Habitat Preferences of Three Sympatric Lacertid Lizards in the Arid Tankwa Karoo Basin of South Africa

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Habitat preferences of three sympatric lacertid lizards in the arid Tankwa Karoo Basin of South Africa

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Four lacertid lizards, *Pedioplanis laticeps, P. lineo-ocellata, Meroles knoxii* and *Nucras tessellata,* occur sympatrically on the arid plains of the Tankwa Karoo Basin in South Africa. The aim of this study was to determine whether the four species are spatially separated in terms of the microhabitat each species occupies, allowing them to occur in sympatry in this structurally simple system with a limited number of potential niches. The habitat preferences of the four species were investigated on the farm Gansfontein in the southwestern parts of the Tankwa Karoo Basin. The area was surveyed by walking transects through different habitat types and recording all active lizards. For each lizard observed, the species was identified and a photograph was taken of its microhabitat. At the end of the sampling period the microhabitats in which lizards were found were sorted into distinct types on the basis of substrate composition. During the survey, only one individual of *N. tessellata* was recorded, but sample sizes for the other three species were sufficiently large to provide a clear perspective of habitat segregation among the three species. The results showed that the three species are spatially separated at the study site, with *P. lineo-ocellata* being restricted to rocky areas, *P. laticeps* preferring gravel substrates and *M. knoxii* frequenting sandy areas. Although only anecdotal information is available, all indications are that the observed spatial separation of the three species is mainly the result of historical adaptation to the different substrate types.

Key words: ***Pedioplanis laticeps, Pedioplanis lineo-ocellata, Meroles knoxii, Nucras tessellata,* resource partitioning, substrate composition.**

INTRODUCTION

Resource partitioning has been well-studied in lizards and in environmental systems ranging from tropical rainforests to deserts (Pianka 1969; Huey & Pianka 1977; Toft 1985; Tracy & Christiansen 1986; Arnold 1987; Vitt & De Carvalho 1995). The degree to which species successfully partition resources within a system can reduce competition, increase feeding efficiency and increase the carrying capacity of the system (Simon & Middendorf 1976). Pianka (1969) describes the three main variables whereby resource partitioning takes place among reptiles as habitat, food and time. These variables represent the three main dimensions of ecological space, referred to as the spatial, trophic and temporal dimensions (Pianka 1973; Hutchinson 1978; Toft 1985). To avoid interspecific competition or total competitive exclusion, coexisting species should partition resources along one or more of these three axes within ecological space (Pianka 1974).

The level of resource partitioning within an area can be directly correlated with the structural complexity of the area (Pianka 1966; Toft 1985). Structural complexity influences microhabitat availability, or, in other words, niche diversity (Pianka 1966). A more heterogeneous environment allows for resource partitioning to take place along various dimensions within the system. Multidimensional resource partitioning will result in greater overlap between different niches, enabling a larger number of species to coexist within a system (Pianka 1974).

Arid environments are examples of ecological systems with low structural complexity in general and accordingly low diversity of potential niches (Pianka 1966). Lizard species occurring in the arid regions of southern Africa have been the focus of several ecological studies, on subjects ranging from community structure (Pianka 1971) to niche partitioning (Huey *et al.* 1974; Huey &Pianka 1977; Pianka& Huey 1978), foraging behaviour (Huey &Pianka 1981; Huey *et al.* 1984; Nagy *et al.* 1984; Cooper *et al.* 1998; Cooper & Whiting 1999), and performance (Huey *et al.* 1984; Nagy *et al.* 1984). Most of this work was done in the Kalahari and Namib Desert systems. One of the driest areas in

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South Africa, however, is the Tankwa Karoo Basin, a large basin between the Great Escarpment and the Cape Fold Mountains in southwestern South Africa. Some parts receive as little as 40 mm of rainfall per year (Mucina *et al.* 2006) and other parts as high as 110 mm (Rubin 1998; Mucina *et al.* 2006). Temperatures range from an average minimum of 5.7°C during winter to an average maximum of 35.9°C during summer (Rubin 1998). The slightly undulating plains are interrupted by a series of solitary dolerite butts and elevated ridges, extensive flat sheet-washes and deeper incised channels of intermittent rivers. The plains are very sparsely vegetated, in extreme precipitation-poor years appearing barren (Mucina *et al.* 2006). The complex geology and the drainage system of the area have resulted in a mosaic of substrate types, varying from sand to various grades of gravel and rock.

