
What Forms an Animal?

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What forms an animal? A likely answer these days is “genes.” Or perhaps: “genes and environment.” Such high-level abstractions reveal how little we actually know and tend to discourage further inquiry. When I hear “genes and environment” I yearn for something more concrete, something I can mentally take hold of. And the only way I know to develop such saturated concepts is to get back to the things themselves – to look carefully at what nature presents and inch my way toward a more full-toned understanding.

Wild and Captive Lions

A few years ago I came across a remarkable article written in 1917 by N. Hollister, then superintendent of the National Zoo in Washington, DC.* He was studying the lion specimen collection at the National Museum, which encompassed over 100 lion skulls and skins. Hollister noticed marked differences between wild-killed specimens and those that had lived for a number of years at the Washington zoo. He proceeded to make a more detailed comparative study.

Since lions from different areas of the world and also different regions of Africa differ substantially from one another, Hollister focused on one subspecies – the Masai lion (*Panthera leo masaica*) from East Africa. Five of the zoo-reared animals were Masai lions and had been captured as small cubs near Nairobi, Kenya. Hollister compared these specimens with wild-killed lions from the same area. He thus had animals from the same subspecies and one regional population. He knew, in other words, that he was comparing fairly close relatives and not genetically and geographically distinct populations.

When the five lions were brought from Kenya to the Washington zoo, they already stood out through their very pale, grayish buff-colored fur. This is the typical coloration of wild-living Masai lions, but contrasted starkly with the much more darkly colored lions at the Washington zoo. Over a period of years the fur of these imported animals darkened considerably, becoming like that of the other lions at the zoo. Moreover, the captive male lions grew much longer manes than wild Masai lions and they also had longer and fuller hair tufts at their elbows.

Immediately we ask, “Why?” But an easy answer is not forthcoming. Hollister was cautious. He believed the higher humidity and precipitation in Washington might have played a role in fur darkening, since humidity has been correlated with darkening of fur, and also feathers in birds. But he also recognized that the quality of light as well as metabolic changes due to the abnormal life and diet in the zoo might have contributed to the differences.

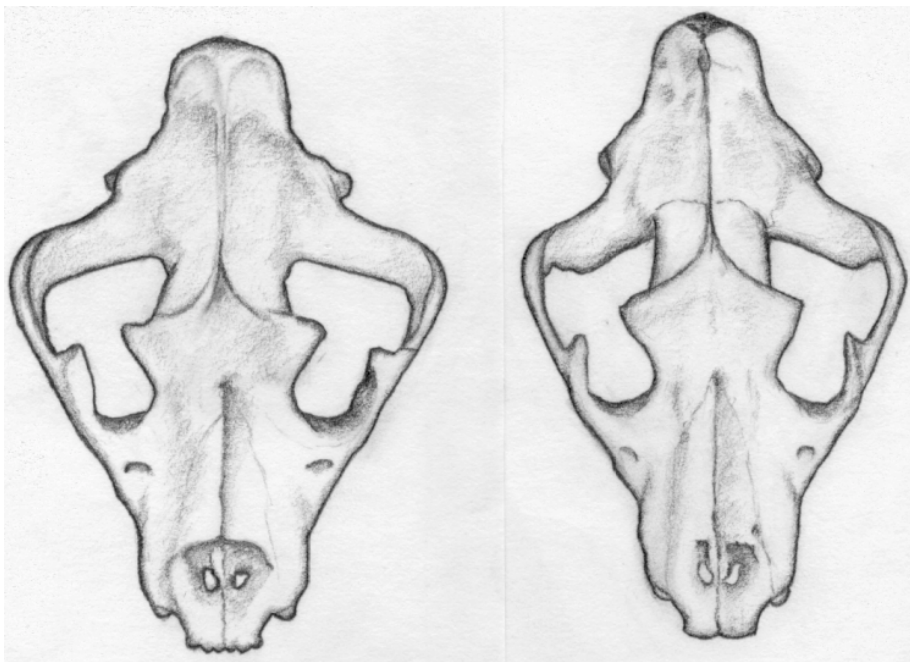
The Skulls of Wild and Captive Lions

Since an animal’s fur is in direct contact with the external environment, we can imagine that it might somehow change in relation to changing environmental conditions. But the solid and complexly formed skull, hidden from the world by skin and muscles, is another matter. And yet, surprisingly, the most striking differences between the wild and zoo-reared animals were in their skulls (see Figures 1, 2 and 3).

The skulls from the zoo-reared animals are much shorter and broader than in the wild animals. They appear compact compared to the more sleek skulls of the wild lions. When I first saw the photographs of the skulls, I thought they had been incorrectly labeled, expecting the more stocky, massive skull to have belonged to a wild animal. But they were correctly labeled and I needed to consider the matter more closely. (A good exercise in overcoming prejudice!)

