Vestnik zoologii, **49**(4): 351–350, 2015
DOI 10.1515/vzoo-2015-0038

DE GRUYTER
OPEN

UDC 598.2:574.2(6–13)

AVIAN DIVERSITY ALONG AN ALTITUDINAL GRADIENT IN HIGHVELD/ DRAKENSBERG GRASSLANDS

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Avian Diversity Along an Altitudinal Gradient in Highveld/Drakensberg Grasslands. Kopij, G. — Temperature and rainfall related to altitudinal gradients influence ecological and evolutionary responses of organisms to physical factors. In this study, the line transect method was used during the years 1996–2001to compare resident (potentially breeding) bird communities in three altitudinal divisions in Highveld/Drakensberg grasslands in Lesotho: lowlands (< 1700 m a. s. l.), foothills (1700–2200 m a. s. l.) and highlands (> 2200 m a. s. l.). In total, 105 resident species were recorded. The total number of species recorded in lowlands was higher than that in highlands and foothills, but this difference was not statistically significant. The highland and foothill did not differ in numbers of species. A group of five species dominated at all three sites, and the proportion of dominant species in relation to the whole assemblage was very similar. The composition of the dominant group (species with more than 5 % of pairs) and the group of species most often encountered (in more than 80 % of transects) was, however, different. Only two species, Cape Canary *Serinuscanicollis* and Karoo Prinia*Priniamaculosa* were dominant in all three study areas, and just one species, the Cape Bunting *Emberizacapensis*, was dominant in two plots. Similarly, only two species, the Cape Turtle-Dove *Streptopelia capicola* and Cape Canary had a high frequency of occurrence in all three study areas, and two otherspecies, theKaroo Prinia and Cape Bunting — in two study areas. Simpson's Diversity Index was strikingly the same (S = 0.96) for all three avian assemblages (lowland, foothill and highland) investigated. However, proportions of breeding pairs of some congeneric species were found to change with the altitude. The granivores were more common (44–45 %) in the foothills and highlands than in lowlands (36%), while insectivores were more common in the highlands (50 %) than in foothills and lowlands (36–37 %). In general, avifauna is relatively diverse and unique in the Highveld/ Drakensberg grasslands. Results presented here provide data for further investigation of the effect of the supposed climate warming on the diversity and structure of avian communities.

Key words: avian assemblages, population densities, 'hot-spot', Lesotho.

Видовое разнообразие птиц вдоль высотного градиента на лугах Хайвельда/Дракенберга. Копий Г. — Температура и осадки, связанные с высотным градиентом, влияют на экологический и эволюционный ответ организмов на физические факторы. В этом исследовании метод линий трансект был использован в течение 1996–2001 гг. для сравнения постоянно обитающих (потенциально размножающихся) сообществ птиц в трех высотных участках на лугах Хайвельда/Дракенберга в Лесото: низинах (< 1700 м н. у. м.), предгорьях (1700–2200 м н. у. м.) и нагорьях (> 2200 м н. у. м.). В общей сложности было отмечено 105 видов-резидентов. Общее количество видов, зарегистрированных в низинах, было выше, чем в горной местности и предгорьях, но это различие не было статистически значимым. Горные и предгорные области не отличаются по количеству видов. Группа из пяти видов преобладала на всех трех участках, а доля доминирующих видов по отношению ко всем птичьим комплексам была очень сходной. Однако состав доминирующей группы (виды более чем с 5 % пар) и группа видов, наиболее часто встречающихся (более чем 80 % трансект), отличается. Только два вида, *Serinus canicollis* и *Prinia maculosa,* были доминирующими во всех трех областях исследований и только один вид, *Emberiza capensis*, доминировал в двух участках. Точно так же, только два вида, *Streptopelia capicola* и *Serinus canicolls,* имели высокую частоту встречаемости во всех трех областях исследований и два других вида, *Prinia maculosa* и *Emberiza capensis* — в двух областях исследований. Индекс разнообразия Симпсона поразительно одинаков (S = 0,96) для всех трех исследованных птичьих комплексов (низменности, предгорных и горных областей). Тем не менее было определено, что доля гнездящихся пар некоторых родственных видов меняется с высотой. Зерноядные были более распространены (44–45 %) в предгорьях и горных районах, чем в низинах (36 %), в то время как насекомоядные были более распространены в горной местности (50 %), чем в предгорьях и долинах (36–37 %). В общем птичья фауна относительно разнообразна и уникальна на лугах Хайвельда/Дракенберга. Представленные здесь результаты — материал для дальнейшего исследования влияния предполагаемого потепления климата на разнообразие и структуру сообществ птиц.

Ключевые слова: птичьи комплексы, плотность населения, «горячие точки», Лесото.

Introduction

Within southern Africa, Cowling and Hilton-Taylor (1994) have distinguished eight so called "hot-spots" — areas with a high species richness and a high concentration of endemic species. Of these the Maloti/Drakensberg hot-spot occupies c. 75 % of the area of Lesotho. All highlands and most of the foothills in this country lie within this hot-spot (Ambrose et al., 2000). Lesotho is thus a key area in biodiversity conservation.