A recent survey of the Tankwa Karoo Basin revealed that at least seven terrestrial, diurnal lizard species frequent the arid plains, one agamid, two scincids, and four lacertids (Meyer *et al.* 2010). The four lacertids, *Pedioplanis laticeps, P. lineo-ocellata, Meroles knoxii* and *Nucras tessellata,* are of similar size and morphology, and are all heliothermic insectivores (Branch 1998). Furthermore, because these species are very closely related phylogenetically, one would expect similarities in ecological traits based on their evolutionary history alone (e.g. Vitt *et al.* 2003; Vitt & Pianka 2004). Given the high likelihood of considerable overlap in times of activity and in diet, a logical first step in the investigation of resource partitioning among the four lacertids of the Tankwa Karoo Basin, would be to investigate the degree of overlap in habitat use. Based on their close genealogical relationship and expected similarities in general ecology, we predicted that the four species will be spatially separated in the Tankwa Karoo Basin. The aim of our study accordingly was to determine whether *P. laticeps, P. lineo-ocellata, M. knoxii* and *N. tessellata,* at any given area in the Tankwa Karoo Basin where they occur sympatrically, are spatially separated in terms of the habitat type each species occupies.

MATERIALS & METHODS

Habitat preferences of the four lacertids were investigated on the farm Gansfontein (32°43′27.32″S, 19°42′55.20″E) in the southwestern parts of the Tankwa Karoo Basin. Data were collected on various occasions from October 2007 to August 2008. The area was surveyed by walking representative transects through the study area and recording all active lizards. For each lizard spotted, a digital photograph was taken of the habitat in which the lizard was found. Species identification, based on colour pattern, was always easy in the case of adults, but for juveniles and subadults the lizards were captured and identified on the basis of diagnostic scale characters. Each transect was walked only once, eliminating the possibility of recording an individual lizard more than once. At the end of the sampling period, the habitats in which lizards were found were categorized into six distinct habitat types on the basis of substrate composition. Species preferences for each habitat type were expressed as the proportion of individuals of each species found in each habitat type. A correspondence analysis was done using the number of observations made per species among the various habitat types to illustrate which habitat type(s) each species was associated with the most, or in other words the composition of species a specific habitat type supports.

Microhabitat types

Rocks on compacted sand (*RCS*). Rounded rocks (with an estimated diameter of 10 cm and larger) on a compacted sand substrate dominate the northwestern section of the study site, usually on slightly elevated ridges and hills (Fig. 1a).

Rocks on loose sand (*RLS*). This habitat type is similar to the previous one, but the compacted sand is now replaced by loose sand. It typically forms a continuation of the previous type into low-lying areas (Fig. 1b).

Loose sand (*LS*). This habitat type completely lacks rocks and gravel. It is typically associated with waterflows and can vary considerably in extent, at places being only small isolated habitat pockets. Due to the occasional presence of water, some areas support a well-structured vegetation component (Fig. 1c).

Compacted sand (*CS*). This type of substrate also seems to be linked to the periodic occurrence of water. It occurs in the low-lying areas where water would occasionally flow during wet spells. It occurs only as narrow strips within low-lying areas of other habitat types, especially on the gravel flats. Vegetation cover within these narrow strips also tends to be more pronounced, forming green belts within more sparsely vegetated areas (Fig. 1d).

