Chapters 5 through 9 presented a survey of the dinosaurs and many conclusions about their biology and behavior. This chapter summarizes some of that information and explores other aspects of dinosaur biology and behavior. The study of dinosaur soft-tissue (non-skeletal) anatomy and behavior is full of speculation, much of it sensational and unwarranted. Here, we shall take a cautious approach to these subjects, presenting reasonable speculation and avoiding science fiction.

**Dinosaur Biology**

Many aspects of dinosaur biology, especially skeletal anatomy, have already been reviewed in this book, and Chapter 13 discusses the complex subject of dinosaur metabolism. The focus of this chapter is on four topics not discussed elsewhere in this book: dinosaur external appearance, weight, growth, and longevity.

**External Appearance**

Fossilized skin impressions are known for ornithopod, theropod, and ceratopsian dinosaurs. They indicate that the skin of these dinosaurs was covered with scales similar to the scales of some living reptiles (figure 12.1). There is no conclusive evidence that any dinosaur was covered with hair or feathers, although some paleontologists believe that small theropods closely related to birds may have had feathers or a feather-like body covering (see Chapter 14).

The color of dinosaurs is totally a matter of conjecture, because the pigment in their skin and scales did not fossilize. Most paleontologists and artists who create paintings or sculptures of dinosaurs use the color patterns of living reptiles, especially lizards, as a guide to the probable colors of dinosaurs. Some artists, however, paint dinosaurs with very flamboyant, bright color patterns unlike those of most living reptiles. These flashy dinosaurs are eye-catching, but no serious student of dinosaurs views the coloration attributed to any dinosaur as anything but speculation.

The posture and overall body shape of a dinosaur is determined by analyzing its skeleton. Skeletal anatomy is a guide to the size, shape, and configuration of the muscles and provides an understanding of how the dinosaur moved (figure 12.2). Of course, this is old news to the readers of this book. What is not old news, and what is not so certain, is how fat or thin a given dinosaur was, whether or not
Figure 12.1
This close-up fossilized skin impression of a hadrosaurid shows reptilian scales only a few millimeters wide. Probably all dinosaurs were covered with such scales.

Figure 12.2
The dinosaur skeleton provides the basis for reconstruction of the shape, size, and arrangement of muscles.
it had flaps of skin on its neck or head as do some modern lizards and birds, and other features of dinosaur external anatomy that are difficult to predict from skeletal anatomy. It is certain that paleontologists' and artists' view of the external appearance of dinosaurs has evolved as new ideas about dinosaur biology and behavior (see Chapter 1) have emerged. Older ideas of sluggish, cold-blooded dinosaurs produced restorations of flabby and lethargic dinosaurs. New ideas of fast, warm-blooded dinosaurs produce renderings of sleek and agile dinosaurs. We can see that ideas about dinosaur external appearance not only involve careful inferences from dinosaur skeletal anatomy, they also require speculation about coloration and soft-tissue anatomy that cannot be directly inferred from skeletal anatomy. Furthermore, paleontological conceptions about dinosaur biology and behavior have always shaped perceptions of dinosaur external appearance.

WEIGHT

Many popular dinosaur books list weights of dinosaurs. These weight estimates are one way to state the size of a dinosaur. Indeed, most dinosaur weight estimates emphasize the very large size of the dinosaurs. How are dinosaur weights estimated?

Two methods are used. One way is measuring the cross-sectional area of a weight-bearing limb bone (figure 12.3). The more weight a limb bone bears, the larger its cross-sectional area, and an equation that predicts weight borne from the cross-sectional area of a limb bone (usually the femur) can be calculated for living vertebrates. The cross-sectional area of the dinosaur limb bone can be plugged into such an equation.

What is determined, of course, is not the weight of the dinosaur but only the weight supported by the limb bone. A further adjustment upward of this value must be made in order to estimate the dinosaur's body weight. This adjustment depends on the dinosaur's posture and shape, leading to some uncertainty in the weight estimate. Also uncertain is just how applicable the cross-section-to-weight-borne equation is to extinct animals much larger, and presumably heavier, than the living animals from which the equation was originally determined.

Because of these uncertainties, the cross-sectional area method is not the ideal method of estimating a dinosaur's weight. Instead, scale models of dinosaurs are the most common way to estimate weights.