The skulls from the zoo-reared animals – whether male or female – are not only broad but also thicker-boned. One can see this in the prominent cheekbones (zygomatic arches, see Figure 1). The arch sweeps out further to the sides and consists of much thicker and more rounded bone. Figure 2 shows a cross section through the bone of the zygomatic arch in a zoo-reared and a wild animal. The difference is glaring. The zoo-reared animal’s bone is triangular in cross section with convex surfaces and rounded corners. It consists largely of porous bone material (spongiosa). In contrast, the wild animal’s arch is narrower and has one concave and one convex surface that meet at the top of the arch, forming a sharp ridge. The arch has little porous bone, consisting mainly of the outer layer of strong compact bone.

* Hollister, N. 1917. Some effects of environment and habit on captive lions. *Proceedings U.S. National Museum* 53: 177-193.



zoo-reared lion

wild-killed lion

Figure 1. Top view of a zoo-reared and a wild-killed lion; both adult males. Drawn to same scale. (Drawings by Christina Holdrege. After Hollister 1917)

Similar differences are visible at the rear of the skull (see Figure 3). Not only is the skull of the zoo-reared animal much broader, the surfaces and forms are more rounded with gradual transitions from convex to concave. The skull of the wild-reared lion has much sharper, more defined edges and angles.

One further interesting contrast between the skulls pertains to the braincase (see Figure 1). Measured externally, the braincase in the skull of a wild lion is smaller than in the zoo-reared lion. When, however, one measures the internal cranial capacity — which is a direct indicator of brain size — the wild lion skull is considerably larger (40 to 50 cubic centimeters greater in size). This apparent paradox is resolved when one considers bone thickness. As in the other parts of the skull, the bones of the braincase are substantially thicker in the skull of the zoo-reared animal. Therefore the braincase appears externally larger but internally leaves less room for the brain. The larger brain of wild lions is covered by thinner, but solid, compact bone.

Hollister writes that even an untrained observer would group the skulls into wild and zoo-reared specimens, so apparent and uniform are the differences. He suggests that if one were dealing with only specimens from wild animals (or fossils), a biologist or paleontologist would think that he or she was viewing specimens of different species (a remark that makes one wonder about the accuracy of fossil classifi-

cations). Where does this contrast come from?

Activity that Sculpts

A primary activity missing from the life of a captive lion is the hunt and kill. A hungry lion in Africa's savannah crouches in the grass, all muscles tensed and its senses focused on the movement of a herd of antelopes or zebras. It stalks slowly and silently toward the herd and then suddenly, in a forceful burst of speed, sprints toward an animal, leaps, grabs onto the neck, and pierces through blood vessels and the wind pipe with its long, pointed canines. It pulls the prey down — using head and paws — and holds it until it dies. If the lion is a female with young cubs, she may drag the prey, locked into her jaws, toward the place where she's hidden them.

All this activity is missing from the life of a captive lion. And this activity forms the skull. The lion uses powerful muscles to grip, bite into and hold the prey in its jaws. The masseter muscle is especially important for the gripping power exercised in using the incisors and canines to pierce and hold the prey. This muscle attaches to the zygomatic arch and to the mandible (lower jaw). A powerful muscle must be rooted in strong bones. As the lion exercises its muscles, they not only grow but also put tension and stress on the bones. Although we tend to think of bones as inert structural elements of the body, they are, in fact, alive and adaptive. With an increase in stress and tension the bones

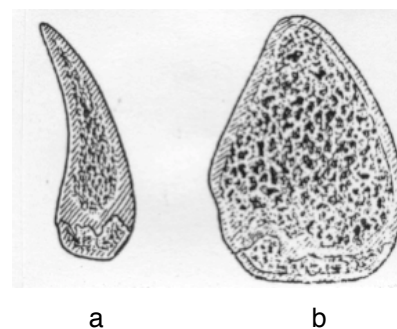


Figure 2. Cross section through the zygomatic arch of a wild-killed (a) and a zoo-reared lion (b). Adult males of same age; natural size (From Hollister 1917)

