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Posted Date: 21 May 2025

doi: 10.20944/preprints202505.1671.v1

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Article

Seasonal Variation in the Diet Composition and Dietary Overlap in Five *Trachylepis* Skink Species in Arid South-Western Africa

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Abstract: Diet of five *Trachylepis* skink (*T.spilogaster, T.acutilabris, T.sulcata, T.hoeschi, T.occidentalis*) was studied through stomach content analysis. Skinks were collected in arid habitats in western Namibia. In all these species, active predatory strategy predominates. All skink species preyed almost exclusively on insects. Among insects four taxa comprised the bulk of diet in all five species investigated: beetles (Coleoptera), grasshoppers (Orthoptera), termites (Isoptera), ants (Hymenoptera: Formicidae) and larvae. Their overall contribution changed from 92.2% to 97.7% of all prey items in the diet of particular skink species. These insects are among the most common invertebrate groups in arid regions of southern Africa. Most prey items (ants, termites, spiders, most beetles, flies) were below 10 mm long. All main prey groups were recorded in dry and wet season in all five skink species. Both males and females fed on the same prey groups, but there were marked differences in the proportions of these groups in particular skink species. In general males preyed more on beetles, while females – more on ants. Niche breadth ranged from 0.25 in *T. occidentalis* to 0.47 in *T.hoeschi*. The highest overlap of feeding niches was recorded between *T. spilogaster* and *T. sulcata*, and between *T.spilogaster* and *T.acutilabris*; while the lowest overlap was recorded between *T.acutilabris* and *T.sulcata*, and between *T.sulcata* and *T. hoeschi.*

Keywords: Scincidae lizards; diet; niche breath; niche overlap

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1. Introduction

Predation and competition play a major role in animal interactions. Competition occurs when individuals, belonging to different species (often closely related), utilize the same environmental resources which are limited. Competition for food resources may lead to character displacement (morphological or behavioural differentiation) among competing species, and this, in turn, may result in the niche segregation (KREBS 2009). Competing species may segregate their food niches in three major ways: trophic (what they eat), spatial (when they forage) and temporal (when they forage).

Closely related species may co-exist in the same habitat if their niches do not overlap to a large extend. This overlap decreases with increasing environmental variability, and/or with increasing diffuse competition (increasing number of competing species). A maximal tolerable niche overlap should, therefore, vary inversely with the intensity of competition (PIANKA 1974). Lizards living in arid environments constitute good study objects to test niche differentiation and similar related issues of interspecific competition (PIANKA 1969, 1974; HUEY ET AL. 1974; TOFT 1985; WINEMILLER, PIANKA 1990; SHENBROT ET AL. 1991; COOPER, WHITING 1999; BAKER ET AL. 2021). Due to the habitat heterogeneity and long isolation, some arid regions, like these in Namibia, support also a high level of lizard endemicity, especially skinks and geckos (MURRAY et al. 2016).

The family Scincidae is the largest and most diverse lizard family represented by more than 1685 species, 158 genera and seven subfamilies (UETZ et al. 2020). One of the subfamily Mabuyinae consists one of the most speciose lizard genus – *Trachylepis* (previously *Mabuya*), with 87 species. Most of them (n=84) are confined to the Afrotropical Region (UETZ et al. 2020). In southern Africa, the genus consists 23 species (ALEXANDER & MARAIS 2017). HUEY & PIANKA (1977) studied diet of *T.spilogaster, T.occidentalis,* in the southern Kalahari. However, no quantitative data on food consumption are available for *T.acutilabris, T.sulcata* and *T.hoeschi* (BRANCH 1992, ALEXANDER & MARAIS 2017).

I set out to investigate whether the feeding niches differ for five common *Trachylepis* species living in arid regions of Namibia: *T.spilogaster* (Kalahari tree skink), *T. acutilabris* (wedge-snouted skink), *T.sulcata* (western rock skin), *T.hoeschi* (Hoesch's skink), and *T. occidentalis* (western-tree-striped skink) (ALEXANDER & MARAIS 2017). Since these species are very similar and often occur sympatrically (ALEXANDER & MARAIS 2017), I hypothesize that there may be differences between the feeding niches of these selected species of the genus *Trachylepis*. I address this hypothesis by analysing the composition of their diet.

