

## On the Factors Determining Desert Lizards' Diet

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A recent publication presents the theory of feeding strategy /Schoener, 1971/ which is discussed as an optimization problem. Optimal diet, optimal foraging space, optimal foraging period and optimal foraging group size are considered in this theory. Some ideas are based on a comparison of two contrasting ways of foraging: widely foraging and a strategy of "sit and wait". Some ecologists assume that foraging technique may be associated with some important ecological and morphological characters, from the length of the tail to learning ability /Regal, 1978; Vitt and Gordon, 1978; Huey and Pianka, 1981; Vitt and Price, 1982/. The correlation between foraging mode and the diet of desert lizards has been noted /Huey and Pianka, 1981/.

The objective of the present work is to study variations in diet and the factors determining it in desert lizards. The morphological, ecological and behavioural aspects of 4 Gekkonidae species /*Crossobamon*, *Teratoscincus*, *Gymnodactylus*/, 5 Agamidae species /*Agama*, *Phrynocephalus*/, 3 Scincidae species /*Eumeces*, *Ablepharus*/, 7 Lacertidae species /*Eremias*, *Mesalina*/ were studied. Field observations were made from 1972 to 1980: 1972 - 1975 in the Eastern Kara-kum desert /near Repetek desert station/; 1976 - 1980 in the Badkhyz region /between Tedzen and Kushka rivers/. The stomach contents in more than 200 specimens and over 100 faecal samples were examined; more than 10,000 items found in stomachs were measured and determined. Some data on the diet were obtained from field observations /over 1,000 hours/ on five species of lizards /*Agama sanguinolenta*, *Eremias grammica*, *E. persica*, *E. lineolata*, *Mesalina guttulata*/. For each lizard we recorded the distances moved, the duration of each stop, all cases of lizard hunting and their reactions to the feeding objects.

Agamids, geckos, lacertids and scincids are characterized by different degrees of skull kinesis, different dentition and limb proportions, which seem to correlate with the diet. We are interested to see if foraging mode is related to feeding selectivity and how it can vary from a specific stereotype.

It is well known that agamids and other members of Camp's /1923/ Ascalabota /iguamids, chameleons, geckos/ are some of the best examples of the "sit and wait" predatory strategy, whereas lacertids, scincids, teiids and varanids are cruising or intensive foragers /Regal, 1978/. Our comparative analysis has shown that all the species studied tend to feed on the largest possible items; the mean prey size is correlated only with the lizard size /Fig. 1/ and shows no expected correlation with other morphological characters. The same relation of prey size to body size  $0.102 \pm 0.022$ ,  $n = 44$ /

has been found in lizards of four families: Gekkonidae, Agamidae, Lacertidae, Scincidae. Other things being equal, feeding reactions are more active the more rare are the food items.

Our data show also the shifts in foraging mode within a species. It was known that the gecko, *Ptenopus garrulus*, will shift foraging mode in response to food availability; the lacertid lizard *Aporosaura anchietae* might alter foraging mode in response to weather condition and the lacertid lizard *Ichnotrophis squamulosa* has a possible ontogenetic shift /Huey and Pianka, 1981/. Feeding strategy in the ground-dwelling agama, *Agama /Trapelus/ sanguinolenta*, can usually be classified as "sit and wait" in sandridge areas /dunes and semistabilized dunes with *Haloxylon persicus/* of Repetek and Badkhyz regions. Moves of more than 1 - 2 m are associated in most cases with nontrophic forms of activity. Feeding intensity shows no correlation with moving activity /Tsellarius and Tsellarius, 1980/. The correlation coefficient between the quantity of invertebrates eaten during each 30 min and distances moved in this time reach 0.28 - 0.34 in different specimens. Maximum moving activity arose some time later than the trophic activity maximum. It is associated with thermoregulatory behaviour of the females and/or territorial behaviour of the males. The number of invertebrates found in active foraging is low and composes only 0 - 13.5 % of all the diet.

A quite different phenomenon has been observed in Badkhyz on the shrubless, grassy, loessy plains. Agamas exhibit active foraging there. The mobility of lizards becomes higher: daily movements of adult agamas extend over  $585.8 \pm 176.7$  m / $n = 5$ / in the grassy plains whereas daily movements of agamas in sandy areas /covered with *Haloxylon/* from Kara-kum are  $100 \pm 78.3$  / $n = 12$ /. The proportion of invertebrates found in active foraging increases here to 45 %. Such variability in foraging mode was also observed for *Phrynocephalus mystaceus*. The males inhabit the slopes of the sand hills /without vegetation/ and have a "sit and wait" strategy. The females are active foragers in low-lying plots between sandhills with variously developed grassy vegetation /Polynova and Lobachev, 1981/.

The *Eremias* lizards are typical active foragers. The quantity of prey captured per unit time is only loosely associated with distances moved. The correlation coefficient between quantity of the prey and distances moved is 0.79. However, we have observed that these lacertid lizards can, to some extent, use both foraging modes: active foraging and "sit and wait".

Huey and Pianka /1981/ observed that among seven species of lacertid lizards, in the Kalahari semidesert of southern Africa, five species forage widely and two others sit and wait. Such syntopic occurrence of both foraging modes in a single, very closely related group or even in the same species is of great interest for current ideas on ecological strategies.

