Subject : Environmental Science (Hons.)

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Name of the teacher: Dr. Arijit Chatterjee

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Box 2.2

BIOGEOGRAPHICAL RULES

Most biogeographical rules were established during the nineteenth century when it was observed that the form of many warm-blooded animal species varies in a regular way with climate.

Gloger's rule

Proposed by Constantin Wilhelm Lambert Gloger in 1833, this rule states that races of birds and mammals in warmer regions are more darkly coloured than races in colder or drier regions. Or, to put it another way, birds and mammals tend to have darker feathers and fur in areas of higher humidity. This is recognized as a valid generalization about clines of **melanism**. A credible explanation for it is that animals in warmer, more humid regions require more pigmentation to protect them from the light. Gloger's rule was first observed in birds, but was later seen to apply to mammals such as wolves, foxes, tigers, and hares. It has also been observed in beetles, flies, and butterflies. Given that colour variation shows a concordance of pattern in birds that have vastly different competitors, diets, histories, and levels of gene flow, some common physiological adaptation seems likely.

Bergmann's rule or the size rule

Established by Carl Bergmann in 1847, this rule states that species of birds and mammals living in cold climates are larger than their **congeners** that inhabit warm climates. It applies to a wide range of birds and mammals. Bergmann believed many species conform to the rule because big animals have a thermal advantage over small ones in cold climates: as an object increases in size, its surface area becomes relatively smaller (increasing by the square) than its volume (increasing by the cube).

Examples of Bergmann's rule, and exceptions to it, abound. In central Europe, the larger mammals, including the red deer (*Cervus elaphus*), roe deer (*Capreolus capreolus*), brown bear (*Ursus arctos*), fox (*Vulpes vulpes*), wolf (*Canis lupus*), and wild boar (*Sus scrofa*), increase in size towards the northeast and decrease in size towards the southwest. In Asia, larger tigers (*Panthera tigris*) tend to occur at higher latitudes. Species that decline to obey Bergmann's rule include the capercaillie (*Tetrao urogallus*), which is smaller in Siberia than in Germany. Also, many widespread Eurasian and North American bird species are largest in the highlands of the semi-arid tropics (Iran, the Atlas Mountains, and the Mexican Highlands), and not in the coldest part of their range. The geographical variation of size in some vertebrate and invertebrate poikilotherms ('cold-blooded') species conforms to Bergmann's rule (e.g. Lindsey 1966).

The explanation of Bergmann's rule is the subject of much argument, but climate does appear to play a leading role (see Yom-Tov 1993). This is borne out by Frances C. James's (1970) study of bird size and various climatic measures sensitive to both temperature and moisture (wet-bulb temperature, vapour pressure, and absolute humidity) in the eastern USA. She found that wing length, a good surrogate of body size, increased in size northwards and westwards from Florida in the following species: the hairy woodpecker (*Dendrocopos villosus*), downy woodpecker (*D. pubescens*), blue jay (*Cyanocitta cristata*), Carolina chickadee (*Parus carolinensis*), white-breasted nuthatch (*Sitta carolinensis*), and eastern meadowlark (*Sturnella magna*). In all

cases, there was a tendency for larger (or longer-winged) birds to extend southwards in the Appalachian Mountains, and for smaller (or shorter-winged) birds to extend northwards in the Mississippi River valley. In the downy woodpecker, female white-breasted nuthatches, and female blue jays, relatively longer-winged birds tended to extend southwards into the interior highlands of Arkansas, and relatively shorter-winged birds to extend northwards into other river valleys. These subtle relations between clinal size variation and topographic features indicated that the link between the two phenomena might involve precise adaptations to very minor climatic gradients. The variation in wing length in these bird species correlated most highly with those variables, such as wet-bulb temperature, which register the combined effects of temperature and humidity. This suggested that size variation depends on moisture levels as well as temperature. James reasoned that a relationship with wet-bulb temperature and with absolute humidity in ecologically different species strongly suggests that a common physiological adaptation is involved. Absolute humidity nearly determines an animal's ability to lose heat: any animal with constant design will be able to unload heat more easily if it has a higher ratio of respiratory surface to body size. This new twist to Bergmann's rule bolsters some aspects of Bergmann's original interpretation about thermal budgets. Climate tends to be cooler, and therefore drier, at high altitudes and latitudes. This accounts for the fact that many clines of increasing size parallel increasing altitude and latitude. Additionally, size tends to increase in arid regions irrespective of altitude and latitude, and widespread species tend to be largest in areas that are high, cool, and dry. James concluded that, if the remarkably consistent pattern of clinal size variation in breeding populations of North American birds represents an adaptive response, then 'Bergmann's original rationale of thermal economy, reinterpreted in terms of temperature and moisture rather than temperature alone, still stands as a parsimonious explanation' (James 1991, 698).

An observed body-mass decline in several resident bird species in Israel since 1950 presents an interesting demonstration of Bergmann's rule in operation (Figure 2.2). Yoram Yom-Tov (2001) found that the body mass of the yellow-vented bulbul (*Pycnonotus xanthopygos*), house sparrow (*Passer domesticus*), Sardinian warbler (*Sylvia melanocephala*), and graceful prinia (*Prinia gracilis*) showed significant declines during the second half of the twentieth century. Minimum summer temperatures in Israel rose by an average of 0.26°C per decade over the same period.

