

happen in a wide variety of ways, whereby the multiplicity of manifestations of reality is produced.

In the book examples from poetry (stanzas from Pushkin's *Eugene Onegin*), music, architecture, and other arts are treated in an interesting metrical manner, showing the analogy with one-dimensional and other structures. For music the locus classicus is the rearrangement of the several fugues of Bach's "Kunst der Fuge" according to symmetry principles by Wolfgang Graeser (1924).

The references given at the end of the book are numerous, valuable, and up to

date. They give, inter pares, a vivid impression of the activity of Russian science and philosophy in the realm of special and general symmetry.

This clearly written, beautifully illustrated book will become a standard work for all who are interested in unifying branches of natural sciences and of art, and we must be grateful to the translator, the editor, and the publisher for having produced such a precious publication.

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Mammals in Motion

How Mammals Run. Anatomical Adaptations. P. P. GAMBARYAN. Translated from the Russian edition (Leningrad, 1972) by Hilary Hardin. Halsted (Wiley), New York, and Israel Program for Scientific Translations, Jerusalem, 1974. xiv, 368 pp., illus. \$26.75.

Most of the bones and muscles of mammals and other vertebrates are directly adapted to the functions of locomotion, and it follows that anyone interested in how mammals have evolved needs to know a good deal about how they move around. In the past, there have been two parallel ways of approaching mammalian locomotion. Morphologists have accumulated innumerable data on the differences between the limb bones and muscles of various mammals, but these data have been related to actual behavior mostly by the loose procedure of comparing animals in different "locomotor categories"—fast runners vs. slow runners, hovering bats vs. swift-flying bats, bipedal primates vs. brachiating primates, and so on. On the other hand, students of behavior from Muybridge onward have recorded locomotion on film and developed elegant and precise systems for recording limb movements and footfall sequences, but few have gone on to seek morphological or adaptive correlates of ob-

served differences in locomotor behavior.

In recent years, however, many morphologists have begun approaching mammals with movie cameras and electromyographic apparatus as well as with scalpels and calipers, and we are beginning to learn a great deal about the correlations between the kinetics of motion and the musculoskeletal machineries that produce the motion. In the West, this new work is being done mostly on primates and bats, and to some extent on marsupials and monotremes; so it comes as a pleasant surprise to learn of the parallel Soviet work summarized in this book, which has been directed toward ungulates, carnivores, rodents, and lagomorphs.

Gambaryan's analysis of locomotor morphology in these terrestrial mammals relies heavily on exactly the kind of studies

of gaits and footfall patterns that have not led to many morphological insights in the hands of his Western predecessors. He begins by summarizing previous work in the analysis and description of symmetrical gaits, culminating in the synthetic system devised by Sukhanov (whose 1968 magnum opus has also just appeared in English translation). Gambaryan's principal interest, however, is in asymmetrical gaits—that is, those in which the gait cycle begins with the movement of both forelimbs, followed by the movement of both hind limbs. These are of particular importance for two reasons: they are the characteristic high-speed gaits of terrestrial mammals, and they are unique to the class Mammalia. Gambaryan divides asymmetrical gaits into two basic types: the ricochet, in which the hind limbs begin to move forward immediately after pushing off and land before the forefeet leave the ground; and the gallop, in which the forefeet push off while the hind feet are still in the air.

Many students of locomotion would have stopped there, or gone on to demonstrate (to nobody's surprise) that kangaroos are adapted for the ricochet and cheetahs are not; but Gambaryan proceeds to draw some very large and ingenious phylogenetic inferences that are central to much of what follows. The ancestors of the therian mammals (marsupials and placentals), he argues, must already have had asymmetric gaits—either the gallop or the ricochet. But the ricochet is less efficient than the gallop, because it necessitates putting more of the propulsive force into vertical oscillations of the center of gravity (Fig. 1). Therefore, since the less advantageous ricochet could not have evolved from the gallop, the ricochet is the primitive fast gait of mammals. Gambaryan goes on to attack the notion that primitive mammals were arboreal, arguing that if they had been slow-climbing animals they would never have developed asymmetrical gaits (since stride length is greater in symmetrical gaits), and that if they had been leaping about in the trees they would have developed the gallop instead of the ricochet (since change in the length of the ricochet changes the footfall pattern and so requires greater coordination in leaping varying distances, and arboreal leaping favors gaits in which the forelimbs touch down first). He concludes that primitive mammals lived on the forest floor, feeding by digging through the litter with their forelimbs while supporting themselves on their hind limbs, and that this explains the evolution of asymmetrical gaits as well as the characteristic mammalian posture, in which the limbs support the body from underneath.

All of this strikes me as tenuous, and many objections could be raised: Jenkins



Fig. 1. Asymmetrical gaits of mammals. The rodent (top) illustrates the ricochet, in which the hind limbs are brought forward together immediately after they leave the ground. The mustelid (bottom) illustrates the "extended flight" phase of the gallop, which is permitted by an increase in the propulsive thrust provided by the forelimbs, and which allows obstacles of a given height to be cleared with a lower center of gravity than that required by the ricochet. [From *How Mammals Run*]

has recently shown that tree shrews get along just fine in the trees using Gambaryan's "primitive ricocheting jump," leaping primates ordinarily land with the hind feet touching down first, and I doubt very much that the quadrupedal ricochet is primitive for marsupials, as Gambaryan says at the end of the book. Whether or not one accepts Gambaryan's arguments of this sort, his efforts to reconstruct the phylogeny and adaptive meaning of different sorts of quadrupedal gait give data of this kind a new significance, and provide us with a model for incorporating such data into our reconstructions of the past.