Little is known about structure of avian assemblages in the whole Grassland Biome of southern Africa (Kopij, 2006), which is also the only biome in Lesotho. Since it occupies areas ranging in altitude from c. 1000 m a. s. l. to 3500 m a. s. l., not only changes in bird species composition, but also dominance structure, population densities and proportions between related species are expected to change along the altitudinal gradient. Although such changes were not studied in southern Africa (Bonde, 1993; Hockey et al., 2005), they are well documented in other regions of the world (e. g. Glutz Von Blotzheim, 1962; Dyrcz et al., 1991; Fischer et al., 2011). It has been shown that with the altitude species diversity declines, but dominance of some of them increases. The dominance structure as a whole changes significantly with the altitude (e. g. Glutz Von Blotzheim, 1962; Mccain, 2009; Reif, Flousek, 2012). Breeding parameters, such as clutch size, breeding success and timing of breeding also change with altitude (Mccain, 2009).

The purpose of this study was to investigate altitudinal differences in the bird species composition, their dominance structure and relative abundance. Special attention was paid to compare changes in relative densities and dominance of closely related congeneric species. It should be pointed out that the aim of the study was not to test other variables, such as season of the year, time of the day or annual differences in rainfall.

Study area and methods

The Maloti/Drakensberg 'hot-spot', also known as the Eastern Mountains, has an area of c. 40 000 km^2, most of which falls within Lesotho. The main vegetation type in this area is the Afromontane Grassland, with Highveld Grassland at the lowest levels (below 1800 m a. s. l.), and Alpine Grassland at the highest altitudes (over 2500 m a. s. l.). The 'hot-spot' lies entirely within the Afromontane and Afroalpine Grasslands, and borders on Highveld Grassland (Ambrose et al., 2000).

Lesotho is divided into lowlands, foothills and highlands (mountains) (fig. 1). Lowlands are regarded as the land below 1700 m a. s. l., foothills are between 1700 and 2200 m a. s. l., and highland above 2200 m a. s. l. Lowlands (total surface — 6 051 km^2) form a strip of land lying along its northeast-southwest border and extending eastward to the Cave Sandstone Foothills. The foothills (total surface — 2964 km^2) form a narrow strip bordering the highlands to the east and lowlands to the west, constituting therefore transitional zone between the highlands and the lowlands (Ambrose et al., 2000).

The study was conducted during the years 1996–2001 in three areas: Koro-Koro, Nyakosoba and Mantsunyane, all in the Maseru District (fig. 1). Koro-Koro (14 transects, with a total length of c. 73 km) is situated in the lowlands

Fig. 1. A map of Lesotho showing three ecozones, and three study areas located within the zones: 1 — Koro-Koro; 2 — Nyakosoba; 3 — Matsunyane.

(29˚32'–29˚29' S; 27˚41'–27˚44' E), Nyakosoba (16 transects, with a total length of c. 120 km) in the foothills (29˚29'–29˚37' S; 27˚42–27˚48' E) and Mantsunyane (10 transects, with a total length of c. 54 km) in the highlands (29˚32'–29˚35' S; 28˚09'–28˚36' E) (table 1). At all three sites, natural habitats, such as grassy plains, bushy slopes, marshlands, riparian vegetation, etc., predominated. Excluded were from the surveys human settlements and river valleys. Transects were designed in such a way as to reflect the proportion of particular habitats in each area.

The line transect method in American version, i.e. without belts (Bibby et al., 1992) was used for counting birds. Each transect was surveyed once, mostly in wet season and in the morning, during the years 1996–2001. A total of 122 h and 15 min. were spent on counting (table 1). Depending on transect length, 45 min. — 5 h and 15 min. were spent on each transect; on average 2.6 h (SD = 1.45). The total length of all transects surveyed was c. 247 km (table 1). Only resident (potentially breeding) species were counted, vagrants and visitors were excluded. As recommended for the line transect method, a pair of the resident species was the census unit (Bibby et al., 1992). In the case of polygamous species and those species which do not form pairs, the number of females was interpreted as being equivalent of the number of pairs. For most species, therefore, numbers given in Appendix 1 refer to the number of encounters, which is usually equal to the number of potentially breeding pairs (compare Bibby et al., 1992).

For each bird species, the following data were calculated (Appendix 1): 1) N — number of potentially resident pairs recorded; 2) % D — dominance expressed as the percentage of resident pairs of a given species in relation to the total number of all resident pairs of all species recorded, 3) F — frequency of occurrence, defined as the percentage of transects, where a given species was recorded relative to the total number of transects in given plot; 4) Ind. — index of abundance calculated as the percentage of the number of resident pairs of a given species in relation to thenumber of the most numerous species (the most numerous species has 100 %); 5) x — average number of resident pairs per transect (only transects where the species were recorded were taken into account); 6) sd — standard deviation of this average.