2. Materials and Methods

I studied food composition of stomachs dissected from museum specimens deposited in the National Museum of Namibia in Windhoek (Table 1). Specimens were collected in various sites in the western part of Namibia, dominated by deserts, and semi-deserts (Figure 1). Specimens were collected throughout the year (Table 1).

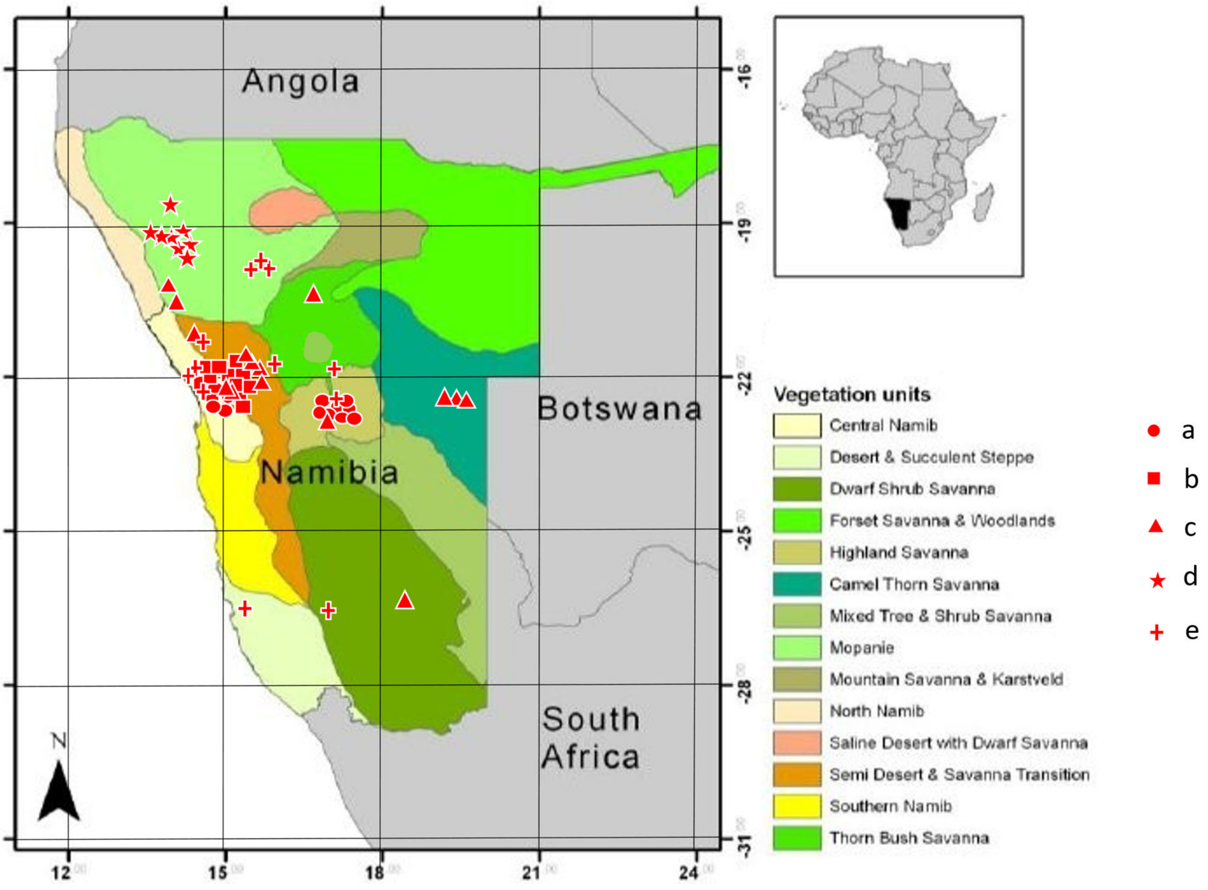

Figure 1. Distribution of the samples (Trachylepis specimens). a – T.spilogaster, b – T.acutilabris, c – T.sulcata, d – T.hoeschi, e – T.occidentalis.

Stomach content was placed in Petri dishes. Prey were identified to the least possible taxon. Food content were assessed in terms of the frequency of occurrence of prey taxa (the percentage of stomachs containing given taxon in relation to the total number of stomachs containing prey) and numerical percentage of prey items (the percentage pf given prey taxa in relation to the total number of prey items identified). Each prey item was measured with a ruler to the nearest 1 mm.