In the body of the text, Gambaryan attempts to relate habitat and food-getting to movements of the limbs in running, and to explain muscular morphology in terms of the ranges of joint motion that various locomotor habits require. An extraordinary quantity of data on gaits, limb lengths, muscle weights and attachments, and joint mobility is brought together in successive chapters on ungulates, elephants, carnivores, lagomorphs, rodents, and kangaroos.

Some of Gambaryan's remarks on carnivores will convey an idea of the scope of these analyses. In both carnivores and ungulates, the forelimbs play an important propulsive role in running; but carnivores differ from ungulates in having a more flexible vertebral column (increasing the length of the stride) and thus having greater mobility between the forelimb and the trunk. This mobility correlates with a locomotor cycle in which the humerus is further protracted at the shoulder joint; therefore, increasing specialization for speed tends to produce enlargement of the pectoral muscles in carnivores, but not in ungulates. The typical fast locomotor pattern of felids is a bounding run, in which both hind limbs move together, whereas canids specialize in a lateral gallop less suited to bursts of speed and more to prolonged running. This obviously reflects typical differences in hunting behavior, and the resulting differences in locomotor pattern are in turn reflected in differences in limb proportions and in joint angulations. Bears have powerful forelimbs used in characteristic foraging behaviors, and their power is utilized in locomotion to produce a distinctive form of gallop in which the phase of "crossed flight" (between forelimb pushoff and hind-limb touchdown) is prolonged. The propulsive functions of the vertebral musculature, which distinguish carnivores from ungulates, are peculiarly exaggerated in the weasel family, whose distinctively long and mobile vertebral column is interpreted by Gambaryan as part of a supposed ancestral adaptation for hunting burrowing prey. The familiar

"humping" gait of mustelids results from these vertebral specializations, which are also reflected in increase in the relative weights of the vertebral extensors, reduction of the interspinous ligaments and spinous processes, and virtual elimination of the "crossed flight" phase of the gait cycle.

Here as elsewhere, objections can be raised to much of what Gambaryan says. For instance, many of his interpretations of muscle functions are based on his electromyographic studies of decerebrate cats going through reflex locomotor movements induced by electrical stimulation of the brain stem. This bizarre procedure simplifies the experimenter's job by allowing him to switch his animal on at the same time as the recording apparatus, but its relevance to normal locomotion is obscure, and I hope that the method will not be imitated by other electromyographers.

Yet for all of that, Gambaryan has collected and synthesized here a vast amount of useful and suggestive information about carnivore locomotion, and his chapters on other orders are equally informative and stimulating. Hardin's translation is lucid and readable, and even corrects a few errors made in the original Russian edition—for example, the use of *Procyon* instead of *Lycaon* for the African wild dog. It would also have been helpful to have some of Gambaryan's anatomical terminology brought into line with Western usage, so that the reader would not have to figure out for himself that "anconeus" means "triceps" and that "talocrural extension" means volar flexion of the ankle joint. Despite these difficulties, and despite the objections that everyone will have to some of Gambaryan's arguments and conclusions, this is an impressive synthesis that needs to be read by anyone with an interest in the evolution of mammalian locomotion.

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Ethological Diversion

Animal Architecture. KARL VON FRISCH with the collaboration of Otto von Frisch. Translated from the German by Lisbeth Gombrich. Harcourt Brace Jovanovich, New York, 1974. viii, 306 pp., illus. \$12.95. A Helen and Kurt Wolff Book.

Animal Architecture, written by Karl von Frisch in collaboration with his son Otto von Frisch, is the modern-day counterpart of a remarkably similar book written by J. G. Wood called *Homes without*

Hands published in England in 1884, just two years before the elder von Frisch was born. It is an informal, affectionate, oh-my book of animal behavior. Written "for light diversion," it is not so much a comprehensive scientific survey of structures produced by animals as an excuse to describe selected, often spectacular, aspects of natural history. Experts will be aware of occasional small inaccuracies, impressed with the amount of specialized literature reviewed, and frustrated at the complete absence of bibliographic references. But the book contains a large collection of generally reliable information about the biology of diverse species, rather casually fitted to the theme of animal architecture and softly stamped with the author's gentle philosophy of nature. Beginning with the sand-grain shells of certain amoebas, it proceeds "up" through the animal kingdom to the loosely woven sleeping nests of chimpanzees. Some of the classic figures of European ethology are included—the feisty three-spined sticklebacks with their releasers and sign stimuli, the slender *Am-mophila* wasp, and Kohler's problem-solving apes. There is a conspicuous absence of any mention of von Frisch's own famous work on communication in bees, even though other notable nonarchitectural capacities are freely discussed for various species. Almost every example cited is illustrated by one or more of the 114 excellent photographic plates (many of which are in color) and 105 drawings (some excellent, others mediocre but adequately illustrating the text).

Although the book jacket rather loudly advertises the author's Nobel laureateship, it is a relief to find the text free of the kind of high-flown philosophizing that sometimes emanates from grand old men of science. An unexpected and valuable feature of the book is its incidentally autobiographical quality. Clearly von Frisch has watched and loved all kinds of animals since he was a small boy. Much of the book is based on firsthand observations, and the most inspired parts deal with personal experiences, such as his own discovery of parthenogenesis in some pet bagworm moths. He was an insect collector, who, instead of instantly killing a captive mason bee, released it and followed it to its home "in a fifty-yard sprint." The book reflects a wide-ranging scholarly interest in animals; it also shows that von Frisch does not always view them with strict scientific detachment. He empathizes with animals, for example (p. 225) expressing sympathy for kingfishers who have to pass through the "stench" of a flight tube coated with excrement from their young and (p. 252) supposing that badgers wall off portions of their tunnels occupied by foxes because