

# Geographic variation in avian clutch size and nest predation risk along a productivity gradient in South Africa

David Hořák<sup>1\*</sup>, Ondřej Sedláček<sup>1</sup>, Anna Tószögyová<sup>1</sup>, Tomáš Albrecht<sup>2,3</sup>, Michal Ferenc<sup>1</sup>,  
Václav Jelínek<sup>1</sup> and David Storch<sup>1,4</sup>

<sup>1</sup> Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic

<sup>2</sup> Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic

<sup>3</sup> Department of Avian Ecology, Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic v.v.i.,  
větná 8, CZ-603 65 Brno, Czech Republic

<sup>4</sup> Center for Theoretical Study, Charles University and the Academy of Sciences of the Czech Republic, Jiřská 1,  
CZ-110 00 Praha 1, Czech Republic

\* Corresponding author, e-mail: david@natur.cuni.cz

Geographic variation in avian clutch size is thought to be related to the variation in nest predation rate and food availability. We studied predation on artificial ground nests along a large-scale geographic gradient in South Africa characterised by increasing productivity from the deserts in the west to humid savannas in the east, and calculated mean clutch sizes of birds occurring in atlas quadrates surrounding our study sites. Clutch sizes generally increased with increasing productivity and seasonality. The least productive desert site was characterised also by the highest predation rate, whereas all the other sites located in savannas revealed much lower and more or less constant predation rate. We found no evidence for relationship between nest predation rates and clutch sizes of ground-nesting birds. This indicates that food availability is the major factor responsible for geographical variation in bird clutch sizes across South Africa, though high predation rate might also contribute to low clutch size in least productive arid environments.

## Introduction

Avian clutch size is believed to be primarily determined by two factors: nest predation and food availability. Nest predation is a major cause of reproductive failure in birds (Ricklefs 1969, Skutch 1985), and therefore represents a strong selective power on the evolution of avian life histories (Martin 1995). To be specific, lower clutch size is thought to have evolved in response to greater predation risk, as it reduces nest exposure time and fitness costs of nest losses (Slagsvold 1982, Skutch 1985). Smaller broods also require fewer visits by parents that may reveal nest location to predators (Skutch 1949, 1985). The second general factor that explains the clutch size variation is food availability. According to Lack (1947) the number of eggs within a clutch corresponds to the number of young which the parents can nourish, i.e. to the actual amount of food during the breeding season. Thus, larger clutch size is expected when higher amount of food is available. Later on, the hypothesis of resource availability was modified by Ashmole (1963) who incorporated population densities. He suggested that population sizes are controlled during the periods when food is scarce, and clutch size is determined by food availability during breeding season relative to population density. For that reason, high seasonality of resources leads to large clutch sizes.

Avian clutch sizes show remarkable geographical variation. The most striking pattern is the decline in clutch size from northern regions to the tropics (Jetz et al. 2008).

It is assumed that corresponding variation in nest predation rate (Skutch 1949) and/or availability of food resources lies behind the spatial variation in clutch size (Ashmole 1963, Ricklefs 1980). It has been shown that nest predation differs among habitats and consistent differences can favour evolution of contrasting life history traits (Martin 1993a). Hence, variation in nest predation among environments and along environmental gradients has attracted much scientific attention. A considerable number of studies have dealt with differential predation rates at small spatial scales. Differences in nest predation rate are commonly tested between edge and interior habitats (Lahti 2001, Batáry and Báldi 2004, Spanhove et al. 2009), but there has also been some focus on environmental gradients such as the gradient of urbanization (e.g. López-Flores et al. 2009) or wetland gradients (e.g. Albrecht et al. 2006).

Analogous studies over larger geographical scales, however, are much less frequent and often have lead to conflicting results. Martin (1995), for example, found no significant relationship between latitude and nest predation rate in a set of 123 North American passerines, while the results of Kulesza (1990) on New World passerines do suggest such an effect. Most recently, McKinnon et al. (2010) showed a clear decline in predation risk along a 3 350 km long south–north gradient in the Arctic region of North America.

