

# Historical introduction: on widely foraging for Kalahari lizards

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This book shows that the field of foraging biology of reptiles is alive and well. We find this exciting, as we've been interested in this field for four decades. No doubt for that reason, we've been asked to describe the history of our thinking about foraging modes. How did we become involved? What were some of the salient experiences we had, and what insights of others helped channel our thinking?

When Eric began studying US desert lizards in the early 1960s, he immediately noted that the teiid *Cnemidophorus* moved much more than did all species of iguanids. This lizard world was clearly dichotomous in terms of foraging behavior. In his 1966 paper in *Ecology*, Eric coined the terms "sit-and-wait" (hereafter SW) and "widely foraging" (hereafter WF) to characterize these different behaviors.

Ray's interest in foraging behavior evolved independently about the same time. As an undergraduate at UC Berkeley in the spring of 1965, he took Natural History of the Vertebrates (taught by R. C. Stebbins and others). Students were required to do a field project: Ray studied the feeding behavior of great blue herons. In his term paper (Huey, 1965), he noted that herons "... use two distinct types of hunting whether on land or in water – stalking and still hunting." Further, he observed that herons hunting in estuaries will switch to "still hunting" when the tide is coming in, letting the moving water bring food to the birds. Thus the dichotomy of foraging behaviors he observed within a species was exactly the same as what Eric had observed between species!

In 1966 Eric headed to Australia on a postdoc, and in 1967 Ray started graduate school at the University of Texas (UT). Ray was fascinated by Eric's work (and also by Tom Schoener's) on species diversity and competition in lizards, and their studies inspired him to do his MA thesis on competitive relations of geckos from the Sechura Desert in Peru. When he read Eric's paper (Pianka,

1966), he found that his own observations on herons fit in neatly within Eric's concept, terminology, and ideas on foraging mode.

By a remarkable and fortuitous coincidence, Eric joined the faculty at UT in fall 1968. Eric and Ray became instant friends and intellectual soul mates, given their many mutual interests (in lizards, foraging mode, and far-away deserts). The next winter Eric received an NSF grant to study species diversity of lizards in the Kalahari; and he hired Ray and Larry Coons to work as his field assistants beginning in November 1969.

Eric arrived in the Kalahari a month later, and the three of us spent two wonderful months observing and collecting lizards in the Kalahari and Namib, drinking non-hot beer, and avoiding lions, leopards, scorpions, puff adders, and cape cobras. We no longer recall who first noticed that different species of lacertids were either WF or SW – given our histories, that pattern was probably immediately obvious to us both!

In any case, Ray had two experiences later on that trip that crystallized our thinking on the ecological significance of foraging mode. First, he realized that we ourselves were widely foraging predators on lizards; and that our foraging behavior must not only increase our encounter rates with lizards, but also influence the *kinds* of lizards we'd encounter. For example, our WF movements would necessarily increase our encounters with sedentary SW lizards. Second, Ray remembers walking one day along a sand ridge, wondering why we always found a WF paired with a SW lizard in a given habitat (e.g. *Meroles suborbitalis* with *Pedioplanis namaquensis* on white interdunal street sands, and *Pedioplanis lineocellata* with *Heliobolus lugubris* on the red sandridges), but never two WF species or two SW species paired in a habitat (see Pianka *et al.*, 1979). Although this pairing could obviously have happened by chance, Ray wondered whether foraging mode might in fact influence the kinds of prey a lizard would encounter. If so, differences in foraging mode might reduce dietary overlap and facilitate spatial overlap. As soon as he posed these issues, he predicted that WF lizards should encounter more patchily distributed and sedentary prey (e.g. termites), whereas SW lizards should encounter mainly moving prey. To our delight, this prediction was validated when we analyzed the dietary data (Huey and Pianka, 1981).

Yet another important insight emerged from our Kalahari peregrinations. All too frequently we stepped on horned adders (*Bitis caudalis*), which hunt by burying themselves (except for their eyes) in the sand, catching unsuspecting lizards that happen to wander by. These vipers responded viciously to our transgressions by "leaping" out of the sand, striking at our feet and legs. Not surprisingly, our initial response was always that of sheer terror; and we were

inspired to invent the 'Kalahari two-step,' an intensely evasive dance that has curiously never caught on with the general public. In any case, once our adrenalin titers dropped, we recognized that these vipers were archetypal (and arch-villain) SW predators.