For each species, also the niche breath, and niche breath overlap were calculated using the following formula:

Niche breadth (PIANKA 1986):

$$B = \sum_i^n 2p_i^2$$

where: i – resource category, p – proportion of resource category i, n- total number of categories

B ranges from 1 to n, indicating whether the species preys upon a wide range of prey (high value, close to n) or specializes on a limited range of prey (low value, close to one).

Table 1. Seasonal distribution of samples (stomachs) of *Trachylepis* skink species. Unmarked cells – wet season, grey cells – dry season. .

Species	**J**	**F**	**M**	**A**	**M**	**J**	**J**	**A**	**S**	**O**	N	D
T.spliogaster		1	1	1	2		1	1	4			
T.acutilabris	2		2			1				4	1	2
T.sulcata			4	1	3			2	2		1	
T.hoeschi			1				5			4		
T.occidentalis	2		2	3				1	1	3		

Niche breadth overlap (PIANKA 1986):

$$O_{jk} = \sum_i^n pij \ x \ pik \ / \sqrt{\sum_i^n pij^2 \sum_i^n pik^2}$$

where: i – resource category, p – proportion of resource category i, n- total number of categories, j – female, k – male

O_{jk} ranges from 0 (no similarity) to 1 (totally similar).

3. Results

All skink species investigated preyed almost exclusively on insects (Table 2). Only in the diet of *T.acutilabris* single spider was recorded (Table 3). Among insects four taxa comprised the bulk of diet in all five species investigated: beetles (Coleoptera), grasshoppers (Orthoptera), termites (Isoptera), ants (Hymenoptera: Formicidae) and larvae. Their overall contribution changed from 92.2% to 97.7% of all prey items in the diet of particular skink species. However, the proportions of particular taxa varied markedly. Beetles were important prey of *T.sulcata*, and *T.occidentalis*; grasshoppers – *T.sulcata*, termites – *T.hoeschi* and *T.acutilabris*; ants – *T.spilogaster* and *T.acutilabris*; while larvae were important diet of *T. sulcata*. Beetles were represented by at least five families, associated mainly with the ground as feeding place. Orthopterans were also represented by at least five families, with clear dominance of locusts (Acrididae) and crickets (Gryllidae), also associated mainly with the ground as foraging place (Table 3). Also termites and ants are typical ground-foraging insects. Insect larvae were represented mainly by Coleoptera, Diptera and Lepidoptera. Other insects were preyed upon only occasionally and belonged to the order Hymenoptera, represented by bees Apionoidea and wasps Vespoidea. These, like ants and termites, are social taxa.

Table 2. General characteristic of diet of *Trachylepis* skink species.

	T.spilogaster	*T.acutilabris*	*T.sulcata*	*T.hoeschi*	*T.occidentalis*
Number of stomachs analysed	12	13	15	11	12
Number of empty stomachs	2	3	5	5	3
Percentage of empty stomachs	14.2	18.8	25.0	31.3	20.0
Number of insect orders in the diet	5	6	5	4	5
Number of prey items	43	105	18	41	84
Niche breath	0.34	0.37	0.30	0.47	0.25

Most prey items (ants, termites, spiders, most beetles, flies) were below 10 mm long, some were 11-20 mm in length (crickets, grasshoppers, larvae, some beetles and wasps) and only two wasp species were 25 mm in length. One exceptionally large prey was recorded in the diet of *T.sulcata* (SMR4607; SVL: 62.3, TL: 7.7 [tail broken off], collected in Suiderhof, Windhoek, on 25 April 1985), a locust (Orthoptera: Acrididae: Acridinae) 30.2 mm long

All main prey groups were recorded in dry and wet season in all five skink species. Ants appear to be more important in dry, while termites – in wet season. *T. hoeschi* preyed mostly on beetles in dry, while on termites – in the wet season (Figures 2, 3 and 5).

Both males and females fed on the same prey groups, but there were marked differences in the proportions of these groups in particular skink species. In general males preyed more on beetles, while females – more on ants (Figure 4).

Niche breath ranged from 0.25 in *T.occidentalis* to 0.47 in *T.hoeschi* (Table 2). The highest overlap of feeding niches was recorded between *T.spilogaster* and *T.sulcata*, and between *T.spilogaster* and *T.acutilabris*; while the lowest overlap was recorded between *T.acutilabris* and *T.sulcata*, and between *T.sulcata* and *T.hoeschi* (Table 4).