Large-scale studies offer a unique opportunity to investigate the effects of variation in food availability because

several correlates of food resources such as humidity, average annual temperature, or seasonality change dramatically over large geographical scales. Although the causality of relationships in correlative studies is often hard to reveal, examination of relations between predation rate, food availability and avian clutch size can be still informative as the directions of possible relationships between the factors determining clutch size evolution seems to be relatively clear. Environmental characteristics may influence both predation rate (e.g. via habitat structure) and clutch size (via food available to birds). Predation rate may subsequently limit clutch size. Variation in environmental conditions over large spatial scales may thus influence avian clutch sizes directly via food availability and/or indirectly via nest predation rate. It follows that, although it may be difficult to distinguish among mechanisms operating behind geographical variation in clutch size, simultaneous investigations of variation in nest predation rate and clutch size over large-scale environmental gradients and subsequent comparison of several such gradients might bring interesting insights into evolution of clutch size in birds.

Here we describe changes in the rate of artificial nest predation among study sites situated along a long geographical productivity gradient, and compare this with large-scale geographic trends in clutch size. For this purpose, we chose a c. 1 550 km long environmental gradient across South Africa, which has several advantages: (1) it is wide enough to cover areas with extremely low environmental productivity and areas with high productivity, (2) changes in productivity are relatively gradual across South Africa, and (3) although the gradient covers a wide range of environments, it is rather longitudinal and thus situated within one biogeographical unit (the whole area is occupied by relatively similar bird taxa). The general aim of the present study is to describe relationships among estimates of food availability (environmental productivity), nest predation risk (artificial nest predation) and avian clutch size over large spatial scale.

## Material and methods

The field work was carried out during November and December 2009 (during the breeding season of birds) at five study sites situated along a gradient of environmental productivity in South Africa (Table 1). Various environments along the transect host considerable number of ground nesting bird species belonging to guineafowls (Numididae), francolins (Phasianidae), bustards (Otididae) and also passerines, especially larks (Alaudidae). Similarly rich communities of potential predators of avian nests occurred at the study sites. Ground nests can be predated by: (1) mammals – including black-backed jackal *Canis mesomelas*, Cape fox *Vulpes chama*, honey badger *Mellivora capensis*, bat-eared fox *Otocyon megalotis*, small spotted genet *Genetta genetta* or yellow mongoose *Cynictis penicillata*; (2) birds – especially crows such as Pied Crow *Corvus albus* or Black Crow *C. capensis*; and (3) snakes – which even include specialists on avian eggs (rhombic egg-eater *Dasypeltis scabra*). Field work proceeded according to the breeding season of birds at each study site, starting in the west (Pofadder) and finishing in the east (Punda Maria; Table 1). For each study site, we obtained the normalised difference vegetation index

(hereafter NDVI), an estimate of environmental productivity based on the spectral properties of vegetation (the average NDVI estimates in January and July—in these months the highest differences in NDVI distribution are observed—were obtained from ARTEMIS; Africa Real Time Environmental Monitoring Information System, Food and Agriculture Organization of the United Nations, <http://www.fao.org/geonetwork/srv/en/>). We also calculated seasonality in NDVI as the difference between NDVI estimates in January and July. Furthermore, we measured relative vegetation cover for 32 plots situated along linear transects within each study site. This was estimated visually as the percentage of the area surrounding each point (radius of 100 m) covered by vegetation for four separate layers (the herb layer up to 1 m, shrub layer between 1–3 m, large shrub and small tree layer between 3–5 m, and tree layer above 5 m) similarly as, e.g., in Reif et al. (2006). The relative cover for these four layers was then summed to get an overall relative cover (i.e. it can be higher than 100%; Table 1).