Ray later made a related, but critical, observation one day near Tsabong, Botswana, while watching a secretary bird foraging for lizards. It would walk briskly up to a bush and suddenly raise its wings, startling any nearby lizard (most likely a SW species), which it then grabbed as the lizard fled. Thus both horned adders and secretary birds preyed on lizards, but did so with polar opposite foraging modes. These differences were striking to us, and we predicted that these two predators should eat different species of lizard. Fitting neatly with our expectations, SW sand vipers preyed relatively heavily on WF lizards, whereas WF secretary birds caught disproportionate numbers of SW lizards. These field observations – and Don Broadley's (1972) remarkable dietary data – led us to propose the idea of crossovers in foraging mode between trophic levels as well as to argue that models of foraging mode needed to incorporate interactions among multiple trophic levels, not just between predator and prey (Huey and Pianka, 1981).

Ray flew back to Austin in late November 1970, and he used the long flight to begin synthesizing our ideas on the ecology of foraging mode. He scribbled these on the back of airline non-slip placemats. Over the next few weeks, we spent many fruitful hours huddled over those placemats; and we talked and talked until our ecological correlates began to gel.

Nevertheless, our foraging mode project soon went into torpor. Other Kalahari projects (and Ray's thesis work on thermoregulation) took precedence. But one important realization that became increasingly apparent to us during this period was the comparative beauty of the Kalahari system – namely, that *close relatives* differed in foraging mode. That was not at all the case in the North American deserts, where any observed difference in ecology between SW vs. WF species might reflect foraging mode, or it might merely reflect long separate phylogenetic histories (iguanids vs. teiids), or both (Huey and Pianka, 1981; Huey and Bennett, 1986, p. 85). One couldn't easily tell which (but see Anderson and Karasov, 1988).

Another reason for delaying publication was simply that we had no quantitative data on foraging movements. So on a return trip in 1975–6 generously sponsored by the National Geographic Society, we (and Carolyn Cavalier) quantified various aspects of foraging behavior of our lacertids among other studies (Huey and Pianka, 1981; Huey *et al.*, 1983). We measured time spent moving and number of moves per minute for six species of lacertid, two of

which were SW and four WF foragers (see also Cooper and Whiting, 1999). With these data, we finally had all of the elements in hand for a paper.

About the same time, many others were working on related aspects of foraging mode in herps. Bennett and Gorman (1979) and Anderson and Karasov (1981) had estimated metabolic costs of different foraging modes. Bennett and Licht (1973) and Ruben (1976, 1977) explored physiological and morphological differences in reptiles with different foraging modes. Vitt and Congdon (1978) drew attention to striking differences in morphology and reproductive effort, and proposed that relative clutch mass, body shape, and foraging mode were co-evolved characters. Regal (1978) argued that WF lizards might have enhanced learning and memory, as well as larger brains. Cathy Toft (1981) noted a number of parallels in frogs, and added the fascinating observation that WF tropical anurans are typically very poisonous. Cathy's observation was especially interesting to us, because we had discovered that the juveniles of one of our WF lacertids (*Heliobolus lugubris*) mimicked a very noxious "oogpister" beetle (Huey and Pianka, 1977; Schmidt, 2004). WF animals are of course relatively conspicuous to visually hunting predators, and thus poisons and mimicry may be relatively common ways of reducing predation on such species.

Foraging mode of herps was obviously a field whose time had come by the 1970s! It was clearly and simultaneously attracting the attention of diverse herpetologists. So when we finally put our thoughts down on paper (Pianka *et al.*, 1979); Huey and Pianka, 1981) we drew on the insights of many others, not just our own. Our synthetic debt to all is clearly evident in Table 8 in our 1981 paper.

Huey returned once more to the Kalahari in 1981–2 to investigate physiological correlates of foraging mode. This time he worked with three top-flight physiological ecologists (Al Bennett, Henry John-Alder, and Ken Nagy). They found that WF vs. SW species differed in locomotor capacity (acceleration, maximal speed, and stamina) (Huey *et al.*, 1984; but see Perry, 1999), differed in field metabolic rates and feeding rates (Nagy *et al.*, 1984), and also differed in some (but not all) lower-level physiological traits (Bennett *et al.*, 1984).