Very high (O_{jk} >0.90) niche overlap was recorded between *T.spilogaster and T.acutilabris, T.subcostata* and *T.occidentalis*, and between *T.acutilabris* and *T. occidentalis*. On the other end, low food niche overlap (O_{jk}<0.40) was recorded between *T.sulcata* and *T.acutilabris,* and between *T.sulcata* and *T.hoeschi* (Table 4).

Table 3. Diet composition of five *Trachylepis* skin species associated with arid habitats in Namibia. %N – numerical percentage (proportion of a given prey taxon in relation to the total number of prey items); %F – frequency of occurrence (percentage of stomachs containing given taxon).

Prey taxa	*T.spilogaster*		*T.acutilabris*		*T.sulcata*		*T.hoeschi*		*T.occidentalis*	
	%N	%F	%N	%F	%N	%F	%N	%F	%N	%F
Coleoptera										
Carabidae	2.3	8	1.0	8	0	0	0	0	0	0
Cerambicidae	0.0	0	1.0	8	0	0	0	0	0	0
Curculionidae	0.0	0	0.0	0	11.1	7	0	0	0	0
Scarabaeidae	0.0	0	0.0	0	5.6	7	0	0	0	0
Tenebrionidae	0.0	0	1.0	8	0.0	0	2.4	9	10.7	42
Unidentified	14.0	25	2.9	23	27.8	33	9.8	27	7.1	33
Total	16.3	33	4.8	46	44.4	47	12.2	36	17.9	75
Orthoptera										
Acrididae	0.0	0	0.0	0	16.7	20	7.3	27	1.2	8
Gryllidae	2.3	8	2.9	23	5.6	7	0.0	0	2.4	17
Pamphagidae	0.0	0	1.0	8	0.0	0	0.0	0	0.0	0

doi:10.20944/preprints202505.1671.v1

Tettigonidae	0.0	0	0.0	0	0.0	0	2.4	9	0.0	0
Tetrigidae	0.0	0	1.0	8	0.0	0	0.0	0	0.0	0
Unidentified	0.0	0	1.0	8	0.0	0	4.9	18	2.4	17
Total	2.3	8	5.7	46	22.2	27	14.6	55	6.0	42
Isoptera	34.9	25	44.8	8	0.0	0	65.9	9	33.3	8
Hymenoptera										
Formicidae	44.2	33	40.0	54	5.6	7	0.0	0	26.2	50
Vespidae	0.0	0	0.0	0	0.0	0	0.0	0	2.4	8
Vespoidea	0.0	0	0.0	0	0.0	0	2.4	9	0.0	0
Apioidea	0.0	0	0.0	0	0.0	0	2.4	9	0.0	0
Total	44.2	33	40.0	54	5.6	7	4.9	18	28.6	58
Diptera										
Imago	2.3	8	1.0	8	5.6	7	0.0	0	0.0	0
Larvae	0.0	0	0.0	0	0.0	0	0.0	0	14.3	8
Total	2.3	8	1.0	8	5.6	7	0.0	0	14.3	8
Lepidoptera – larvae	0.0	0	1.9	8	0.0	0	0.0	0	0.0	0
Insecta – larvae	0.0	0	0.0	0	22.2	13	2.4	9	0.0	0
ARANEAE	0.0	0	1.0	8	0.0	0	0.0	0	0.0	0

Table 4. Niche breath overlap between five *Trichylepis* skin species.

	T.spilogaster	*T.acutilabris*	*T.sulcata*	*T.hoeschi*	*T.occidentalis*
T.spilogaster					
T.acutilabris	0.96				
T.sulcata	0.99	0.17			
T.hoeschi	0.68	0.79	0.25		
T.occidentalis	0.94	0.92	0.43	0.77	

