in the transcription of a eukaryotic gene would TFII factors be active?

- a. elongation
- b. initiation
- c. processing
- d. termination

13. Which polymerase is responsible for the synthesis of

5S rRNA?

- a. polymerase I
- b. polymerase II
- c. polymerase III
- d. ribonuclease I

14. What transcripts will be most affected by low levels of α -amanitin?

- a. 18S and 28S rRNAs
- b. 5S rRNAs and tRNAs
- c. other small nuclear RNAs
- d. pre-mRNAs

15. Which of the following features distinguishes eukaryotic transcription from bacterial transcription?

- a. Eukaryotic transcription does not start at a consensus sequence.
- b. Eukaryotic transcription does not require an initiation complex.
- c. Eukaryotic transcription and translation do not take place at the same time.
- d. Eukaryotic transcription does not require a termination sequence.

16. A poly-A sequence is added at the:

- a. 5' end of a transcript in the nucleus
- b. 3'-end of a transcript in the nucleus
- c. 5' end of a transcript in the cytoplasm
- d. 3'-end of a transcript in the cytoplasm

17. Which pre-mRNA processing step is important for initiating translation?

- a. poly-A tail
- b. RNA editing
- c. splicing
- d. 7-methylguanosine cap

18. Where are the RNA components of ribosomes synthesized?

- a. cytoplasm
- b. endoplasmic reticulum
- c. nucleus
- d. nucleolus

19. What processing step enhances the stability of pre-tRNAs and pre-rRNAs?

- a. cleavage
- b. methylation
- c. nucleotide modification
- d. splicing

20. What are introns?

- a. DNA sequences to which polymerases bind
- b. the processed mRNA
- c. translated DNA sequences in a gene
- d. untranslated DNA sequences in a gene

21. What is often the first amino acid added to a polypeptide chain?

- a. adenine
- b. leucine
- c. methionine
- d. thymine

22. In any given species, there are at least how many types of aminoacyl tRNA synthetases?

- a. 20
- b. 40
- c. 100
- d. 200

23. In prokaryotic cells, ribosomes are found in/on the:

- a. cytoplasm
- b. mitochondrion
- c. nucleus
- d. endoplasmic reticulum

24. The peptide bond synthesis in prokaryotic translation is catalyzed by:

- a. a ribosomal protein
- b. a cytoplasmic protein
- c. mRNA itself
- d. ribosomal RNA

25. What would happen if the 5' methyl guanosine was not added to an mRNA?

- a. The transcript would degrade when the mRNA moves out of the nucleus to the cytoplasm.
- b. The mRNA molecule would stabilize and start the process of translation within the nucleus of the cell.
- c. The mRNA molecule would move out of the nucleus and create more copies of the mRNA molecule.
- d. The mRNA molecule would not be able to add the poly-A tail on its strand at the 5' end.

26. Which of the following is associated with the docking of mRNA on a ribosome in eukaryotic cells?

- a. Kozak's sequence
- b. poly-A sequence
- c. Shine-Dalgarno sequence
- d. TATA box

CRITICAL THINKING QUESTIONS

27. If mRNA is complementary to the DNA template strand and the DNA template strand is complementary to the DNA non-template strand, why are base sequences of mRNA and the DNA non-template strand not identical? Could they ever be?

- a. No, they cannot be identical because the T nucleotide in DNA is replaced with U nucleotide in RNA and AUG is the start codon.
- b. No, they cannot be identical because the T nucleotide in RNA is replaced with U nucleotide in DNA.
- c. They can be identical if methylation of the U nucleotide in RNA occurs and gives T nucleotide.
- d. They can be identical if de-methylation of the U nucleotide in RNA occurs and gives T nucleotide.

28. Imagine if there were 200 commonly occurring amino acids instead of 20. Given what you know about the genetic code, what would be the shortest possible codon length? Explain.

- a. Four
- b. Five
- c. Two
- d. Three

29. What part of central dogma is not always followed in viruses?

- a. The flow of information in HIV is from RNA to DNA, then back to RNA to proteins. Influenza viruses never go through DNA.
- b. The flow of information is from protein to RNA in HIV virus, while the influenza virus converts DNA to RNA.
- c. The flow of information is similar, but nucleic acids are synthesized as a result of translation in HIV and influenza viruses.
- d. The flow of information is from RNA to protein. This protein is used to synthesize the DNA of the viruses in HIV and influenza.