Compacted sand with gravel (*CSG*). This habitat

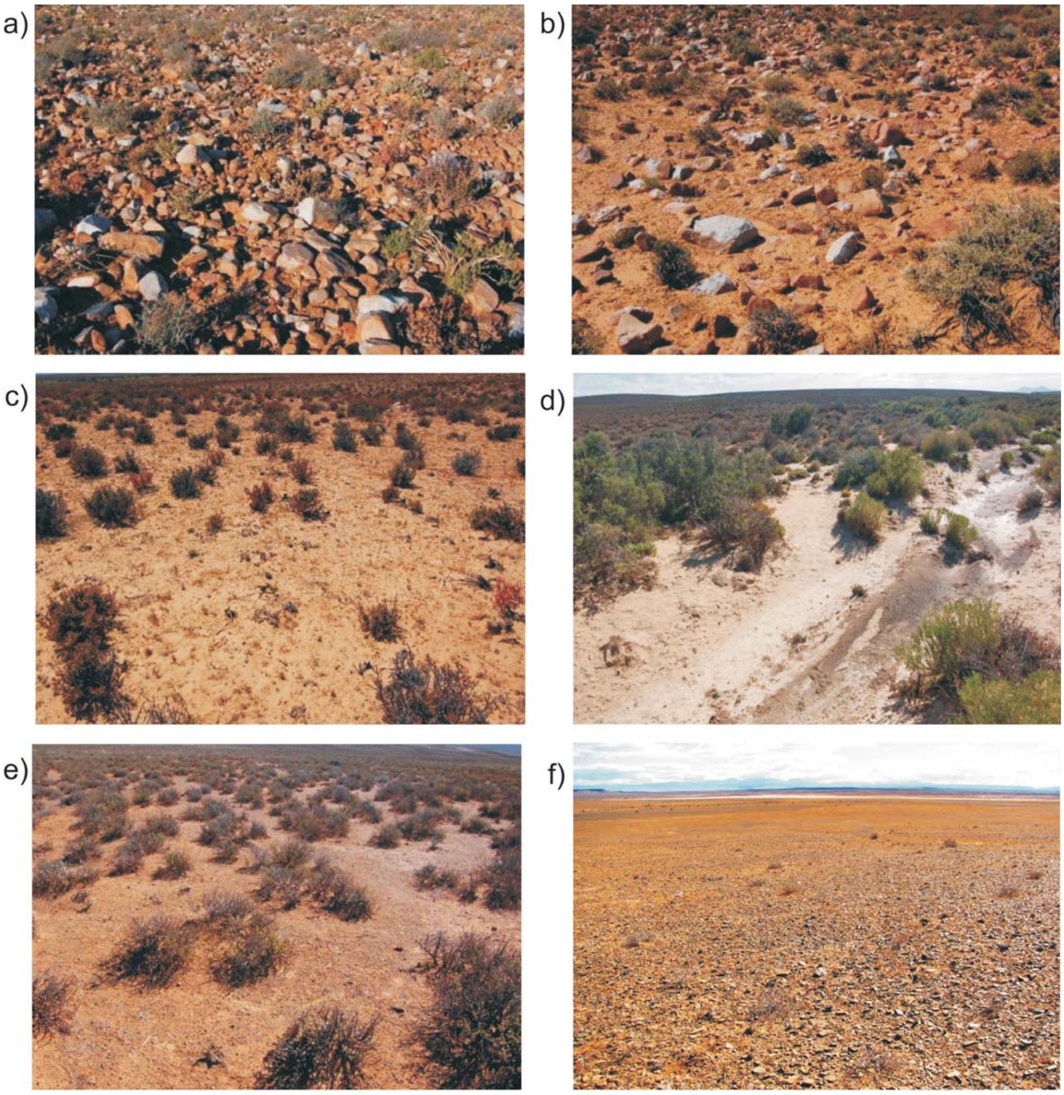

Fig. 1. Different microhabitat types identified in the study area at Gansfontein in the Tankwa Karoo: **a**, rocks on compacted sand (RCS); **b**, rocks on loose sand (RLS); **c**, loose sand (LS); **d**, compacted sand (CS); **e**, compacted sand with gravel (CSG); **f**, gravel-dominated (G).

type consists of a compacted sand layer in combination with a diffuse layer of gravel. As one moves away from the more sandy regions surrounding the river the presence of gravel becomes more prevalent. This habitat type forms a transition between the more sand-dominated areas and the unique gravel-dominated eastern parts of the study site. The vegetation structure is similar to that of the more gravel-dominated regions, however, with some areas completely lacking vegetation (Fig. 1e).

Gravel (*G*). This habitat type represents almost the entire eastern section of the study site. Gravel hills and plains dominate most of eastern landscape directly adjacent to the Doring River. The general composition of the gravel layer changes throughout the habitat type, varying from small rocks to a more gravel-like composition. Vegetation within this habitat type is limited, but is dominated by woody plants; some areas also support small succulent species. Gravel flats cover vast areas infrequently interrupted by other habitat types (Fig. 1f).