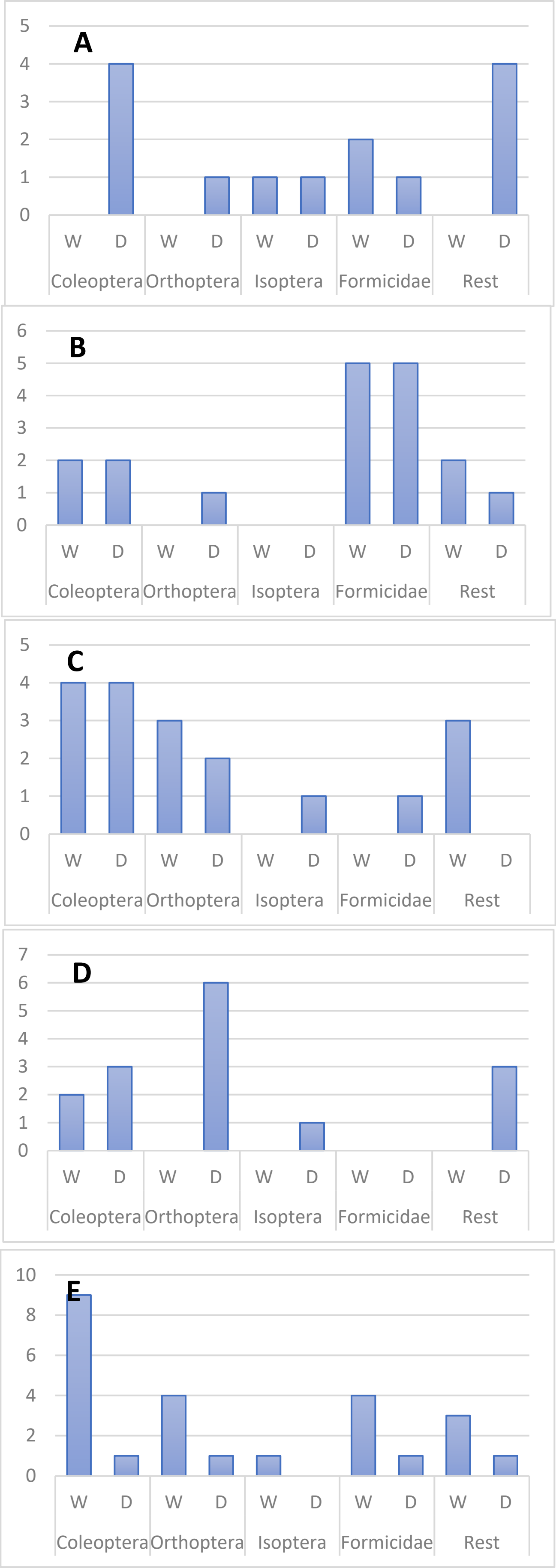
A
5
4
3
2
1
0
W D W D W D W D W D
Coleoptera Orthoptera Isoptera Formicidae Rest
B
6
5
4
3
2
1
0
W D W D W D W D W D
Coleoptera Orthoptera Isoptera Formicidae Rest
C
5
4
3
2
1
0
W D W D W D W D W D
Coleoptera Orthoptera Isoptera Formicidae Rest
D
7
6
5
4
3
2
1
0
W D W D W D W D W D
Coleoptera Orthoptera Isoptera Formicidae Rest
E
10
8
6
4
2
0
W D W D W D W D W D
Coleoptera Orthoptera Isoptera Formicidae Rest

Figure 2. Seasonal variation in the diet of *T. spilogaster* (A), *T. acutilabris* (B), *T. sulcata* (C), *T. hoeschi* (D) *and T. occidentalis* (E). Number of prey items are shown on vertical axis.