Estimating dinosaur weights from scale models is relatively straightforward once a model of known scale (say one-fiftieth the length of the dinosaur) is available. The volume of the model is calculated by displacement of water. That volume is multiplied by the cube of the linear scale of the model so that it becomes the volume of a full-size dinosaur identical in shape to the model. This volume of

![Figure 12.3](image)
The cross-sectional area of a limb bone is related to the weight that bone must bear.
the “real” dinosaur is then multiplied by 0.9 kg/liter, which is the mass of a liter of living crocodile, to arrive at a mass (weight) in kilograms (box 12.1).

This method is simple, and it forms the basis of most published dinosaur weight estimates (table 12.1). However, these estimates are only as accurate as the models (figure 12.4). Because we are uncertain exactly how “fleshy” or “lean” dinosaurs were, dinosaur model-making is an imprecise art. Dinosaur weight estimates are full of uncertainty, which is why this book uses skeletal lengths, not weight estimates, to convey the size of a given dinosaur.

Growth and Longevity

Living reptiles grow throughout their lives, although the rate at which they grow decreases as they age (figure 12.5). This type of growth, called indeterminate growth, contrasts with the determinate growth of mammals and birds. Determinate growth means that after the animal grows to adulthood it stops growing (figure 12.5). In general, rates of determinate growth are faster than those of indeterminate growth (figure 12.6). Another factor affecting growth rate is metabolism; on average, warm-blooded vertebrates grow at least 10 times faster than cold-blooded vertebrates.

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Most paleontologists estimate the weight of dinosaurs by using scale models. The more accurate the scale model, the more accurate the weight estimate. You can use this method by using available scale models, such as the plastic dinosaurs you can purchase at a toy store. Here's how to do it.

First, you need the following tools: a waterproof plastic scale model of a dinosaur, a water-filled graduated cylinder, and a hydrometer to measure the density of the water or graduated cylinder from a chemistry lab. The more precise the calibrated in your graduated cylinder, the more accurate your estimate.

Next, fill the graduated cylinder with water, weigh the graduated cylinder with water, and record the weight in milliliters. Then determine the density of the water using the hydrometer. Multiply the density of the water by the number of milliliters contained in the graduated cylinder, and divide the result by 100 to get the density of the water. This value is approximately 60% of the model's volume.

Now measure the model in millimeters from the bottom to the top of the model. Next, measure the length of the model in millimeters. Finally, multiply the height and length of the model by the density of the water to get the volume of the model. Next, multiply the volume of the model by the density of the water to get the weight of the model in milliliters. Finally, divide the weight of the model in milliliters by the density of the water to get the weight of the model in grams. This value is approximately 60% of the size of the dinosaur.

Now measure the model in millimeters from the bottom to the top of the model. Next, measure the length of the model in millimeters. Finally, multiply the height and length of the model by the density of the water to get the volume of the model. Next, multiply the volume of the model by the density of the water to get the weight of the model in milliliters. Finally, divide the weight of the model in milliliters by the density of the water to get the weight of the model in grams. This value is approximately 60% of the size of the dinosaur.

What type of growth did dinosaurs have, and how long did an individual dinosaur live? These questions are difficult to answer directly from dinosaur fossils because they provide little direct evidence of the age, in years, of an individual dinosaur. (Recent identification of growth rings in some dinosaur bones may change this, but it is difficult to be certain how long a time interval is represented by each ring.) But if we examine dinosaurs for which eggs or hatchlings and full-size adults are known, we can use the growth rates of living vertebrates as a guide.

The ceratopsian Protoceratops is a good example. The adult weight of a full-size Protoceratops has been estimated, from scale models, to have been 177 kilograms. The estimated weight of the hatchling is 0.43 kilograms, if hatching
weight represents 90 percent of the weight of the egg, which is calculated from egg volume (= 0.5 liter in Protoceratops). If the maximum growth rate for living reptiles applies to this dinosaur, it would have taken 26 to 38 years to reach adult size. A similar calculation for the European sauropod Hypselosaurus (adult weight = 5,300 kilograms, hatchling weight = 2.4 kilograms) indicates 82 to 118 years of growth to reach adulthood. Because much larger sauropods, such as Brachiosaurus, weighed four or five times as much as Hypselosaurus, the estimated time they would have taken to reach adult size would have been much more than one century, perhaps centuries!