Finally, Huey and Bennett (1986) were invited to contribute a chapter to a volume on predator–prey relationships in lower vertebrates (Feder and Lauder, 1986). This was right at the beginning of the "Felsenstein era" of comparative biology, marked by Felsenstein's remarkable, now classic, 1985 paper. We were already well aware of the suitability of lacertids for comparative studies of foraging mode and had noted (Huey and Pianka, 1981, p. 991) that the close relationships of these lizards provided "a substantial measure of

control over phylogenetic and sensory differences.” Huey and Bennett (1986) now took that a step further and speculated on the direction of evolutionary change within this lineage. They used a crude phylogeny of the lacertids to suggest that SW was derived in this group, and next explored various selective factors that might have favored this evolutionary transition. Improved phylogenies (see, for example, Harris *et al.*, 1998) and reconstructions in Perry (1999) and McBrayer (2004) seem to support the suggestion (Huey and Bennett (1986) that SW is derived.

The two of us are rapidly approaching our academic dotage (but we’re not there yet!), and we take this opportunity to reflect on our own foraging-mode work as well as add a few observations on current research in this field today. On a personal level, our Kalahari studies of foraging mode were great fun to do and had a big effect on our academic development. Those studies were growth experiences for us: in the process, we taught ourselves the critical importance of integrating field studies of behavior and ecology with laboratory and field studies of physiology (energetics and locomotor capacity). Moreover, we taught ourselves the importance of conducting comparative studies within an explicit phylogenetic context. We admit to some pride, of course, in the continuing impact of our studies (Fig. A1, and this volume) and those of others involved at the same time.

When we reflect on our old work, several things strike us as worth emphasizing.

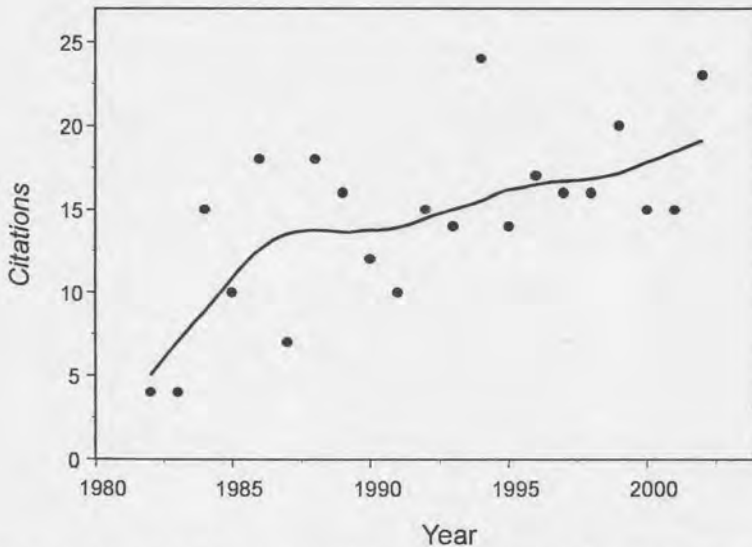


Figure A1. Number of citations per year of Huey and Pianka (1981). The curve is a non-parametric super-smoother.

First, our experiences reinforce the often-forgotten view that novel ideas can emerge from seemingly trivial natural history observations of animals in nature (Gans, 1978; Bartholomew, 1986; Greene, 1986, 2005). Who would have ever guessed that so much work would evolve in part from Eric's observations of the movement patterns of North American lizards or of Ray's of great blue herons? Or who would have thought that our stepping on horned adders would inspire the arcane idea of trophic crossovers?

Second, our work with lacertids helped make us both keenly aware of the importance of phylogeny and phylogenetic control in comparative biology. This is old news now, but it certainly was not in 1981 or even in 1986. In those "dark days of ecology" (W. L. Hodges, personal communication), comparative studies almost invariably involved distant relatives (cf. Huey, 1987), were generally restricted to only two species (Garland and Adolph, 1994), and rarely considered phylogeny (but see Greene and Burghardt, 1978!). Times have changed, and explicit phylogenetic approaches involving many species are now standard.