30. Suppose a gene has the sequence ATGCGTTATCGGGAGTAG. A point mutation changes the gene to read ATGCGTTATGGGGAGTAG. How

would the polypeptide product of this gene change?

31. Explain the initiation of transcription in prokaryotes. Include all proteins involved.

- a. In prokaryotes the polymerase is composed of five polypeptide subunits, two of which are identical. Four of these subunits, denoted α , α , β , and β' , comprise the polymerase core enzyme. The fifth subunit, σ , is involved only in transcription initiation. The polymerase comprised of all five subunits is called the holoenzyme.
- b. In prokaryotes the polymerase is composed of four polypeptide subunits, two of which are identical. These subunits, denoted α , α , β , and β' , comprise the polymerase core enzyme. There is a fifth subunit that is involved in translation initiation. The polymerase comprised of all four subunits is called the holoenzyme.
- c. In prokaryotes the polymerase is composed of five polypeptide subunits, two of which are identical. Four of these subunits, denoted α , α , β , and β' , comprise the polymerase holoenzyme. The fifth subunit, σ , is involved only in transcription initiation. The polymerase comprised of all five subunits is called the core enzyme.
- d. In prokaryotes the polymerase is composed of five polypeptide subunits, two of which are identical. Four of these subunits, denoted α , α , β , and β' , comprise the polymerase core enzyme. The fifth subunit, σ , is involved only in termination. The polymerase comprised of all five subunits is called the holoenzyme.

32. In your own words, describe the difference between ρ -dependent and ρ -independent termination of transcription in prokaryotes.

- a. Rho-dependent termination is controlled by rho protein and the polymerase stalls near the end of the gene at a run of G nucleotides on the DNA template. In rho-independent termination, when the polymerase encounters a region rich in C-G nucleotides the mRNA folds into a hairpin loop that causes the polymerase to stall.
- b. Rho-independent termination is controlled by rho protein and the polymerase stalls near the end of the gene at a run of G nucleotides on the DNA template. In rho-dependent termination, when the polymerase encounters a region rich in C-G nucleotides, the mRNA folds into a hairpin loop that causes polymerase to stall.
- c. Rho-dependent termination is controlled by rho protein and the polymerase begins near the end of the gene at a run of G nucleotides on the DNA template. In rho-independent termination, when the polymerase encounters a region rich in C-G nucleotides, the mRNA creates a hairpin loop that causes polymerase to stall.
- d. Rho-dependent termination is controlled by rho protein and the polymerase stalls near the end of the gene at a run of G nucleotides on the DNA template. In rho-independent termination, when the polymerase encounters a region rich in A-T nucleotides, the mRNA creates a hairpin loop that causes polymerase to stall.

33. What is the main structure that differentiates between ρ -dependent and ρ -independent termination in prokaryotes?

- a. Rho-independent termination involves the formation of a hairpin.
- b. Rho-dependent termination involves the formation of a hairpin.
- c. Rho-dependent termination stalls when the polymerase begins to transcribe a region rich in A-T nucleotides.
- d. Rho-independent termination stalls when the polymerase begins to transcribe a region rich in G nucleotides.