Simpson's Diversity Index (D) was used to calculate diversity of avian assemblages: $D = 1-\Sigma (n/N)^2$, where: n — total number of pairs of particular bird species; N — total number of pairs of all bird species; no diversity if $D = 0$; infinite diversity if $D = 1$.

Sörensen's Coefficient: $S = 2C/A+B$ (A — the number of bird species in area A, B — the number of bird species in area B, C — the number of bird species shared by both areas) was used to compare similarities between assemblages. A dominant bird species is defined as comprising at least 5 % of the total number of all resident pairs; while subdominant species comprised 2–4.9 % of that total. The nomenclature of bird species follows Hockey et al. (2005).

Results

In total, 105 resident species were recorded (γ-diversity = 105). The total number of species recorded in lowlands (α-diversity = 81) was higher than that that in highlands (α-diversity = 72) and foothills (α-diversity = 71), but this difference was not statistically significant ($x^2 = 0.53$, $p > 0.05$). The β-diversity between lowlands and foothills was 38, between foothills and highlands — 24, and between lowlands and highlands – 40 resident species. Simpson's Diversity Index was strikingly the same (S = 0.96) for all three avian assemblages (lowland, foothill and highland) investigated.

The number of dominant species was the same (N = 5) in all three areas. Also the proportion of dominant species in relation to the whole assemblage was very similar. The composition of dominant group (species with more that 5 % of pairs) and the group of most often encountered species (in more than 80 % of transects) was, however, different. Only two species, the Cape Canary *Serinus canicollis* and Karoo Prinia *Prinia maculosa* were dominant in all three study areas compared, and only a single species, the Cape Bunting *Emberiza capensis*, was dominant in two study areas. Similarly, only two species, the Cape Turtle-Dove *Streptopelia capicola* and Cape Canary had a high frequency of occurrence in all three study areas, and two other species, the Karoo Prinia and Cape Bunting — in two study areas (Appendix 1).

Sörensen's Coefficient was the highest between the foothill and highland assemblages (S = 0.83), and the lowest between the lowlands and the highlands (S = 0.67). The index was intermediate (S = 0.71) between the lowland and foothill assemblages. The proportions between some congeneric species (African *Anthus cinnamomeus* to Mountain Pipit *A. hoeschi*, Familiar *Cercomela familiaris* to Sickle-winged Chat *C. sinuata*, Cape *Monticola rupestris* to Sentinel Rock-thrush *M. explorator*, Grey-headed *Passer diffusus* to Cape Sparrow *P. melanurus*, and Laughing *Streptopelia senegalensis* to Cape Turtle-Dove *S. capicola*) were found to significantly change with the altitude (table 2). Among *Cisticola*-

Table 1. Transects designed to study avian diversity, date and time of counts

Area	Length, km	Date	Time
Koro Koro lowlands	**c. 73.2 km**		**34h45'**
Marshlands near Koro Koro	c. 4.0 km	06.04.1996	08.20–10.20
Farmland between Koro Kora and Mokuoane	c. 5.2 km	06.04.1996	10.20–12.45
Farmland between Ha Phokleli and Mofoka	c. 4.3 km	06.04.1996	14.20–16.30
Hillsides between St Joseph and Ha Moitšupeli	c. 3.3 km	01.08.2001	10.20–12.00
Hillsides between St Joseph and Ha Moitšupeli	c. 6.0 km	01.08.2001	12.00–15.00
Sandstone cliff near Koro Koro	c. 6.7 km	21.11.2000	07.40–11.00
Sandstone cliff between Makulele and Molibe	c. 7.3 km	21.11.2000	11.00–14.40
Sandstone cliff between Molibe and St. Joseph	c. 6.7 km	21.11.2000	14.40–17.30
Farmland between St. Joseph and Ha Melefaani	c. 3.7 km	14.12.2001	07.45–09.35
Top and afforested slopes of sandstone plateau near Ha Motibe	c. 8.1 km	14.12.2001	09.35–14.40
Farmland near Koro Koro	c. 1.2 km	12.12.2000	07.30–08.40
Plateau near Koro Koro	c. 4.7 km	12.12.2000	08.40–11.00
Molhaeng surroundings	c. 4.0 km	12.12.2000	11.00–13.00
Molhaeng-Koro Koro	c. 8.0 km	12.12.2000	13.00–17.00
Nyakosoba foothills	**c. 119.8 km**		**59h40'**
Nyakosoba — Popa — Popanyane	c. 7.7 km	16.10.1999	08.10–12.00
Popanyene — Lebe Me	c. 4.0 km	16.10.1999	12.00-14.00
Popanyane — Ha Noka	c. 4.5 km	11.08.2000	09.45–12.00
Ha Noka — Ha Maama	c. 4.0 km	11.08.2000	12.00–14.00
Nyakosoba-Ha Mofolisi-Ha Tsomo — Ha Ntsane — Nyakosoba	c. 10.0 km	20.03.1999	06.30–11.30
Nyakosoba — Ha Moke — ThabaChitja	c. 8.0 km	02.04.1999	06.40–10.40
Nyakosoba — Pheuoeng	c. 4.7 km	28.10.2000	08.00–10.20
Ha Moitšupeli — Mokheseng — Ha Lekhonoto — Thabana-li-Mele	c. 12.0 km	30.01.1999	06.45–14.00
Thabana-li-Mele — Ha Moitšupeli	c.4.6 km	30.01.1999	14.00–16.20
Ha Moitšupeli — Matamo — Ha Hubeum	c. 6.0 km	15.08.2000	09.00–12.00
Ha Hubeum — Ha Moitšupeli	c. 7.0 km	15.08.2000	12.00–15.30
Ha Moitšupeli — St John's — Patsi Ha Mohake	c. 6.0 km	12.12.2001	07.20–10.15
Patsi Ha Mohake — Ha Moitšupeli	c.10.0 km	12.12.2001	10.15–15.15
Ha Moitšupeli — Thaba-Telle — Ha Tlali — ThabaNtšonyana	c. 6.5 km	22.02.1999	07.00–10.15
ThabaNtsonyana (Terea) — Thaba-Telle	c. 10.0 km	22.02.1999	10.15–15.00
Ha Moitšupeli — Therea — Motlepu — Nkoeng — Ha Takate	c. 4.8 km	15.05.1999	08.15–10.30
Mantsonyane mountains	**c. 53.7 km**		**27h50'**
Marakabei — Ha Seqoe	c. 3.7 km	22.12.2000	05.40–07.20
Ha Seqhoe — radio station	c. 5.3 km	22.12.2000	07.20–10.00
Crossd. Ha Seqhoe/Aurey — Ha Thabo — Ha Sootho — Ha Felete	c. 8.7 km	22.12.2000	10.40–15.00
Ha Tsoane — Ha Rantelali	c. 7.7 km	23.12.2000	05.30–09.20
Ha Rantelali — Marakabei	c. 5.3 km	23.12.2000	09.20–12.00
Mantša — Qasamo	c. 4.0 km	21.12.2000	15.00–17.00
ThabaTseka surroundings	c. 10.0 km	04.03.2001	05.00–10.00
ThabaTseka surroundings	c. 2.0 km	04.03.2001	17.00–18.00
ThabaTseka surroundings	c. 5.0 km	05.03.2001	06.45–09.15
ThabaTseka surroundings	c. 4.0 km	04.03.2001	10.00–12.00