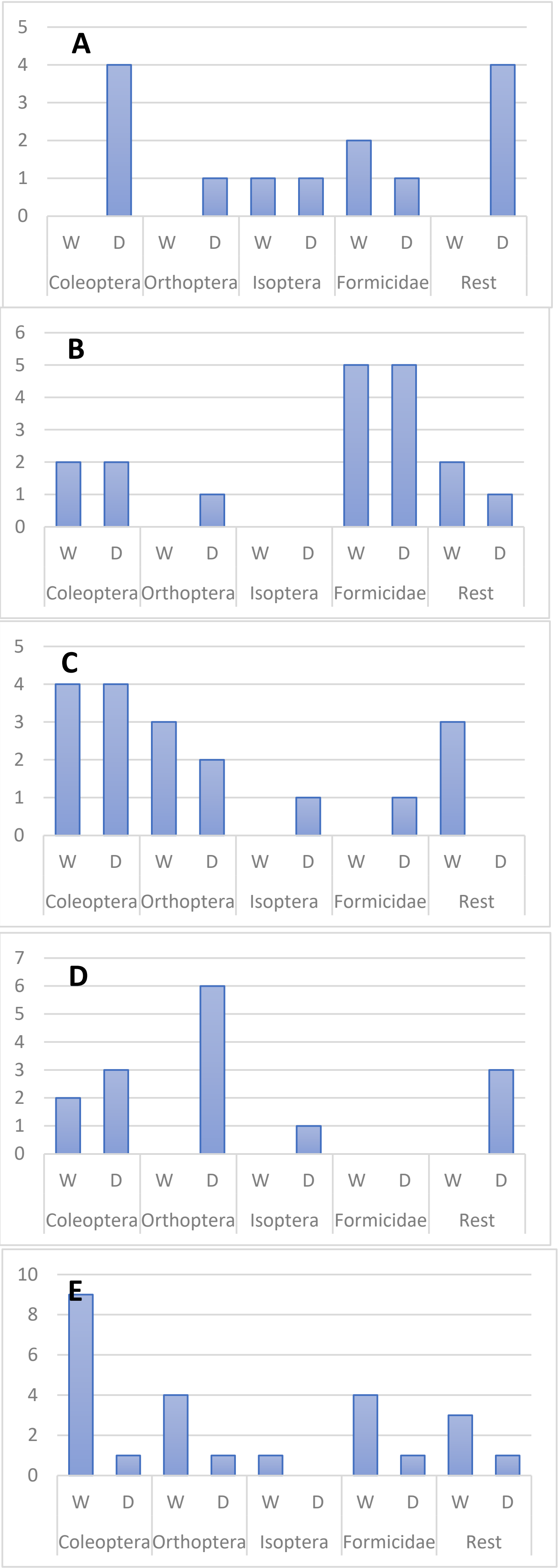

Figure 3. Seasonal variation in the frequency of occurrence of main prey groups in the diet of *T. spilogaster* (A), *T. acutilabris* (B), *T. sulcata* (C), *T. hoeschi* (D) and *T. occidentalis* (E). Number of prey items are shown on vertical axis.

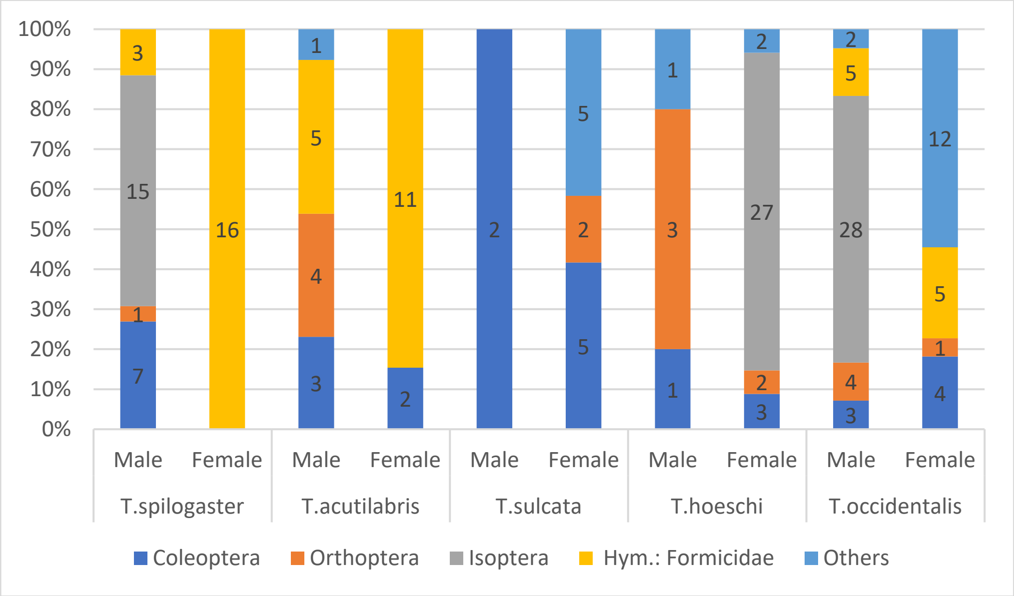

Figure 4. Proportions of main prey groups in the diet of male and female of five *Trachylepis* species occurring in arid south-west Africa. The number of prey items are indicated in each bar (prey group) of each column.