34. Which step in the transcription of eukaryotic RNA differs the most from its prokaryotic counterpart?

- a. The initiation step in eukaryotes requires an initiation complex with enhancers and transcription factors. Also, the separation of the DNA strand is different as histones are involved.
 - b. The initiation step in prokaryotes requires an initiation complex with enhancers and transcription factors. Also, the separation of the DNA strand is different as histones are involved.
 - c. The elongation step in eukaryotes requires an initiation complex with enhancers and transcription factors. Also, the separation of the DNA strand is different as histones are involved.
 - d. The initiation step in eukaryotes requires an initiation complex with enhancers and transcription factors. Also, the separation of the DNA strand is different as histones are not involved.
- 35.** Would you be able to determine which RNA polymerase you isolated from a eukaryotic cell without analyzing its products?
- a. No, because they have the same α -amanitin sensitivity in all products.
 - b. No, quantitative analysis of products is done to determine the type of polymerase.
 - c. Yes, they can be determined as they differ in α -amanitin sensitivity.
 - d. Yes, they can be determined by the number of molecules that bind to DNA.
- 36.** Can you predict how alternative splicing may lead to an economy of genes? Do you need a different gene for every protein that the cell can produce?
- a. Alternative splicing can lead to the synthesis of several polypeptides from a single gene.
 - b. Alternative splicing can lead to the synthesis of several forms of mRNA from a single gene.
 - c. Alternative splicing can lead to the synthesis of several forms of codons from a set of genes.
 - d. Alternative splicing can lead to the synthesis of several forms of ribosomes from a set of genes.
- 37.** What is the major challenge in the production of RNA in eukaryotes compared to prokaryotes?
- a. exporting the mRNA across the nuclear membrane
 - b. importing the mRNA across the nuclear membrane
 - c. the mRNA staying inside the nuclear membrane
 - d. the mRNA translating into proteins within seconds
- 38.** What would happen if the 5' methyl guanosine was not added to an mRNA?
- a. The transcript would degrade when the mRNA moves out of the nucleus to the cytoplasm.
 - b. The mRNA molecule would stabilize and start the process of translation within the nucleus of the cell.
 - c. The mRNA molecule would move out of the nucleus and create more copies of the mRNA molecule.
 - d. The mRNA molecule would not be able to add the poly-A tail on its strand at the 5' end.
- 39.** Transcribe and translate the following DNA sequence (nontemplate strand): 5'-ATGCCCGTTATTAAGCA-3'
- a. The mRNA would be 5'-AUGGCCGGUUAUUAAGCA-3' and the protein will be MAGY.
 - b. The mRNA would be 3'-AUGGCCGGUUAUUAAGCA-5' and the protein will be MAGY.
 - c. The mRNA would be 5'-ATGCCCGTTATTAAGCA-3' and the protein will be MAGY.
 - d. The mRNA would be 5'-AUGGCCGGUUAUUAAGCA-3' and the protein will be MACY.
- 40.** The RNA world hypothesis proposes that the first complex molecule was RNA and it preceded protein formation. Which major function of the ribosomal RNA supports the hypothesis?
- a. rRNA has catalytic properties in the large subunit and it assembles proteins.
 - b. rRNA is a protein molecule that helps in the synthesis of other proteins.
 - c. rRNA is essential for the transcription process.
 - d. rRNA plays a major role in post-translational processes.
- 41.** A tRNA is chemically modified so that the amino acid bound is different than the one specified by its anticodon. Which codon in the mRNA would the tRNA recognize: the one specified by its anticodon or the one that matches the modified amino acid it carries?
- a. The anticodon will match the codon in mRNA.
 - b. The anticodon will match with the modified amino acid it carries.
 - c. The anticodon will lose the specificity for the tRNA molecule.
 - d. The enzyme amino acyl tRNA synthetase would lose control over the amino acid.

TEST PREP FOR AP® COURSES

42. What characteristic of the genetic code points to a common ancestry for all organisms?

- a. The code is degenerate
- b. The code contains 64 codons.
- c. The genetic code is almost universal.
- d. The code contains stop codons

43. What process transfers heritable material to the next generation?

- a. replication
- b. splicing
- c. transcription
- d. translation

44. When comparing transcription of heritable information in prokaryotes and eukaryotes, which events are the same?

- a. Transcription by polymerase, recognition of a consensus sequence in the promoter, and termination by a hairpin loop are conserved.
- b. Translation by polymerase, recognition of a consensus sequence in the promoter, and termination by a hairpin loop are conserved.
- c. Transcription by polymerase, recognition of a highly variable sequence in the promoter, and termination by a hairpin loop are conserved.
- d. Transcription by polymerase, recognition of a consensus sequence in the promoter, and elongation by a hairpin loop are conserved.

45. Which of the following cell structures does not contain heritable information?

- a. chloroplast
- b. cytoplasmic membrane
- c. mitochondria
- d. nucleus

46. How does the enzyme reverse transcriptase violate the central dogma of molecular biology in HIV?

- a. The enzyme reverse transcriptase reverse transcribes the RNA in the genome of HIV to DNA.
- b. The enzyme reverse transcriptase translates the RNA of the HIV into protein and then back to DNA.
- c. The enzyme reverse transcriptase transcribes the DNA straight into the protein molecules.
- d. The enzyme reverse transcriptase transcribes DNA to RNA, then again to DNA. There is no protein synthesis.

47. Radioactive deoxythymidine triphosphate is supplied to the protist *Euglena*. After an interval of time, the cells are homogenized and different fractions are analyzed for radioactivity content in large nucleic acid molecules.

Which fraction will not be labeled?