species, the Neddicky *C. fulvicapilla* was the commonest in the lowlands, the Wailing Cisticola *C. lais* in the foothills and the Wing-snapping Cisticola *C. ayresii* in the highlands. Among the *Euplectes*-species, the Southern Red Bishop *E. orix*, Red-collared Widowbird *E. ardens* and Long-tailed Widowbird *E. progne* were equally common in the lowlands (together making up 96 % of all *Euplectes* pairs); the Yellow-crowned Bishop *E. afer* and Red-collared Widowbird were most common in the foothills (83 %); while the Long-tailed Widowbird and Yellow-crowned Bishop in the highlands (78 %) (table 2).

Of three species endemic to the Maloti/Drakensberg hot-spot, the Drakensberg Siskin *Pseudochloroptila symonsi* and Mountain Pipit were recorded only in the highlands, while the Drakensberg Rock-jumper *Chaetops aurantius* occurred both in foothills and in highlands, but not in the lowlands. Two other species near-endemic to the region, the Sentinel Rock-thrush, and Wing-snapping Cisticola were recorded both in foothills and highlands, although they were much more common in the highlands. Another near-endemic, the Sickle-winged Chat was only recorded in the highlands. Some non-endemic species, such as the Large-billed Lark *Galerida magnirostris* and Yellow Canary *Serinus flaviventris* were also confined to the highlands, while the Swee Waxbill *Coccopygia melanotis* and Karoo Scrub-Robin *Erythropygia coryphaeus* occurred only in the lowlands.

Members of the granivorous guild were more common (44–45 %) in the foothills and highlands than in lowlands (36 %), while insectivores were more common in the highlands (50 %) than in foothills and lowlands (36–37 %). Therefore, both granivores and insectivores were more common in highlands than in lowlands. However, the number of species in each

Table 2. Changes in proportions of breeding pairs among related commonbird species along altitude gradient in the Moloti/Drakensberg 'hot-spot' area