The spatial distribution of the different micro-

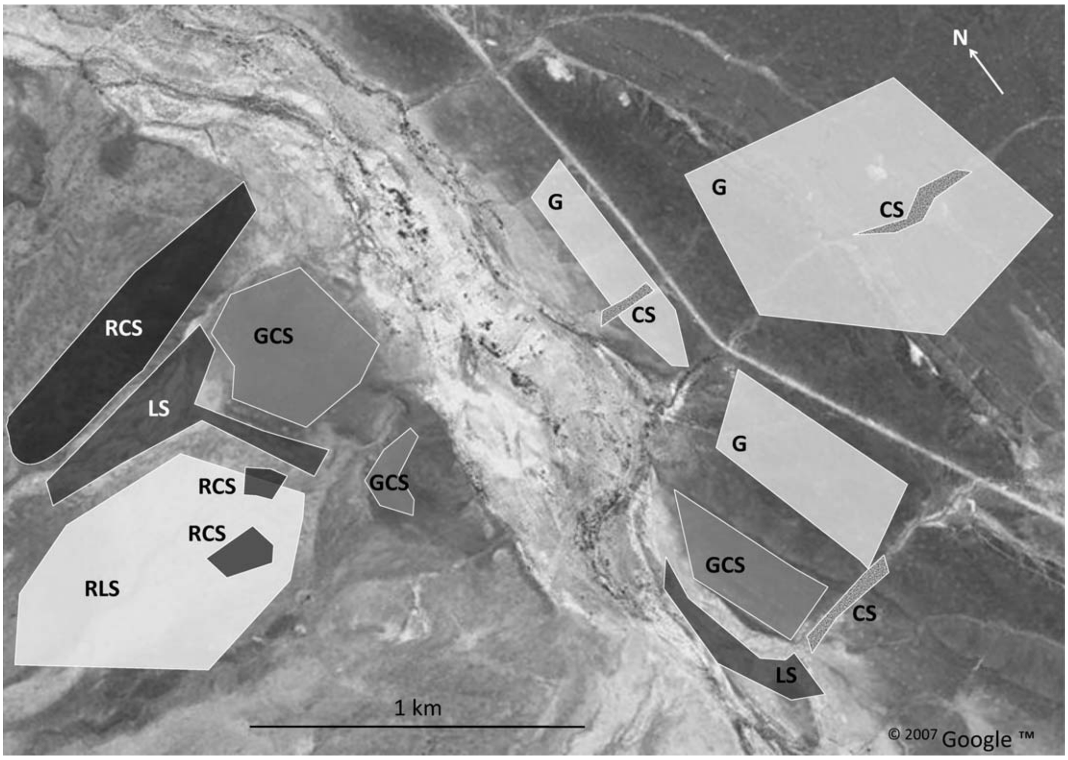

Fig. 2. Areas and microhabitats surveyed in the study area at Gansfontein in the Tankwa Karoo. RCS = rocks on compacted sand, RLS = rocks on loose sand, LS = loose sand, CS = compacted sand, CSG = compacted sand with gravel, G = gravel-dominated.

habitat types and areas surveyed in the study area is depicted in Fig. 2. The Doring River cuts across the study area in a northerly direction. The area west of the river encompasses several elevated areas of rocks on loose or compacted sand, with loose sand along the drainage lines. Vast stretches of gravel occur east of the river, with compacted sand, free of gravel, along the drainage lines.

RESULTS

During the survey, habitat data were obtained for 161 individuals of the four lacertid species occurring sympatrically in the Tankwa Karoo Basin. The sample included only one individual of *Nucrastes sellata* (a juvenile recorded on a sandy flood plain), but samples sizes for *Pedioplanis laticeps* (*n* = 73), *P. lineo-ocellata* (*n* = 57), and *Meroles knoxii* (*n* = 30) were sufficiently large to obtain a clear perspective of habitat segregation among these three species. All three species were restricted to a specific set of habitat types, with limited overlap among the three (Table 1). *Pedioplanis lineo-ocellata* was restricted to rocky habitats; it was the only species present in the RCS habitat and was also found in the RLS habitat, but was absent in habitat types lacking rocks (Table 1). *Pedioplanis laticeps* was extremely abundant on the gravel plains and was the only one of the three lacertids that frequented this habitat type (Table 1). It was also the dominant species in the CSG habitat (81.08% of observations) and shared this habitat with *M. knoxii* (18.92% of observations) (Table 1). *Meroles knoxii* was the only one of the three species observed in the LS habitat (Table 1). It was also the dominant species in the CS habitat (83.33% of observations) and shared this habitat with *P. laticeps* (16.67% of observations) (Table 1). The RLS habitat was the only habitat in which all three species were found, but *P. lineo-ocellata* (85.71% of observations) was by far the most dominant species in this habitat type (Table 1).