- a. nucleus
- b. mitochondrion
- c. chloroplast
- d. plasma membrane

48. You sequence a gene of interest and isolate the matching mRNA. You find that the mRNA is considerably shorter than the DNA sequence. Why is that?

- a. There was an experimental mistake. The mRNA should have the same length as the gene.
- b. The mRNA should be longer than the DNA sequence because the promoter is also transcribed.
- c. The processed mRNA is shorter because introns were removed.
- d. The mRNA is shorter because the signal sequence to cross the nuclear membrane was removed.

49. A mutation in the promoter region of the gene for the beta-globin can cause beta-thalassemia, a hereditary condition which causes anemia. Why would mutations in the promoter region lead to low levels of hemoglobin?

- a. The globin chains produced are too long to form functional hemoglobin.
- b. The globin chains are too short to form functional hemoglobin.
- c. Fewer globin chains are synthesized because less mRNA is transcribed.
- d. Globin chains do not fold properly and are non-functional.

50.

Codon on mRNA	Amino Acid
GCA	alanine
AAG	lysine
GUU	valine
AAU	asparagine
UGC	cysteine
UCG	serine
UCU	serine
UUA	leucine
UAA	stop

You are given three mRNA sequences:

1. 5'-UCG-GCA- AAU-UUA -GUU-3'
2. 5'-UCU-GCA- AAU-UUA -GUU-3'
3. 5'-UCU-GCA- AAU-UAA -GUU-3'

Using the table, write the peptide encoded by each of the mRNA sequences.

- a.
 1. Serine-alanine-asparagine-leucine-valine
 2. Serine-alanine-asparagine-leucine-valine
 3. Serine-alanine-asparagine(-stop)
- b.
 1. Serine-phenylalanine-asparagine-leucine-valine
 2. Serine-alanine-asparagine-leucine-valine
 3. Serine-alanine-asparagine (-stop)
- c.
 1. Serine-alanine-asparagine-leucine-valine
 2. Serine-alanine-asparagine (-stop)
 3. Serine-alanine-asparagine-leucine-valine
- d.
 1. Serine-alanine-asparagine-leucine-valine
 2. Serine-arginine-asparagine-leucine-valine
 3. Serine-alanine-asparagine(-stop)

51.

Codon on mRNA	Amino Acid
GCA	alanine
AAG	lysine
GUU	valine
AAU	asparagine
UGC	cysteine
UCG	serine
UCU	serine
UUA	leucine
UAA	stop

You are given three mRNA sequences:

1. 5'-UCG-GCA- AAU-UUA -GUU-3'
2. 5'-UCU-GCA- AAU-UUA -GUU-3'
3. 5'-UCU-GCA- AAU-UAA -GUU-3'

Using the peptide encoded by each of the above, compare the three peptides obtained. How are peptides 2 and 3 different from 1? What would be the consequence for the cell in each case?

- a. There is a silent mutation in peptide 2 and peptide 3 has a stop codon due to mutation.
- b. There is a silent mutation in peptide 3 and peptide 2 has a stop codon due to mutation.
- c. There is a different amino acid in peptide 2 and peptide 3 has a stop codon due to mutation.
- d. There isn't a mutation in peptide 2 and peptide 3 has a stop codon due to mutation.

SCIENCE PRACTICE CHALLENGE QUESTIONS

52. Gamow (1954) proposed that the structure of DNA deduced by Watson and Crick (1953) could be interpreted as a way of forming roughly 20 "words" of the common amino acids from the four "letters" A, T, C, and G that represent DNA nucleotides.

Crick and coworkers (1961) used a method developed by Benzer to induce mutations in the DNA of a virus by the insertion of a single nucleotide. The mutant could not infect the bacterium *Escherichia coli* and neither could viruses with a second insertion of a second DNA nucleotide. However, a third nucleotide insertion restored the ability of the virus to infect the bacterium.

In 1961, Nirenberg and Matthaei conducted a series of experiments to better understand the flow of genetic information from gene to protein. They discovered that in solutions containing the contents of ruptured *E. coli* bacterial cells from which DNA had been removed, polymers containing only one repeating amino acid, phenylalanine, would be synthesized if synthetic mRNA composed of only the single nucleotide, uracil (U), was added to the solution in which phenylalanine was also present. In solutions containing mRNA with only adenine

(A) or cytosine (C) and the amino acids lysine or proline, polymers containing only these amino acids would be synthesized. The researchers found that when ribosomes were removed by filtration, these polymers did not form. Nirenberg and Leder (1964) extended this work to include other nucleotides.