These estimates, of course, assume cold-blooded dinosaurs with reptilian growth rates. But if many dinosaurs were warm-blooded (see Chapter 13), they would have had growth rates comparable to those of living birds and mammals. The time taken by warm-blooded dinosaurs to reach adult size would have been about one-tenth of the estimates given above. Protoceratops would have reached adult size in about 3 years, and Hypselosaurus would have taken about 10 years. In comparison, living African elephants reach adult size in about 10 years.

Where does this leave us with the question of dinosaur growth rates and longevity? The answer depends on how we view dinosaur metabolism. Because much evidence suggests that many dinosaurs were warm-blooded, dinosaur growth rates and longevity estimates based on living warm-blooded vertebrates are probably correct. This means that it is reasonable speculation that many dinosaurs grew as fast as living warm-blooded vertebrates, and probably lived at least as long as large mammals and birds.

**Dinosaur Behavior**

Although Chapters 5 through 9 discussed many aspects of dinosaur behavior, it is useful to summarize them here and to discuss some subjects mentioned briefly at greater length. Important aspects of dinosaur behavior were feeding and locomotion, reproduction and parenting, attack and defense, and social (group) behavior.
FEEDING AND LOCOMOTION

Tooth and jaw structure allow paleontologists to easily distinguish plant-eating from meat-eating dinosaurs (figure 12.7). As we repeatedly saw in Chapters 6 through 10, meat-eating dinosaurs had numerous sharp, serrated, blade-like teeth set in powerful jaws. This was a feeding mechanism designed to stab, tear, and slice flesh. Plant-eating dinosaurs, in contrast, had flatter, leaf-shaped teeth, sometimes arranged in dental batteries, set in massive jaws and skulls. This was a feeding mechanism designed to tear, slice, pulp, and/or grind vegetation. Nevertheless, the feeding of some toothless theropods, such as oviraptorosaurs, and some sauropods, such as diplodocids, is less certain.

It is extremely difficult to determine exactly what kinds of plants or animals a given kind of dinosaur ate. Stomach contents—conifer twigs and needles in hadrosaur mummies, a lizard in Compsognathus, and so forth—provide some direct evidence. Gut contents even indicate some meat-eating dinosaurs resorted to cannibalism (box 12.2). Inferences of the feeding range of plant-eating dinosaurs—how far above the ground the dinosaur could crop vegetation—suggest some specific types of plant food that may have been favored by different kinds of dinosaurs (figure 12.8). But preserved gut contents are not known for most dinosaurs, and inferences about feeding narrow little the range of possible plant foods. So it remains difficult to identify the specific food items most dinosaurs ate.

**Figure 12.7**
The teeth, jaws, and skull structure of meat-eating *Tyrannosaurus* contrast with those of plant-eating *Parasaurolophus*.

**Figure 12.8**
Feeding range may provide some clues to the types of plants eaten by some dinosaurs.
One of the principal reasons most animals, including dinosaurs, move (locomote) is to obtain food. Dinosaur locomotion has been discussed at various points in this book, and we can draw some general conclusions.

Dinosaur skeletons indicate, almost without exception, that they were ground-dwelling walkers and runners. There is no strong evidence that any dinosaur was arboreal (lived in trees), although some paleontologists speculate that some small theropods may have been tree climbers. Other than some hadrosaurids, no compelling argument can be presented that any dinosaur was aquatic (living in the water). Indeed, as we saw in Chapter 6, earlier ideas that sauropods were aquatic do not stand up to a critical analysis of sauropod anatomy. Therefore, dinosaurs stand out as a remarkable group of ground-dwelling animals.

Reproduction and Parenting
Chapter 11 discussed the evidence suggesting that dinosaurs reproduced by laying eggs. Clutches of eggs are particularly well known for coelurosaurians in Mongolia, the hadrosaurid Maiasaura in Montana, and the French sauropod Hypselosaurus.
Most significant for interpretations of dinosaur reproductive and parenting behavior have been the Montana egg sites. There, at a place called "egg mountain" (figure 12.9), a number of clutches of eggs attributed to two dinosaurs—the hadrosaurid Maiasaura and the hypsilophodont Orodromeus—have been discovered (figure 12.10). These clutches are in oval to subcircular crater-like depressions with raised rims. It is almost certain the eggs were not exposed to the air after being laid, but were covered with a thin layer of soil or vegetation (figure 12.11).