Species	Lowlands	Foothills	Highlands
Anthus cinnamomeus	1.00	0.78	0.21
Anthus hoeschi	0.00	0.22	0.79
Number of pairs	11	25	50
x^2-test	5.5*	9.0**	15.7**
Cercomela familiaris	1.00	1.00	0.14
Cercomela sinuata	0.00	0.00	0.86
Number of pairs	15	8	14
x^2-test	15.0**	–	7.1**
Emberiza tahapisi	0.37	0.03	0.02
Emberiza capensis	0.63	0.97	0.98
Number of pairs	120	103	100
x^2-test	45.6**	94.3**	92.2**
Monticola rupestris	1.00	0.50	0.05
Monticola explorator	0.00	0.50	0.95
x^2-test	–	–	15.2**
Number of pairs	5	4	19
Passer diffusus	1.00	0.54	0.25
Passer capensis	0.00	0.46	0.75
Number of pairs	27	37	80
x^2-test	27.0**	0.24	10.0**
Ploceus velatus	1.00	0.25	0.18
Ploceus capensis	0.00	0.75	0.82
Number of pairs	10	4	32
x^2-test	10.0**	–	12.5**
Streptopelia senegalensis	0.55	0.42	0.24
Streptopelia capicola	0.45	0.58	0.76
Number of pairs	134	175	37
x^2-test	1.5	4.2*	17.0**
Cisticola fulvicapilla	0.91	0.37	0.13
Cisticola lais	0.09	0.56	0.36
Cisticola ayresii	0.00	0.07	0.50
Number of pairs	173	87	135
x^2-test	517.5**	64.7**	56.6**
Euplectes orix	0.33	0.00	0.13
Euplectes ardens	0.30	0.38	0.08
Euplectes progne	0.33	0.09	0.44
Euplectes afer	0.05	0.45	0.00
Euplectes capensis	0.00	0.09	0.34
Number of pairs	61	47	59
x^2-test	454.1**	376.4**	457.1**

Note. x^2-test: * $p<0.05$; ** $p<0.01$.

Appendix 1. Breeding bird assemblages in Lesotho lowland, foothill and highland mosaic habitats during the years 1996–2001

1) N — number of potentially resident pairs recorded; 2) % D — dominance expressed as the percentage of resident pairs of a given species in relation to the total number of all resident pairs of all species recorded; 3) % F — frequency of occurrence, defined as the percentage of transects, where a given species was recorded relative to the total number of transects in given plot; 4) *x* — average number of resident pairs per transect (only transects where the species were recorded were taken into account); 5) sd — standard deviation of this average; 6) Ind. — index of abundance calculated as the percentage of the number of resident pairs of the most numerous species.

Species name	Lowlands (14 transects; c. 73 km)						Foothills (16 transects; c. 120 km)						Highlands (10 transects; c. 54 km)					
	N	% D	% F	*x*	sd	Ind.	N	% D	% F	*x*	sd	Ind.	N	% D	% F	*x*	sd	Ind.
Accipiter melanoleucos	1	0.1	7.1	1		0.6												
Accipiter rufiventris	2	0.1	14.3	1	0	1.3	1	0.1	6.3	1	0	1	1	0.1	10	1		1
Acrocephalus baeticatus	3	0.2	7.1	3		1.9							1	0.1	10	1		1
Alcedo cristata	1	0.1	7.1	1		0.6												
Anas sparsa							1	0.1	6.3	1	0	1	1	0.1	10	1		1
Anthus cinnamomeus	11	0.7	21.4	3.7	4.6	7	25	2	62.5	2.5	3.2	24.8						
Anthus crenatus							7	0.6	37.5	1.2	1	6.9	13	1.2	30	4.3	1.5	13.3
Anthus hoeschi													50	4.6	40	12.5	7.9	51
Apus barbatus	45	2.7	57.1	5.6	5.9	28.7	22	1.8	18.8	7.3	3.5	21.8	45	4.1	40	11.3	19.2	45.9
Apus horus	5	0.3	7.1	5		3.2	1	0.1	6.3	1	0	1	6	0.6	20	3	1.4	6.1
Aquila verreauxii							1	0.1	6.3	1	0	1						
Ardea cinerea	1	0.1	7.1	1		0.6												
Ardea purpurea	2	0.1	7.1	2		1.3												
Batis capensis	1	0.1	7.1	1		0.6												
Bostrychia hagedash	14	0.8	57.1	1.8	1.5	8.9	3	0.2	18.8	1	0.3	3	1	0.1	10	1		1
Bubo africanus	3	0.2	21.4	1	0	1.9												
Buteo rufofuscus	5	0.3	28.6	1.3	0.5	3.2	8	0.6	37.5	1.3	1	7.9	5	0.5	30	1.7	0.6	5.1
Calandrella cinerea							4	0.3	25	1	0.3	4	12	1.1	30	4	1.7	12.2
Cecropis cucculata	20	1.2	50	2.9	2.3	12.7	4	0.3	25	1	0.3	4	5	0.5	50	1	0	5.1
Cercomela familiaris	15	0.9	50	2.1	1.2	9.6	8	0.6	37.5	1.3	1	7.9	2	0.2	20	1	0	2
Cercomela sinuata													12	1.1	30.0	4.0	5.2	12.2
Chaetops aurantius							10	0.8	31.3	2	1	9.9	14	1.3	30	4.7	5.5	14.3
Chrysococcyx caprius	1	0.1	7.1	1		0.6							1	0.1	10	1		1
Circus maurus							1	0.1	6.3	1	0	1	1	0.1	10	1		1
Cisticola ayresii							6	0.5	12.5	3	1	5.9	68	6.3	80	8.5	10.8	69.4
Cisticola fulvicapilla	157	9.4	100	11.2	10.4	100	32	2.6	68.8	2.9	2.9	31.7	18	1.7	40	4.5	3.1	18.4
Cisticola juncidis	3	0.2	7.1	3		1.9												
Cisticola lais	16	1	35.7	3.2	3.3	10.2	49	3.9	75	4.1	2.7	48.5	49	4.5	60	8.2	4.8	50
Cisticola tinniens	6	0.4	14.3	3	2.8	3.8	2	0.2	6.3	2	0.3	2	11	1.0	40	2.8	1.7	11.2