The foraging of such typical cruising predators as *Ablepharus* species /Scincidae/ or *Eremias* /Lacertidae/ is usually an alternation of periods of active foraging and searching for prey with periods of searching while relatively immobile. During such periods of immobility the lizards are basking but they captured and ate prey just like the typical "sit and wait" predators. Our data show that the periods of "sit and wait" predation increase in the biotope with the better forage reserves. Active foraging is more typical for all the species /both foraging types/ in the beginning of the activity period and "sit and wait" is more typical towards the end of this period. All the species tend to forage actively under low availability and to use the "sit and wait" strategy with high food resources. In spite of some variability, usually one mode of foraging prevails in most

species. It is interesting that the food availability, which appears to be correlated with the foraging mode, is associated with a prey detecting mode. Regal /1978/ believed that primitive lizards were generally cruising foragers. There were two evolutionary trends toward specialization as /1/ visually oriented "sit and wait" predators among *Ascalabota* and /2/ "olfactory" as well as "visual" searchers and active foragers among the *Autarchoglossa*. "Sit and wait" predation seem to be more often displayed in lizard families with social systems based on territoriality /*Iguanidae*, *Agamidae*, *Chamaeleonidae*, *Gekkonidae*/. The correlation between territoriality and foraging mode has been shown by Polynova /1983/.

The conservation of a relative constancy in foraging mode in different taxonomic groups appear to be associated with the limitation imposed by the morphophysiological type of lizard organization. In this respect, of great importance may be the locomotion systems in different lizard families. It is known /Suchanov, 1967/ that among desert lizards in the USSR fauna three main types can be distinguished. The geckos are the relatively slow forms with a narrow range of velocity changes. The agamids are considered as specialists capable of high velocities. Lacertids exhibit a wide range of velocity changes. These lizards are able to move both very quickly and slowly. Such types of locomotion can influence the predominance of a particular foraging mode within the species. Such fundamental morpho-functional differences are of great importance for an understanding of the origin of foraging mode. Historical factors seem to be very important in the divergence of the major predation strategies.

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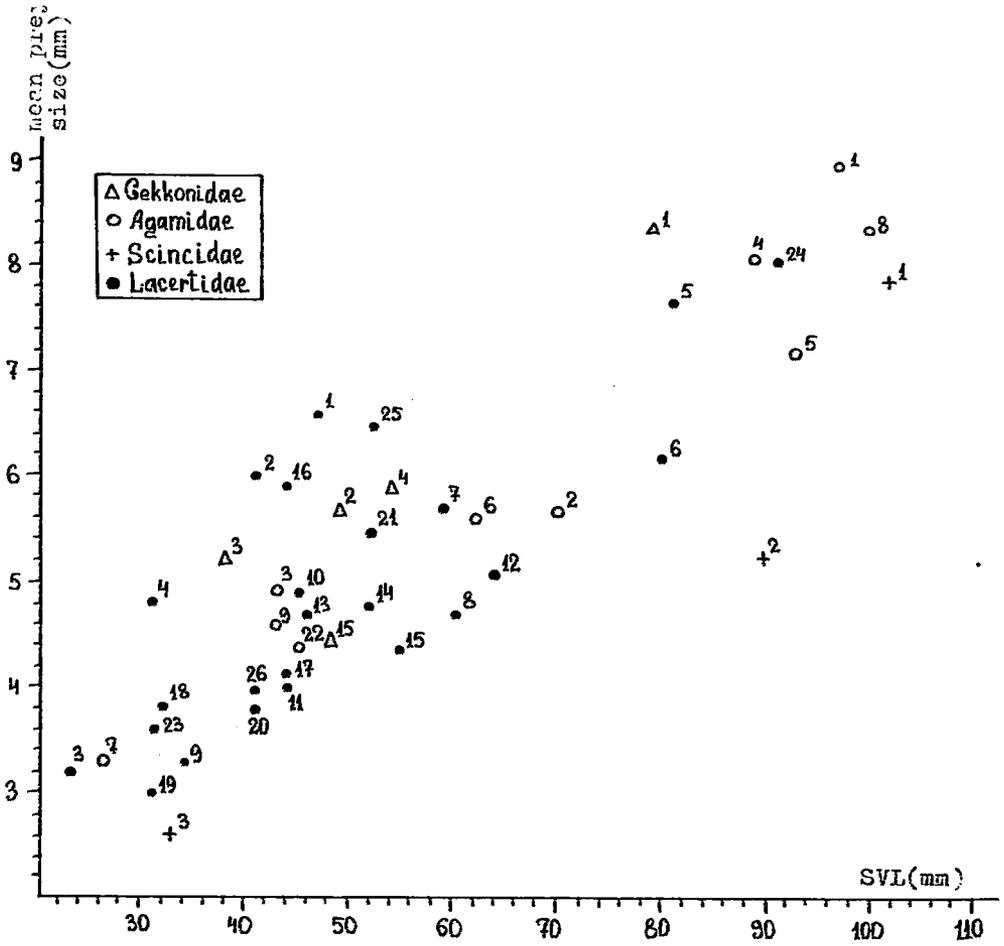


Fig. 1: Relationship of mean prey size to body size in various families of lizards.