Numerous skeletons of hatchling dinosaurs are found around these nests, as are some bones and footprints of adult dinosaurs of the same species as the hatchlings. This provides circumstantial (though not incontrovertible) evidence of parental care.

**Figure 12.9**
Nests and dinosaur bones have been discovered at egg mountain in Montana.

**Figure 12.10**
These three views: (top, oblique, and side) are of an Orodromeus clutch from egg mountain. Each egg is about 20 cm long.
There is very suggestive evidence of parental care of young dinosaurs in the hadrosaurid *Maisaura* (figure 12.12), but what of other dinosaurs? Certainly the nests and hatchlings of coelurosaurs and *Hypselosaurus* could have been cared for as were those of *Maisaura*. But no evidence of such care is preserved. Other dinosaurs, such as the cannibalistic *Coelophysis* (see box 12.2), probably did not care for their young beyond the amount of care characteristic of living crocodilians. There may have been a spectrum of parental care among dinosaurs, ranging from no care to the feeding and protection of hatchlings among some types of hadrosaurids.

**ATTACK AND DEFENSE**

How predatory dinosaurs hunted and how they and other dinosaurs defended themselves are subjects for which there is some good hard evidence and much unfounded speculation.

Chapter 5 discussed ideas about how carnosaur hunted. In general, most paleontologists view the very large carnosours, the tyrannosaurs, as solitary hunters, and smaller carnosours as pack hunters when taking big game, such as sauropods. Pack-hunting in dromaeosaurids is also reasonable speculation, but most other coelurosaurs probably were solitary hunters of small animals such as insects and lizards.

Defensive behavior varied greatly in dinosaurs. Among the predatory dinosaurs, perhaps the most that can be said is that they followed the maxim "the best defense is a good offense." Their speed and agility, and their slashing teeth and claws, must have been used to defend against enemies, as do many predators today.
Among the plant-eating dinosaurs, three different defensive strategies appear to have evolved (figure 12.13). In the sauropods, huge body size and powerful whip-like tails provided defense against enemies. Some sauropods, such as titanosaurids, evolved body armor. But defensive armor was the hallmark of most ornithischians. This armor ranged from the impervious plating of ankylosaurs to the spiked tails of stegosaurs, and from the horns of ceratopsids to the thickened skulls of pachycephalosaurids.

Ornithopods were the exception. They lacked body armor and must have defended themselves from attackers in other ways—by speed, by camouflage, or by fleeing to the water or by some sort of group defensive behavior. But it is not clear which one (or more) of these strategies ornithopods employed. Indeed, defensive behavior probably varied greatly among the ornithopods, from the small and speedy hypsilophodontids to the large, spike-thumbed iguanodontids.

**GROUP BEHAVIOR**

The evidence for group behavior (gregariousness or sociality) among dinosaurs can be listed as follows:

1. Display structures—ceratosaur crests, tubes and crests on hadrosaur skulls, and so forth—suggest sociality among some groups of dinosaurs. These display structures presumably would have enabled the recognition of potential mates or opponents in a social group.

2. Sexual dimorphism (differences between males and females of the same species) of these display features and other structures (for example, tusks) in some dinosaurs also supports sociality. Often (though not always), sexual dimorphism among living social animals allows them to distinguish males from females and provides males with display/defensive structures that aid in the defense of territory and the acquisition of mates.

3. The change in shape during growth of some dinosaur display structures could indicate the need to distinguish juveniles from adults in a social group.
The dinosaur skeletons and bones at Dinosaur National Monument, Utah, were accumulated primarily by river transport, not by the sudden death of a group of dinosaurs.

Courtesy Dinosaur National Monument, Herm Hoopes.
FIGURE 12.15
Most of these Early Jurassic dinosaur trackways in Massachusetts are heading in the same direction and suggest the possibility of group behavior. Note that 20 trackways of the same kind of dinosaur are heading west.
4. Multiple dinosaur fossils (mass-death assemblages) might also indicate group behavior. Dinosaurs that lived in groups would, occasionally, die in groups. However, many dinosaur mass-death assemblages, such as the Late Jurassic fossils at Dinosaur National Monument in Utah, represent river-transported accumulations of carcasses (figure 12.14). Few dinosaur mass-death assemblages may actually represent groups of animals that lived and died together.