Figure 3 depicts the results of a correspondence analysis using the proportion of observations made of each of the three species in each of the six habitat types. Within two-dimensional space, the three species were well separated according to habitat type(s) each species was mostly associated with. *Pedioplanis laticeps* was closely associated

Table 1. The number of individuals of *Pedioplanis laticeps, P. lineo-ocellata* and *Meroles knoxii* observed in each of the six different habitat types at the farm Gansfontein in the Tankwa Karoo Basin. The total number of individuals observed of *P. laticeps, P. lineo-ocellata* and *M. knoxii*, and the total number of observations per habitat type are provided (RCS = rocks on compacted sand, RLS = rocks on loose sand, LS = loose sand, CS = compacted sand, CSG = compacted sand with gravel and G = gravel dominated).

	Habitat type						
Species	RCS	RLS	LS	CS	CSG	G	Total
P. laticeps	0	1	0	1	30	41	73
P. lineo-ocellata	39	18	0	0	0	0	57
M. knoxii	0	2	16	5	7	0	30
Total	39	21	16	6	37	41	160

with CSG and GD, whereas *P. lineo-ocellata* in turn was closely associated with RCS and RLS. The correspondence analysis indicated that *M. knoxii* was mostly associated with LS and CS.

DISCUSSION

The results obtained in this study show that *Pedioplanis laticeps, P. lineo-ocellata,* and *Merolesknoxii* are spatially separated at the study site, *P. lineo-ocellata* being restricted to rocky areas, *P. laticeps* preferring gravel substrates and *M. knoxii* sand substrates. Very limited spatial overlap was recorded in transitional habitats. Of 45 studies dealing with resource partitioning among lizards, 53% ranked habitat (spatial dimension) as the most important ecological dimension according to which resource partitioning takes place in lizard communities (Toft 1985). Pianka (1973) compared lizard communities occurring within three different desert systems (Australia, Kalahari and North America) and in all three of these very little overlap in the spatial dimension occurred among species, with the greatest overlap on the trophic and temporal dimensions.

The distinct spatial separation of the three lacertid species observed in this study can be the result of either adaptation or interspecific competition, or a combination of the two. In the case of the former, there is a distinct possibility that the three lacertid species may be adapted to different habitat types, allowing allotopic, but not syntopic occurrence. If this is the case, one would expect that where the species occur allopatrically they will still display the same habitat preferences as in

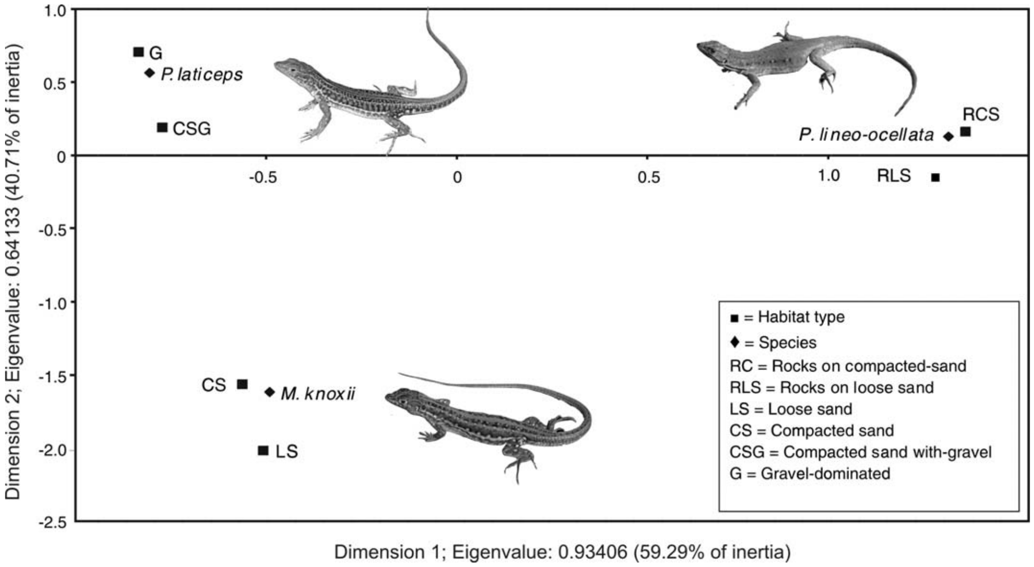

Fig. 3. The results of a correspondence analysis indicating the associations between the three species and the six different habitat types identified within the study area.