Clamator jacobinus	2	0.1	14.3	1	0	1.3	1	0.1	6.3	1	0	1						
Coccopygia melanotis	6	0.4	21.4	2	1.7	3.8												
Colius striatus	17	1	57.1	2.1	1.2	10.8	17	1.4	18.8	5.7	1.9	16.8						
Columba guinea	24	1.4	71.4	2.4	1.8	15.3	23	1.8	43.8	3.3	3.2	22.8	4	0.4	30	1.3	0.6	4.1
Corvus albicollis	3	0.2	21.4	1	0	1.9	4	0.3	25	1	0.4	4						
Corvus albus	4	0.2	21.4	1.3	0.6	2.5												
Corvus capensis	7	0.4	35.7	1.4	0.5	4.5	13	1	56.3	1.4	0.8	12.9	12	1.1	30	4	3.5	12.2
Cossypha caffra	118	7	71.4	11.8	6.2	75.2	52	4.2	81.3	4	2.7	51.5	13	1.2	40	3.3	1.5	13.3
Coturnix coturnix	13	0.8	21.4	4.3	3.2	8.3	19	1.5	18.8	6.3	2.5	18.8	60	5.5	90	6.7	6.5	61.2
Cuculus solitarius	2	0.1	14.3	1	0	1.3												
Elanus caeruleus							4	0.3	25	1	0.3	4						
Emberiza capensis	76	4.5	78.6	6.9	5.1	48.4	100	8	93.8	6.7	3.8	99	98	9.0	80	12.3	9.7	100
Emberiza flaviventris	1	0.1	7.1	1		0.6												
Emberiza tahapisi	44	2.6	78.6	4	2.5	28	3	0.2	12.5	1.5	0.4	3	2	0.2	10	2		2
Erythropygia coryphoeus	8	0.5	50	1.1	0.4	5.1												
Estrilda astrild	10	0.6	14.3	5	2.8	6.4	27	2.2	50	3.4	2.9	26.7	16	1.5	40	4	2.9	16.3
Euplectes afer	3	0.2	21.4	1	0	1.9	21	1.7	18.8	7	3.2	20.8						
Euplectes ardens	18	1.1	42.9	3	2.7	11.5	18	1.4	31.3	3.6	2.1	17.8	5	0.5	30	1.7	1.2	5.1
Euplectes capensis							4	0.3	25	1	0.3	4	20	1.8	50	4	2.4	20.4
Euplectes orix	29	1.7	28.6	7.3	8.6	18.5							8	0.7	20	4	1.4	8.2
Euplectes progne	20	1.2	7.1	20		12.7	4	0.3	18.8	1.3	0.4	4	26	2.4	30	8.7	0.6	26.5
Falco biarmicus	2	0.1	14.3	1	0	1.3	2	0.2	12.5	1	0.2	2	1	0.1	10	1		1
Falco tinnunculus	7	0.4	35.7	1.4	0.9	4.5	1	0.1	6.3	1	0	1	2	0.2	20	1	0	2
Fulica cristata	2	0.1	14.3	1	0	1.3												
Galerida magnirostris													41	3.8	40	10.3	6.2	41.8
Gallinula chloropus	1	0.1	7.1	1		0.6												
Geocolaptes olivaceus	26	1.5	71.4	2.6	1.6	16.6	9	0.7	37.5	1.5	1	8.9	6	0.6	20	3	1.4	6.1
Geronticus calvus							3	0.2	18.8	1	0.3	3	1	0.1	10	1		1
Gypaetus barbatus													2	0.2	20	1	0	2
Hirundo albigularis													1	0.1	10	1		1
Hirundo fuligula	50	3	64.3	5.6	3.9	31.8	19	1.5	50	2.4	2.5	18.8	5	0.5	30	1.7	0.6	5.1
Lagonostica senegala	1	0.1	7.1	1		0.6												
Lanius collaris	16	1	71.4	1.6	0.8	10.2	25	2	56.3	2.8	3.1	24.8	6	0.6	40	1.5	1	6.1
Macronyx capensis	2	0.1	14.3	1	0	1.3	11	0.9	31.3	2.2	0.9	10.9	10	0.9	30	3.3	2.5	10.2
Megaceryle maxima	1	0.1	7.1	1		0.6												
Monticola rupestris	5	0.3	21.4	1.7	0.6	3.2	2	0.2	12.5	1	0.3	2	1	0.1	10	1		1
Monticola expolorator							2	0.2	6.3	2	0.3	2	29	2.7	40	7.3	5.3	29.6
Motacilla capensis	7	0.4	21.4	2.3	1.5	4.5	10	0.8	50	1.3	1	9.9	11	1.0	50	2.2	1.6	11.2