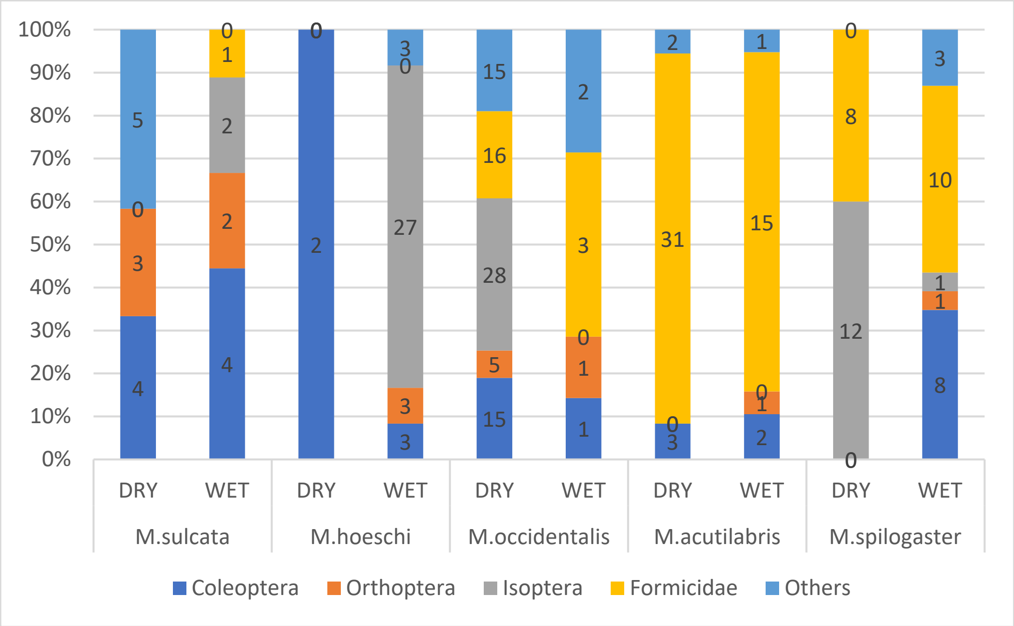

Figure 5. Seasonal variation in the proportions of main prey groups in the diet of five *Trachylepis* species occurring in arid south-west Africa. The number of prey items are indicated in each bar (prey group) of each column.

4. Discussion

In *Trachylepis punctatissima* and *T. varia* from the Free State, South Africa, females had wider niche breadths than males and isopterans comprised the bulk of the diet. The diet was supplemented by larvae in both species, and arachnids in T. varia (Heidemann et al. 2024). Lizards represented by *Mabuya, Agama, Ichnotropis* and *Lygodactylus* from Dambwa Forest Reserve, Livingstone, Zambia, fed mainly on termites and supplemented the diet with ants, beetles, grasshoppers and other insects

(Simbotwe, Garber 1979). In southern Africa, the diet of *Trachylepis margarifer* was dominated by termites (WYMANN & WHITING 2002); geckos preyed mainly on *Hodotermes mossambicus* termites (48.2v%), beetles (10.6v%), and grasshoppers (9.1v%) (PIANKA & HUEY 1978); the tree agama *Acanthocercus a. atricollis* preyed mainly upon ants (92.8 % of all prey items, 17.9 % of total prey volume) and beetles (4n% vs. 26.3v%) (REANEY & WRITING 2002); *Pedioplanis husabensis* and *Rhoptropus bradfieldi* mainly on beetles (MURRAY et al. 2016); *Acanthocercus atricollis* mostly on ants (REANEY & WHITING 2002); *Meroles cuneirostris* fed mainly (in the order of preference): Curculionidae > Tenebrionidae larvae > Tenebrionidae imagi > ants > other Hymenoptera; while *Aporosaura anchietae*: Tenebrionidae larvae > Lepidoptera > Tenebrionidae imagi > Pentatonidae > other beetle larvae (ROBINSON & CUNNINGHAM 1978). BAUER et al. (1989) recorded *Hodotermes mossambicus* termites as main prey of lizards.

Beyond southern Africa, beetles constituted the main prey of three skin species (*Chalcides ocellatus, Scincus scincus* and *Sphenops sepsoides*) in Sinai, Egypt (ATTUM et al. 2004); *Trachylepis quinquetaeniata* in Egypt (KADRY et al. 2017); *Chalcides ocellatus* in Cyprus Island (CICEK & GOCMEN 2013). While ants, bugs and grasshopper often supplemented their diet (ATTUM et al. 2004, KADRY et al. 2017, CICEK & GOCMEN 2013). The staple diets of *Trachylepis adamastor* and *T. thomensis* from the Gulf of Guinea consisted of mites, ants, spiders, flies and beetles (SOUSSA ET AL. 2022).