A. Summarize the conclusions regarding the encoding and decoding of heritable information supported by these studies. Explain how these studies provided evidence to support the Triplet Code.

Khorana (1960) developed a technique for synthesizing RNA composed of predictable distributions of repeated pairs or triplets of nucleotides. He found, for example, that RNA synthesized when A and U were present in relative concentrations of 4:1, respectively, will produce RNA sequences with these distributions determined by their relative probabilities: AAU:AAA, AUA:AAA, and UAA:AAA; $0.8^2 \times 0.2/0.8^3 = 1/4$ [calculated as follows: i) 4/5 of the bases are A, so the likelihood of selecting A is 0.8; ii) the selection is repeated to determine the second letter of the three-letter codon; iii) the likelihood of selecting a U is 1 in 5; iv) the probability of selecting the

set AUU is the product; v) similarly, the probability of AAA is $(4/5)^3$; and vi) the ratio of these probabilities is their relative likelihood]: AUU:AAA, UUA:AAA, and UAU:AAA; $0.8 \times 0.2^2/0.8^3 = 1/16$; and UUU:AAA; $0.2^3/0.8^3 = 1/64$.

B. Based on Khorana's findings, calculate the relative distributions of the following ratios of concentrations of RNA triplet sequences from mixtures in which the relative concentrations of guanine and cytosine, G:C, are 5:1.

Ratio	Relative Probabilities
GGC:GGG	
GCG:GGG	
CGG:GGG	
GCC:GGG	
CGC:GGG	
CCG:GGG	
CCC:GGG	

Table 15.2

C. Based on the work of Nirenberg, Matthaei, Leder, and Khorana, the following table was constructed (taken from Khorana's Nobel Prize address):

		Second letter					
		U	C	A	G		
First letter	U	UUU } Phe UUC } UUA } Leu UUG }	UCU } UCC } Ser UCA } UCG }	UAU } Tyr UAC } UAA Stop UAG Stop	UGU } Cys UGC } UGA Stop UGG Trp	U C A G	Third letter
	C	CUU } CUC } Leu CUA } CUG }	CCU } CCC } Pro CCA } CCG }	CAU } His CAC } CAA } Gln CAG }	CGU } CGC } Arg CGA } CGG }	U C A G	
	A	AUU } AUC } Ile AUA } AUG Met	ACU } ACC } Thr ACA } ACG }	AAU } Asn AAC } AAA } Lys AAG }	AGU } Ser AGC } AGA } Arg AGG }	U C A G	
	G	GUU } GUC } Val GUA } GUG }	GCU } GCC } Ala GCA } GCG }	GAU } Asp GAC } GAA } Glu GAG }	GGU } GGC } Gly GGA } GGG }	U C A G	

Figure 15.18

A solution containing the amino acids shown in the table above and equal concentrations of the two nucleotides C and G is prepared. Predict the proteins that can be synthesized from this mixture in terms of each possible codon and their relative concentrations in terms of their amino acid repeat sequences.

D. Describe the effects of the codons UAA, UAG, and UGA on protein synthesis.

53. The yeast life cycle is usually dominated by haploid cells, each with a single set of unpaired chromosomes. The cell propagates asexually, and the genetic material is

replicated through mitosis. Cell division occurs every 2–4 hours, leading to 60–100 generations in a single day. Yeast also reproduce sexually, particularly under adverse environmental conditions. When two haploid cells—with DNA containing complementary mating-type alleles—conjugate, a diploid zygote results. The diploid zygote can then complete the sexual segment of the life cycle through meiosis. After meiosis, four haploid spores are produced, which can germinate.

Researchers can grow yeast easily on nutrient-containing plates. Because both asexual and sexual reproduction is rapid, yeast has become an important organism for the experimental investigation of mutagenesis and evolution among eukaryotes. Environmental factors, such as chemicals or radiation, induce mutations. High-energy UV-c radiation of less than 1 minute in duration will result in many mutated yeast cells. UV-c can be used to mutate a strain of yeast in which the synthesis of adenine is blocked. This mutation is observable because the *ade-2* mutant has a red color when cultured on nutrient-containing plates. Exposure to uv-c also can result in additional mutations. In particular, one mutant, *ade-7*, changes the color of the *ade-2* mutant to white.