Nectarinia famosa	68	4.1	71.4	6.8	5.1	43.3	11	0.9	37.5	1.8	0.8	10.9	5	0.5	30	1.7	1.2	5.1
Numida meleagris	18	1.1	21.4	6	4.6	11.5	2	0.2	12.5	1	0.3	2						
Oenanthe monticola	5	0.3	35.7	1	0	3.2	1	0.1	6.3	1	0	1	9	0.8	40	2.3	2.5	9.2
Onychognathus morio	24	1.4	64.3	2.7	2	15.3	36	2.9	62.5	3.6	3	35.6	4	0.4	30	1.3	0.6	4.1
Ortygospiza atricollis	10	0.6	42.9	1.7	1.2	6.4	22	1.8	56.3	2.4	3.5	21.8	13	1.2	60	2.2	1.5	13.3
Parisoma layardi	1	0.1	7.1	1		0.6												
Passer capensis							17	1.4	37.5	2.8	2	16.8	60	5.5	70	8.6	6.9	61.2
Passer diffuses	27	1.6	78.6	2.5	1.6	17.2	20	1.6	43.8	2.9	2.5	19.8	2	0.2	10	2		2
Passer domesticus	2	0.1	14.3	1	0	1.3	6	0.5	12.5	3	0.7	5.9	3	0.3	30	1	0	3.1
Ploceus capensis							3	0.2	12.5	1.5	0.4	3	27	2.5	80	3.4	2.8	27.6
Ploceus velatus	10	0.6	28.6	2.5	2.4	6.4	1	0.1	6.3	1	0	1	5	0.5	40	1.3	0.5	5.1
Prinia maculosa	113	6.7	78.6	10.3	5.6	72	92	7.4	81.3	7.1	3.4	91.1	54	5.0	90	6	2.6	55.1
Pseudochloroptila symonsi													2	0.2	10	2		2
Pycnonotus nigricans	47	2.8	71.4	4.7	2.6	29.9	25	2	75	2.1	3	24.8						
Quelea quelea	1	0.1	7.1	1		0.6												
Riparia paludicola	1	0.1	7.1	1		0.6							2	0.2	20	1	0	2
Saxicola torquata							23	1.8	56.3	2.6	3.2	22.8	37	3.4	80	4.6	3.7	37.8
Scleroptila africanus							17	1.4	43.8	2.4	2	16.8	6	0.6	30	2	1	6.1
Scleroptila swainsonii	13	0.8	50	1.9	0.7	8.3	7	0.6	18.8	2.3	1	6.9	1	0.1	10	1		1
Scopus umbretta	2	0.1	14.3	1	0	1.3	2	0.2	12.5	1	0.3	2	2	0.2	20	1	0	2
Segittarius serpentarius							1	0.1	6.3	1	0	1						
Serinus albogularis	2	0.1	14.3	1	0	1.3	2	0.2	12.5	1	0	2	1	0.1	10	1		1
Serinus atrogularis	2	0.1	14.3	1	0	1.3												
Serinus canicollis	124	7.4	85.7	10.3	6.7	79	70	5.6	81.3	5.4	2.9	69.3	78	7.2	90	8.7	6.7	79.6
Serinus flaviventris													4	0.4	20	2	1.4	4.1
Serinus gularis	18	1.1	50	2.6	2.2	11.5							12	1.1	30	4	5.2	12.2
Sphenoeacus afer	16	1	42.9	2.7	1.6	10.2	18	1.4	56.3	2	2	17.8	2	0.2	10	2		2
Spreo bicolor	29	1.7	50	4.1	4.8	18.5	1	0.1	6.3	1	0	1	5	0.5	30	1.7	1.2	5.1
Stenostira scita							2	0.2	12.5	1	0.3	2						
Streptopelia capicola	60	3.6	92.9	4.6	2.8	38.2	101	8.1	87.5	7.2	3.9	100	28	2.6	80	3.5	3.1	28.6
Streptopelia semitorquata	3	0.2	14.3	1.5	0.7	1.9	1	0.1	6.3	1	0	1						
Streptopelia senegalensis	74	4.4	92.9	5.7	5.3	47.1	74	5.9	87.5	5.3	3.1	73.3	9	0.8	50	1.8	1.1	9.2
Sturnus vulgaris	2	0.1	7.1	2		1.3												
Tachymarptis melba	16	1	21.4	5.3	4.5	10.2	8	0.6	25	2	1	7.9	8	0.7	20	4	1.4	8.2
Telophorus zeylonus	45	2.7	92.9	3.5	2.4	28.7	61	4.9	87.5	4.4	2.8	60.4	9	0.8	40	2.3	1.5	9.2
Vanellus armatus	1	0.1	7.1	1		0.6												
Vidua macroura	4	0.2	28.6	1	0	2.5	7	0.6	25	1.8	1	6.9	3	0.3	20	1.5	0.7	3.1
Zosterops pallidus	104	6.2	71.4	10.4	7.2	66.2	38	3	62.5	3.8	2.5	37.6						
Number of pairs recorded	1679						1248						1075					

feeding guild remained very similar in all regions (no statistical differences). On the other hand, the frugivores were much more numerous in the lowlands (26 %) than in foothills (16 %) and highlands (3 %). The percentage of other feeding guilds was low (2–3 %) in all areas, although they were represented by more species in lowlands (16) than in highlands (8).