the Tankwa Karoo Basin where they occur sympatrically. Only anecdotal information is available on habitat specificity by the three species elsewhere within their distribution ranges. Branch (1998) described *P. lineo-ocellata* as preferring flat, rocky veld, but remarks that in Botswana it is restricted to hard soil around pans. De Waal (1978) described the habitat of this species in the Free State Province as sandy areas or rocky flats with scattered rocks and scant vegetation. There is similarly no information available on *P. laticeps,* but Mouton & Van Wyk (1993) remarked that *P. burchelli,* the sister species of *P. laticeps* (Makokha *et al.* 2007), seems to thrive in areas of exposed bedrock or gravel patches with sparse vegetation. The *burchelli-laticeps* clade appears to be basal in the genus (Makokha *et al.* 2007) and indications are thus that habitat specificity displayed by *P. laticeps* at our study site reflects historical adaptation and not a local, competition-induced shift in habitat use. FitzSimons (1943) described *Meroles knoxii* as an active, quick-moving lizard, living in sandy, scrub-covered areas. Along the southwestern coast of South Africa, from the Cape Peninsula to Lambert's Bay, i.e. outside the ranges of the other two species, *M. knoxii* also occurs in sandy areas (personal observation). The majority of species in this small genus are furthermore restricted to coastal sand dunes (FitzSimons 1943; Branch 1998; Harris *et al.* 1998) and one can thus with reasonable certainty conclude that *M. knoxii*'s affinity for sandy habitats in our study area is because it is adapted to this habitat type and not because it is forced into it by competition with any of the other lacertids occurring at the site.

Although the information at hand suggests that spatial separation of the three species in the study area is the result of historical adaptation to different substrate types, interspecific competition may also play a significant role in shaping the realized niches of the three lacertids in the area. In fact, many studies have indicated that interspecific competition within an ecological system plays a crucial role in determining the position a species will occupy within ecological space (Ricklefs & Miles 1994; Vanhooydonck *et al.* 2000). The fundamental niche describes the species' potential without the presence of interspecific competition and the realized niche is the actual niche breadth used by the species when faced with a competitor within the same system (Hutchinson 1957; Miller 1967). Owing to the patchy nature of different substrate types and the transitional nature of some of these substrates in our study area, one would expect that without interspecific competition, all three species would probably have been able to inhabit a much broader range of habitat types than when faced with interspecific competition.

Spatial overlap at our study site was marginally greater between *P. laticeps* and *M. knoxii* than between *P. laticeps* and *P. lineo-ocellata.* This was to be expected as the two *Pedioplanis* species are genealogically more closely related (Makokha *et al.* 2007) and the possibility of large niche overlap is thus greater (Losos 2008). Although no active competition or interspecific aggression was witnessed, one could assume that the more aggressive species would force a rival species out of an area where it has the competitive edge. It is most likely that the most intense competition would occur between the two *Pedioplanis* species, explaining the very narrow sympatry in which they occur within the study area.

The patchy distribution of the various habitat types across the study site could have resulted in the varying degrees of spatial overlap indicated by the data. Schoener (1970) found a similar degree of habitat overlap in two *Anolis* species. In an area where different habitat types occurred scattered throughout the environment, more spatial overlap occurred amongst the preferred habitats of the constituent species (Schoener 1970). The patchy nature of the different habitat types within the system increased the degree of overlap at the margins of the habitats (Schoener 1970).

In conclusion, three of the four lacertids inhabiting the arid Tankwa Karoo Basin in South Africa, are spatially separated. Although only anecdotal information is available, all indications are that this spatial separation is mainly the result of historical adaptation to different substrate types. In transitional habitats, interspecific competition may play a limited role in shaping the realized niches of the three species. It is expected that the three species will largely overlap along the trophic and temporal axes of ecological space, but this needs to be verified.

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