Allen's rule or the proportional rule

Joel A. Allen's (1877) rule extends Bergmann's rule to include protruding parts of the body, such as necks, legs, tails, ears, and bills. Allen found that protruding parts in wolves, foxes, hares, and wild cats are shorter in cooler regions. Like large body-size, short protruding parts help to reduce the surface area and so conserve heat in a cold climate. The jackrabbit (subgenus *Macrotolagus*), which lives in the southwestern USA, has ears one third its body length; in the common jackrabbit (*Lagus campestris*), which ranges from Kansas to Canada, the ears are the same length as the head. Another observation conforming to Allen's rule is that such mammals as bats, which have a large surface area for their body mass, are found chiefly in the tropics. Allen's rule has been observed in poikilotherms as well as homeotherms.

Guthrie's or Geist's rule

This is a modern biogeographical rule based on the observation that the seasonal amount of food

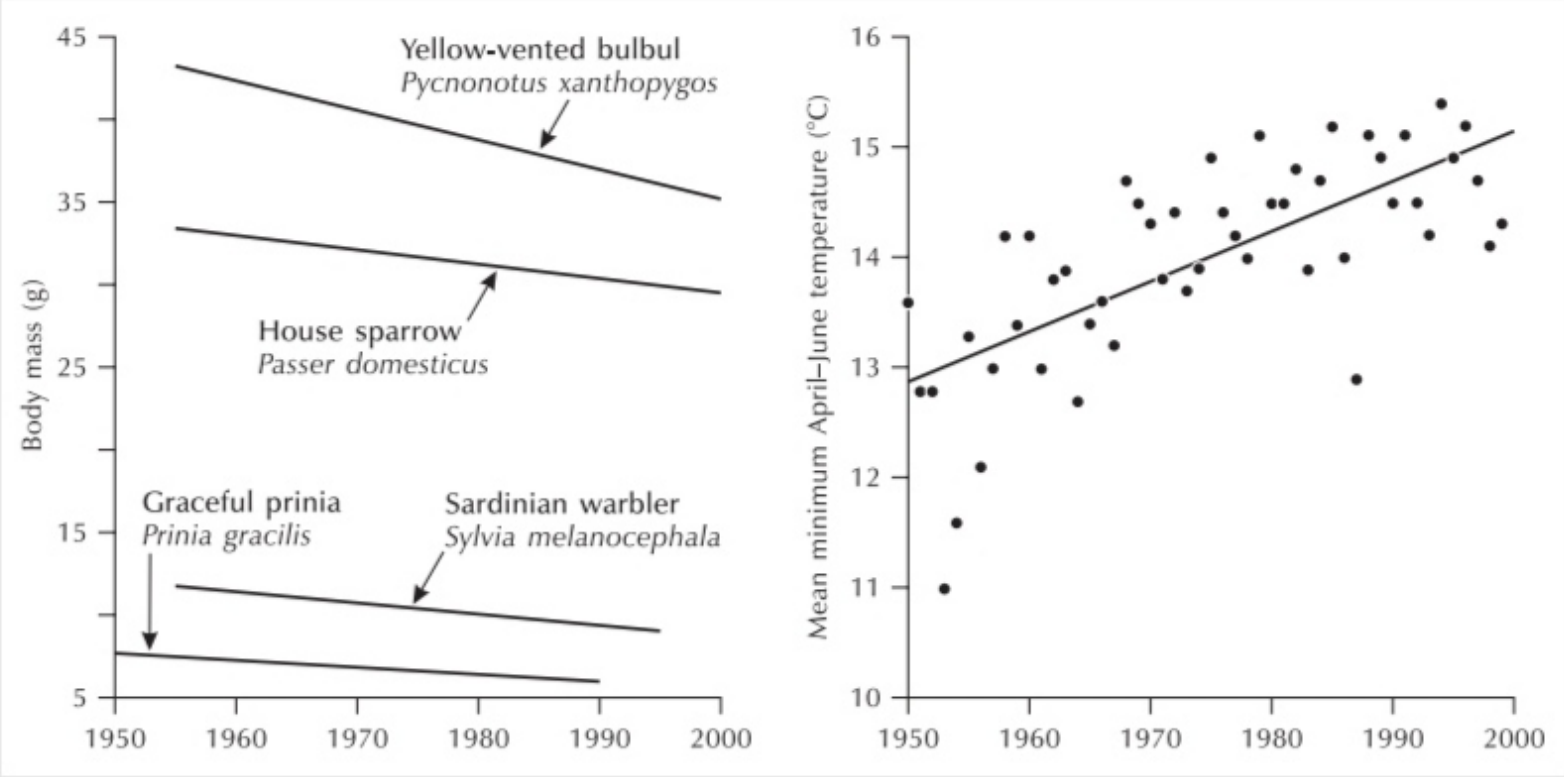

Figure 2.2 Body-mass decline in several resident bird species in Israel since 1950.
Source: Adapted from Yom-Tov (2001)

available influences body size in large mammals. Proposed by R. Dale Guthrie (1984) and Valerius Geist (1987), the basis of this rule is that animals in areas of high seasonal food abundance can achieve a greater proportion of their potential annual growth and therefore develop bigger bodies.