Almost half (48 %) of all birdspotentially breeding in lowlands nested in trees or shrubs, while in the highlands this group formed only 28 %. A similar trend was recorded for hole-nesting birds. Contrary to the expectation, the proportion of cliff-nesting birds also decreased with the increase in the altitude. In the highlands, most species nested on the ground (42 %), while in the lowlands, only 15 % of birds nested on the ground, in foothills — 23 %. The percentage of birds breeding in low herbaceous vegetation remained similar (20–24 %) in all areas compared.

Discussion

In this study, counts were conducted in different time of the day, in different months of the year, and in different years. It might be, therefore, assumed that differences in bird communities along the altitude gradient shown in this study cannot be attributed to the altitude only, as other variables were not controlled. It should be pointed out that these variables were, however, similar in all three eco-zones, having, therefore, a similar 'distorting' effect on the findings in all three eco-zones compared.

The major findings of this study are general changes in avian communities along the altitude gradient, such as species richness, diversity, dominance structure, proportions of feeding guilds and proportions of nesting guilds. The transect line method with single counts is suitable to show such changes, as repeat visits will count many of the same birds. The sample size appears to be increasing, but this is not creating a real increase in precision, because the counts are not independent. It is better, therefore, to use the time to include more different routes in different microhabitats, rather than count the same individual birds several times (Bibby et al., 1992). By including different routes, avian diversity will be also more representative for the whole eco-zone.

Since proportions of some congeneric species were compared in this study within the same eco-zone and not between zones (table 1), the effect of different variables has little effect on the results. In fact, such variables as different months of the year, different years, different time of the day may even increase the precision of results. Furthermore, species within the same genus have similar behavior, breeding season, territorial behavior and detectability in the field, the line transect method suffices, therefore, to study numerical proportion between them.

The species richness depends to certain extend also on the time spend on study. The longer is the study time, the higher is the level of species richness, but after reaching a threshold the time factor does not play any significant role. In this study the time devoted for study in lowlands and in highlands was much the same. However, due to diverse microhabitats, the time was almost doubled in the foothills. It might be expected, therefore, that the number of species in foothills should be slightly overestimated in relation to those in the lowlands and highlands. However, the number in the foothills was in fact almost the same as in highlands, and only slightly lower (not statistically significant) than that in the lowlands.

Data on the dominance, frequency of occurrence, and relative abundance of each species are in this study of much lower importance than above mentioned findings. These data should be treated with certain precaution, as elusive and silent species were underestimated, while large conspicuous and vocal species were most probably overestimated. The data can be, however, used as initial for further monitoring.

Altitudinal gradients are among the most powerful 'natural experiments' for testing ecological and evolutionary responses of plants and animals to abiotic factors (Körner, 2007). Mountain ecosystems are also regarded as hot-spots of biodiversity (Fishcher et al., 2011). Measuring the shifts in altitudinal ranges and densities of species may provide useful information for conservation assessment of terrestrial species prone to climate changes (Sekercioglu et al., 2007). Studies of changes in species composition along altitudinal gradient have been, therefore, increasingly implemented since the 1990s (Fishcher et al., 2011). Such analyses are especially important if confounding effects driving species assemblages along altitudinal gradients can be separated (Fishcher et al., 2011).

The Highveld/Drakensberg region is relatively uniform, as grassland is the only biome at all altitudes (Ambrose et al., 2000). Physical changes (temperature and rainfall) with the altitude in this region can be, therefore, easily separated from changes which are not altitude specific (e. g. moisture, geology, wind and season duration). Despite these advantages, the region attracted little attention of researchers. If the global changes in climate will continue, which probably also affect the Drakensbergs/Maloti region, significant changes in the bird assemblages might be expected. Although some authors have documented climatically induced altitudinal range shifts, with species moving upwards with increasing temperature to track their climatic optima, interspecific variability in such altitudinal shifts remains largely unexplored (Reif, Flousek, 2012). Results of this study provide data to explore changes in avian α- and β-diversities, their dominance structure as well as changes in relative population densities of particular species.

In conclusion, it should be stressed that the Highveld/Drakensberg avifauna is relatively diverse and unique. Species diversity decreases with the altitude, while the level of endemicity increases. Some species show also clear altitudinal trends in relative abundance. This is especially evident in the case of some congeneric species. Results presented in this paper provide valuable data for further investigation of the effect of the supposed climate warming on the diversity and structure of avian communities.

I would like to express my thanks to Prof. A. Craig from Rhodes University, Grahamstown, RSA, for corrections and constructive comments on the earlier draft of this paper.

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Received 23 February 2015
Accepted 4 August 2015