A. You have a uv-c lamp, culture plates, and growth chambers at 23 °C and 37 °C. You also have available known haploid strains that are (*ade-2*, +, +), where + denotes the wild type. **Design** a plan to determine the rate of uv-c-induced mutations in nutrient-containing plates inoculated with yeast.

Earth's ozone layer removes high-energy ultraviolet radiation, uv-c, from the solar radiation received at the surface. Lower-energy ultraviolet radiation, uv-b, strikes Earth's surface. Damage to DNA induced by ultraviolet radiation occurs with the formation of bonds between an adjacent pair of pyrimidine nucleotides, thymine and cytosine, on the same strand of DNA. A repair enzyme, photolyase, which is activated by visible light, is present in plants and most animals, but not in humans. In characterizing the relationship between environmental mutagens and cell damage, a useful assumption is often made and referred to as the linear hypothesis. This assumption states that the extent of damage is proportional to the amount of radiation received.

Mutation rates for a strain (*preac*) that does not produce photolyase and a wild-type (+) strain were studied. Cultures of the two strains of yeast were diluted, and nutrient-containing plates were inoculated in triplicate at 23 °C. The plates were exposed to bright sunlight for varying time intervals. After exposure, the plates were incubated in the dark at 23 °C. After incubation between 1 and 8 hours, data shown in the table below were collected by counting the density of living cells relative to the control, and averaging these among replicates.

B. Using the data table below, **graph** the average survival fraction, relative to the wild-type control. Predict the number of mutations in a sample of 1,000 cells of the *preac* type that are exposed to bright sunlight for 15

seconds.

Incu- bation Time(hr)	10-S Exposure	20-S Exposure	30-S Exposure	40-S Exposure	50-S Exposure
1	0.83	0.58	0.33	0.17	0.08
2	1.00	0.43	0.17	0.09	0.04
3	0.92	0.38	0.12	0.03	0.01
4	0.75	0.35	0.08	0.01	0.00
5	0.99	0.49	0.11	0.01	0.00
6	0.81	0.42	0.12	0.01	0.00
7	0.80	0.32	0.09	0.01	0.00
8	1.05	0.59	0.11	0.01	0.00
Mean	0.89	0.45	0.14	0.04	0.02
Standard Deviation	0.11	0.10	0.08	0.06	0.03

Figure 15.19 This is a 5 column table, showing Incubation time, in hours in the left most column, ranging from 1 to 8. A 10 second exposure has the following values for an incubation time of 1 to 8: 0.83, 1.00, 0.92, 0.75, 0.99, 0.81, 0.80, 1.05 and 0.89 with a standard deviation of 0.11. A 20 second exposure has the following values for an incubation time of 1 to 8: 0.58, 0.43, 0.38, 0.35, 0.49, 0.42, 0.32, 0.59, 0.45, with a standard deviation of 0.10. A 30 second exposure has the following values for an incubation time of 1 to 8: 0.33, 0.17, 0.12, 0.08, 0.11, 0.12, 0.09, 0.11, 0.14, with a standard deviation of 0.08. A 40 second exposure has the following values for an incubation time of 1 to 8: 0.17, 0.09, 0.03, 0.01, 0.01, 0.01, 0.01, 0.04, with a standard deviation of .006. A 50 second exposure has the following values for an incubation time of 1 to 8: 0.08, 0.04, 0.01, 0.00, 0.00, 0.00, 0.00, 0.00, 0.02 with a standard deviation of 0.03

Yeast can also be used to study sexual reproduction, a somewhat puzzling phenomenon. Cloning of cells through mitosis is molecularly much less complex than meiosis, consumes less energy, and is less risky. Two alternative explanations for the evolution of sexual reproduction are popular. In one model, through assortment of genes, meiosis leads to an increase in the frequency of beneficial mutations. In the second model, detrimental mutations are purged from a population through sex. Studies using yeast (Gray and Goddard, *Evol. Biol.*, 2012 and McDonald et al., *Nature* 2012) have provided a mechanism to study these models. As shown below, the fitness (defined as the log of the ratio of the number of cells in successive generations) of yeast is graphed as a function of number of mitotic reproductions in yeast grown in low-stress and high-stress environments, and with and without alternating induction of sexual reproduction.