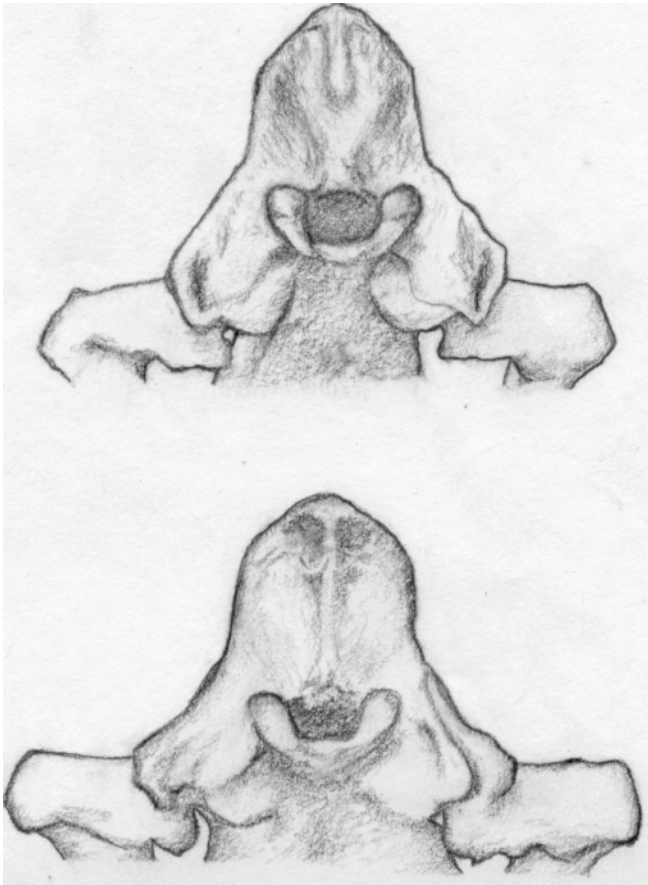


Figure 3. View from the rear of a wild-killed (top) and a zoo-reared (bottom) lion, both adult males. Drawn to same scale. (Drawings by Christina Holdrege. After Hollister, 1917)

change form and structure to meet the demands of the activity. The zygomatic arch remolds to form a sharp ridge of compact bone as the ideal attachment for the masseter muscle. In the same way the mandible forms thinner, more compact bone with ridges and rougher surfaces for the strong muscles attached to it. In contrast, the rounded, smooth zygomatic arch and mandible in the zoo-reared lions reveals a lack of activity. The bones grow and billow out, being hardly influenced by muscular stress and strain. Hollister notes their juvenile appearance, which reflects the lack of change due to inactivity.

Likewise, the sculpting of the rear of the wild lion's skull discloses activity. The wild lion uses its neck muscles in holding, pulling, lifting, shaking, and dragging prey. At least seven different neck muscles attach to the rear of the skull and every contraction sculpts the bones these muscles are rooted in. As in the jaw, the rear of the skull forms defined ridges and rough surfaces where the muscles attach. The little-used neck muscles of the captive lion leave the rear of the skull largely unaltered; the bones become more rounded and have smoother surfaces.

The Formative World

In the life of an animal, activity is a key formative factor. The active, hunting lion takes on a modified form compared to the inactive zoo lion. The muscle-orchestrated movement of the lion shapes the bones. This movement, in turn, is stimulated internally by the animal's drives (hunger) and externally by the perception of the antelope or the zebra. In this sense the antelope and the zebra form the lion. A remarkable thought. We all know that the flesh of these animals nourish the lion, but now we can recognize that the activity these animals call forth in the lion sculpts the lion's very bones. We can go even further and say that the savannah — its soil, light, warmth and moisture, its grasses and trees, its other animals — forms the lion. But it becomes increasingly difficult to say precisely *how* this larger world influences the lion.

The outer world that forms the lion points us to the lion. By "lion" I mean the specific way-of-being that, for example, is open to and reacts to antelopes and zebras in a particular way. A lion doesn't see the grass it's crouching in as something to feed on, as does the antelope. Grass is something to hide in and move through. In this sense the lion is a specific world, a way to be and behave. This aspect of the lion is centered in the bodily form it is born with. This form is given through inheritance and then molded by activity. The hereditarily given model is something dynamic and plastic, waiting to be filled and formed by the animal's activity. This is what we should be picturing when we speak of a "genetic background" or genes, not some fixed plan.

The vast and rich ecology of the savannah stimulates the lion to activity. In a sense it brings forth the lion and allows it to unfold its life. This stimulation influences the whole metabolic activity of the animal, not only the muscles and the bones. Every sense perception forms nerve activity and influences the formation and function of the brain. The zoo lion lives in a world that calls forth little activity. Its bones grow large and thick, expressing the weight and inertia of its existence, while muscles and nerves receive little stimulation. One can sense the responsibility one takes on in having captive animals — knowing that we are cutting them off from part of the world that enlivens and forms them. How can we create a surrogate environment that at least to a degree is appropriate to their needs?

So when you hear that an animal is a product of its genes and its environment, think of the lion. Think of the most solid part of the body — bone — being molded by the animal's activity. In activity, the lion's specific anatomical and behavioral readiness takes hold of a world without — the kill at a watering hole at dusk. The antelope shapes — and so is part of — the lion.