Ants, termites, small beetles and grasshoppers comprise, therefore, the main diet of skins both in southern Africa and other regions of Africa. Results of the present study also this general statement. Most of the insects preyed upon by the *Trachylepis* skinks are among the most common invertebrate groups in arid regions of southern Africa (own observ.). However, contrary to expectations, Tenebrionidae beetles comprised a low contribution to the diet of all skink species studied. This is the most diverse, widespread and commonest terrestrial beetle family in arid regions of Namibia and other regions of southern Africa (BRANCH 1992). Probably they are poisonous to the lizards and their exoskeletons may be too hard for digestion.

Morphological, ecological, and behavioural characters may influence feeding techniques in lizards. Two main hunting strategies can be distinguished in this group living in arid regions of southern Africa: sit-and-wait predatory strategy recorded among others in geckos and chameleons; and cruising (intensive) predatory strategy known among others in skinks and lacertids (ANANJEVA & TSELLARIUS 1986, WYMANN & WHITING 2002). The sit-and-wait strategy increases with the increase of food resources, while the intensive strategy is linked to territoriality (WYMANN & WHITING 2002). In all *Trachylepis* skink species studied here, the intensive predatory strategy predominates.

Mean prey size is correlated with the mean size of lizards of Gekkonidae, Scincidae, Lacertidae and Agamidae (ANANJEVA & TSELLARIUS 1986). Since skinks are relatively small, prey longer than 20 mm were rare, and longer than 30 mm were preyed upon sporadically. In most cases, larger preys were slow-moving insects, such as larvae.

Most *Trachylepis* skinks preyed mostly on termites and ants. These are social insects living mainly on the ground or underground. This suggests patchy resource utilization by these lizards. The contribution of these insects may be much higher at the beginning of rainy season, when alate termites swarm usually 3-5 days after first heavy rain (in Namibia usually in October/November) (BAUER et al. 1989).

Trophic niche overlap between the male and female of the same species was low suggesting strong competition for the food resource. Lower niche breadth in males compared to females may be due to morphological and behavioural differences and merits further investigation (HEIDEMANN ET AL. 2024).

As shown in this study, *Trachylepis* skinks living in Namibia (KOPIJ 2021; this study) are food generalists, preying upon the most common and most easily available insect prey, such as beetles, locusts, ants and termites. In fact, most lizard species worldwide are generalist foragers and are probably relatively unselective of the various types of arthropods available in their environment (TOFT 1985, LUISELLI 2008).

doi:10.20944/preprints202505.1671.v1

The *Trachylepis* skinks studied here may avoid competitive exclusion by foraging among a different microhabitats, by using different foraging mode (most lizard species are sit-and-wait foragers), and by preying upon insects (e.g., termites and ants) occurring in higher aggregations.

The niche overlap hypothesis of PIANKA (1972) holds that maximal tolerable niche overlap should vary inversely with the intensity of competition for the resource. A review of more than 50 studies conducted by LUISELLI (2008) concludes, however, that trophic niche separation was not a general rule among sympatric lizards. This has been also supported by TOFT (1985), KOPIJ (2021), HEIDEMANN ET AL. (2024), and the present study.

In order to co-exists at the same place, the *Trachylepis* species have to partition their temporal (diurnal or nocturnal), spatial (habitat or micro habitat), and trophic niche axes to reduce interspecific competition and enable co-existence.

The method for identifying dietary items (mostly stomach or faecal-pellet content analysis) does not allow for accurate prey identification. Prey items (mostly insects) in majority of cases are identified to order level. For studies of niche segregation, diet should be analyzed at least to the family or genus level. Inappropriate methods may lead to the erroneous conclusion on feeing niche partitioning in most diet studies.

Structure has a temporal dimension (GOTELLI AND GRAVES 1996). In most cases, data on diet composition are obtained in different seasons of the year and over several years. Id averaged, results of such studies provide mean values, which may obscure short-term dietary differences, more important for studies on food niche segregations.

5. Conclusions

This section is not mandatory but can be added to the manuscript if the discussion is unusually long or complex.

Funding: This research received no external funding.

Conflicts of Interest: The author declare no conflicts of interest.

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