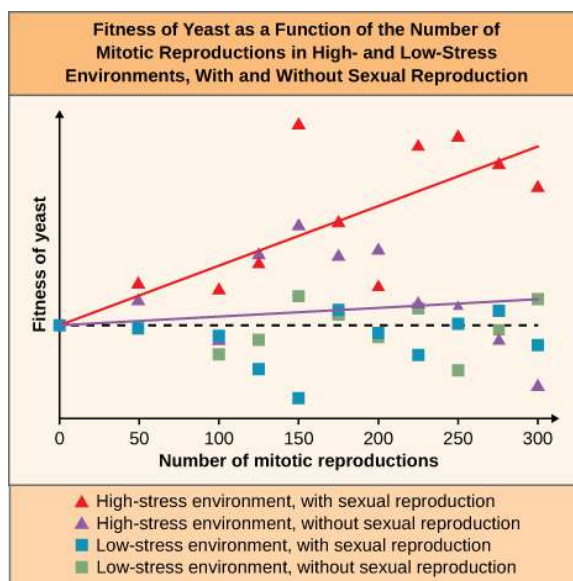


Figure 15.20

C. Based on these data, **evaluate** the merits of the alternative theories of the adaptive advantage provided by sexual reproduction.

54. A. Describe the storage and retrieval of genetic information with the following model. Use the list to fill in the blanks with the letter corresponding to the correct term.

- amino acid
- tRNA
- DNA
- transcription
- mRNA
- translation
- protein
- RNA polymerase
- rRNA

Within the cytoplasm, ___ is synthesized from ___ bound to ___ in a sequence that corresponds to information provided by ___. This process is called ___.

Within the nucleus, information originating in ___ is encoded as a sequence of bases in ___, which is synthesized by the enzyme ___ that is embedded in the ___. This process is called ___.

B. During development, cell differentiation occurs, and the expression of genes is permanently switched off. Using the model summarized above, **explain** where information flow is most effectively blocked.

C. A chemical message is received by the cell regulating the timing of events controlled by gene expression. Using the model summarized above, **explain** where information flow is most effectively managed.

55. Structure and function in biology result from both the presence of genetic information and the expression of that information. Some genes are continually expressed, whereas the expression of most genes is regulated, commonly at the level of transcription. At the initiation of transcription, the TATA-binding protein (TBP) provides access to the DNA strand to be transcribed. The 5'TATAAA3' sequence called the TATA box is found in prokaryotes, archaeobacteria, and eukaryotes. Even among eukarya, when the TATA box is not present among eukaryotes, the initiation of transcription involves TBP. Scientists attribute this common characteristic to the relative thermostability of the A-T interaction. Hydrogen bonds hold the two strands of the DNA double helix together. This type of bond has the smallest interaction energy of all intermolecular forces; as temperature increases, these bonds are broken.

A. **Explain** the advantage, in terms of the energy required, which is provided by an AT-rich region in the sequence where transcription is initiated.

B. The fact that the TATA box or the associated TBP are common to all domains provides evidence of common ancestry among all life. **Pose a scientific question** that would need to be addressed by a valid alternative explanation of this fact.

C. A whole-genome survey of prokaryotes (Zheng and Wu, *BMC Bioinformatics*, 2010) showed that the relative amounts of guanine and cytosine in DNA poorly predicted the temperature range conditions that are suitable for an organism. **Refine the question** posed in part B, taking this result into account.

56. Only a fraction of DNA encodes proteins. The

noncoding portion of a gene is referred to as the intron. The intron fraction depends upon the gene. Introns are rare in prokaryotic and mitochondrial DNA; in human nuclear DNA, this fraction is about 95%. The intron is transcribed into mRNA, but this noncoding mRNA is edited out before translation of the coding portion, or exon, of a gene. The edited exon segments are then spliced together by a spliceosome, a very large and complex collection of RNAs and proteins.

Although introns do not encode proteins, they have functions. In particular, they amplify expression of the exon, although the mechanism is unknown. When introns are very long, which is common among mammalian genes with roles in development, they can significantly extend the time required to complete transcription. Analysis of genes common to different plant and animal species shows many shared intronic positions and base sequences, although in some organisms, such as yeast, many introns have been deleted. Because introns do not encode proteins, mutations can remain silent and accumulate.

A. As described above, introns are ancestral remnants that are replicated because they do not disadvantage the organism. Consider the claim that introns are “junk DNA.” **Evaluate the claim** with supporting evidence.

B. Introns may be retained during transcription. **Explain** how the retention of a transcribed intron between two transcribed exons within a gene could do the following:

- block expression of one polypeptide sequence
- increase expression of a polypeptide
- alter the polypeptide expressed