5. The evidence for parental care and nesting behavior discussed earlier also suggests some sort of group behavior among hadrosaurids.

6. Finally, and regarded by many paleontologists as the strongest evidence, multiple trackways of dinosaurs that walked in the same direction suggest social behavior. Indeed, many dinosaur track sites preserve more than one trackway of the same type of dinosaur, all heading the same way (figure 12.15). Because so many track sites document this pattern, an alternative interpretation—that at each site individual dinosaurs walked, at different times, to a common goal—seems unlikely.

The six points of evidence above suggest some form of group behavior among dinosaurs, especially theropods, ornithopods, and sauropods. But they don't allow us to infer the exact types of social structures of these dinosaurs. Some books talk of dinosaurs living in "herds." But a herd is a complicated and specific kind of social group in which a dominant animal (usually a male) leads other animals. No unequivocal evidence for herd behavior exists among dinosaurs, although much evidence for social groupings exists for many different types of dinosaurs.

**SUMMARY**

1. Fossilized skin impressions suggest all dinosaurs had reptilian scales covering their bodies. There is no conclusive evidence of hairy or feathered dinosaurs.

2. Dinosaur coloration does not fossilize and is usually arrived at in renderings by analogy to the coloration of living reptiles.

3. Restorations of the external appearance of dinosaurs have evolved with changing ideas about the biology and behavior of dinosaurs.

4. Dinosaur-weight estimates are based mostly on scale models and are only as accurate as the models.

5. Living reptiles have indeterminate growth, whereas mammals and birds have determinate growth.

6. Dinosaur growth rates and longevity based on living reptilian growth rates are those of very slow-to-mature and long-lived dinosaurs. However, dinosaur rates based on living warm-blooded-animals are much faster and suggest times of dinosaur maturation and longevity comparable to those of living mammals and birds.

7. Although jaw and tooth structures allow paleontologists to distinguish meat-eating from plant-eating dinosaurs, it is seldom possible to determine exactly what food a dinosaur ate.

8. The skeletons of all dinosaurs identify them as ground-dwelling walkers and runners. Few, if any, dinosaurs lived in the trees or in water.

9. All dinosaurs probably laid eggs, some in nests that may have been protected and, after hatching, tended by adult dinosaurs.

10. Dinosaurs defended themselves in a variety of ways, from speedy escape to impervious body armor.

11. Several lines of evidence suggest group behavior, especially in some theropods, ornithopods, and sauropods. But the exact kinds of social structures of these dinosaurs cannot be determined, and there is no evidence of herd behavior among dinosaurs.

**KEY TERMS**

- armor
- cannibalism
- clutch
- Coelophysis
- coloration
- cross-sectional area
- determinate growth
- feeding range
- group (social) behavior
- herd
- Hypselosaurus
- indeterminate growth
- locomotion
- Malanosaura
- mass-death assemblage
- nest
- scale models
- skin impressions
- social structure
- soft-tissue anatomy
- weight estimates
**Review Questions**

1. When you examine a restoration of a dinosaur, what features are inferred from sound skeletal evidence and what features are based on speculation?

2. Critique the dinosaur restoration in figure 14.9.

3. How have changing ideas about dinosaurs influenced dinosaur restorations?

4. How are dinosaur weights estimated?

5. Which estimate of the growth rate of a dinosaur is preferable, one based on growth rates of living reptiles or one based on living mammals and birds? Why?

6. How long did an individual Brachiosaurus live? What variables affect your estimate?

7. How do paleontologists determine what dinosaurs ate, and what are the limitations of these determinations?

8. What does the locomotion of dinosaurs tell us about where they lived?

9. What sort of parental care did hadrosaurids confer on their young? What evidence supports your answer?

10. List the defensive strategies employed by different types of dinosaurs. What is the evidence to indicate which dinosaurs employed a particular strategy?

11. What is the evidence for group behavior among dinosaurs?

**Further Reading**


Dinosaur Biology and Behavior 195