Third, we note that our paper is commonly viewed as advocating a strictly dichotomous view of foraging mode (Pietruszka, 1986; McLaughlin, 1989; Helfman, 1990). To be sure, we did emphasize the bimodality of foraging mode in our lacertids. But what is often overlooked is that we explicitly discussed *flexibility* in foraging mode and its consequences and constraints (see also Norberg, 1977). To us, this is an area of foraging mode that remains severely understudied (but see Dunham, 1981; Karasov and Anderson, 1984).

The flexibility of foraging mode is directly relevant to continuing attempts to quantify whether foraging modes are really dichotomous (vs. continuous) among species of lizards. Those analyses proceed by pooling data from different taxa with different habits and habitats into a single analysis, and then testing for bimodality. In our view such approaches – though well motivated and often statistically elegant – are weak comparative tests and in fact are potentially biased in favor of a continuum of foraging modes. Why? Foraging mode isn't an invariant behavior but varies with the immediate environmental conditions (Norberg, 1977; Huey and Pianka, 1981; Karasov and Anderson, 1984). If that environmental sensitivity is general, then composite analyses of movement rates of diverse species that forage in habitats as different as temperate-zone deserts and tropical forests (or that forage on substrates as different as ground or on branches; or that forage at different times) will necessarily blur any potential divergence in foraging mode. Such comparisons may be meaningful only when habit and habitat as well as phylogeny are controlled.

Moreover, Laurie Vitt (personal communication) has cautioned that foraging analyses that are based on movement rates must consider the context of movement (or lack thereof) – otherwise data can be misleading. For example,

some WF species periodically punctuate their active foraging and sit for extended periods to bask or to cool (Hillman, 1969; van Berkum *et al.*, 1986). Conversely, males of some SW species start moving extensively during the breeding season (Pietruszka, 1986), but their movements are likely related to searching for mates, not food. By failing to consider the natural history context of movement, an incautious investigator quantifying movement of the above species could grossly misrepresent true foraging rates.

To us, the proper way to address this issue is to select a single habitat and taxonomic group as *the unit* for analysis, to appreciate the ecological context of observed movement patterns, and to assay whether the lizards in that habitat have dichotomous, continuous, or invariant foraging modes. Then to determine generality for lizards, one would need to iterate that procedure through additional habitats and taxa and ultimately determine the proportion of cases showing bimodality versus a continuum. We took a first step with Kalahari lacertids, but we are fully aware that seemingly limited variation in foraging behavior within most other taxa (Perry, 1999; Vitt and Pianka, 2005) hinders or even precludes parallel analyses in most environments. Unfortunately, evolution hasn't always cooperated with the analytical needs of comparative biologists (Huey, 1987)!

What's happened to our own interests since those wonderful days of our youth, foraging widely over the red dunes of the Kalahari? In his old age, Eric has switched from being a WF to a SW hunter of lizards. He notes that he can't hear or see as well as he once could, and that his bad leg can't support his new huge mass as well as it could when he weighed only 140–155 pounds. So now he pit traps lizards, almost exclusively, except for monitor lizards, large ones of which are too big to trap. But he is still avidly pursuing foraging mode. With the help of Bill Cooper and Kurt Schwenk, Pianka and Laurie Vitt recently achieved a synthesis of the history of evolutionary innovations that led to the evolution of widely foraging (Pianka and Vitt 2003; Vitt *et al.* 2003). Recently, they demonstrated that 28% of the variance in diets of 184 extant lizard species in 12 families from 4 continents can be attributed to the first split in squamate phylogeny 200 Ma when Iguania and Scleroglossa split (Vitt and Pianka 2005). Iguanians retained ancestral traits including tongue prehension and ambush foraging, whereas scleroglossans switched from tongue prehension to jaw prehension. This freed the tongue to evolve along new lines (Schwenk and Wagner, 2001), ultimately leading to much keener vomerolfaction, which in turn promoted a more active lifestyle and facilitated a shift to wide foraging.

Ray on the other hand has largely moved away from the world of lizards and foraging biology. He claims to have good reasons for doing so (see Huey, 1994), but many herpers no doubt see his departure as clear evidence of moral

deterioration and premature senility – what else could explain his evolutionary transition to the worlds of fruit flies and mountain climbers? He still does field work but is no longer a WF hunter of wily lizards in remote deserts – instead he is reduced to running a trap line and collecting piddly *Drosophila* on rotting, smelly banana baits. Perhaps this book will inspire him back into the fold.

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