We then placed 100 artificial ground nests along each vegetation plot transect, with one chicken egg put in the middle of an artificially made shallow depression in the ground (about 20 cm in diameter). The artificial nests thus did not simulate complete natural nests of any species. They rather resembled a clutch at the beginning of its formation. Brown chicken eggs are reported to be suitable for ground nest studies because of inconspicuous colouration (Yahner and Mahan 1996) and were used also in other studies on African birds (Carlson and Hartman 2001). However, chicken eggs are larger and more durable than those of small passerines and it can be difficult for some small predators (e.g. mice) to break into them (cf. DeGraaf and Maier 1996). Consequently, the guild of small predators is presumably excluded from our experiment and potential differences in the importance of small predators among study sites may influence our results. Nevertheless, estimates of predation rates on nests of avian species laying larger eggs are not affected. We used artificial ground nests because ground-nesting birds (in contrast to shrub or tree-nesting birds) occur naturally at all study sites and form an important component of local avian communities (Hockey et al. 2005, DS et al. unpublished data). Moreover, ground nests generally experience high nest predation (Ricklefs 1969, Söderström 1999), which allowed us to reveal significant differences between the study sites after a relatively short period of exposure. We placed nests systematically 300 m apart from each other, and determined distances between them using a global positioning system (Garmin GPSMAP 60 CX). All nests were further marked by a small piece of red tape, which we placed on the vegetation about 3 m away from the nest. We avoided placing flags closer to the nests as they might have attracted predators (Green 2004). We controlled for nest visibility and location by consistently placing them in places with no overhead cover (100% visibility from above) and outside the vegetation. We checked all the nests and recorded their fate after 8 d of exposure. We distinguished three categories of nest condition: (1) the egg remained untouched in the nest, (2) egg shell remnants present in the nest, and (3) egg absent. In the course of analyses, nests in the first category were classified as 'unpredated' and nests in the latter two categories as 'predated'. We omitted

**Table 1:** Basic environmental characteristics of the study sites in South Africa where artificial nest experiments were carried out

| Study site name | GPS coordinates             | Elevation† | Dates‡       | NDVI§  | NDVI seasonality†† | Habitat‡‡ | Cover§§ |
|-----------------|-----------------------------|------------|--------------|--------|--------------------|-----------|---------|
| Pofadder        | 29°07'40" S,<br>19°23'46" E | 988        | 7–15 Nov     | 0.1229 | 0.0024             | Kr        | 21.4    |
| Molopo          | 25°48'02" S,<br>22°53'10" E | 1 000      | 25 Nov–3 Dec | 0.1836 | 0.0280             | Ka        | 54.3    |
| Kuruman         | 27°27'42" S,<br>23°25'52" E | 1 324      | 14–22 Nov    | 0.2176 | 0.0452             | aSW       | 106.5   |
| Marakele        | 24°28'45" S,<br>27°32'32" E | 1 450      | 29 Nov–8 Dec | 0.3384 | 0.1436             | mSW       | 150.5   |
| Punda Maria     | 22°41'29" S,<br>31°00'39" E | 482        | 11–20 Dec    | 0.3304 | 0.1183             | mSW       | 151.8   |

† Approximate elevation above sea level (m)

‡ Dates of artificial nest exposure in 2009

§ Normalised difference vegetation index estimated in January

†† Absolute difference between mean normalised difference vegetation indices estimated in January and July

‡‡ Habitat type: Kr = Karoo, Ka = Kalahari, aSW = arid savanna woodland, mSW = moist savanna woodland

§§ Relative vegetation cover (sum of four vegetation layers in %)

one nest from the analyses (placed in Marakele) because it may have been destroyed by human activity (DH et al. pers. obs.). We compared nest predation estimates among study sites using chi-square statistics.

To investigate spatial variation in avian clutch size across South Africa, we compiled information about all breeding bird species found in  $0.25 \times 0.25$  degree grid cells from Hockey et al. (2005). For each grid cell, we calculated the mean clutch size of birds occurring there. We tested the differences in average clutch sizes among our study sites using mean assemblage clutch size values for 21–25 grid cells (according to the availability of data) surrounding each location. In order to filter out a taxonomic (phylogenetic) effect in geographical distribution of avian clutch sizes we performed ANOVA with a family as an explanatory factor. Then we used residuals from this analysis as well as raw clutch size data for further calculations. As we carried out artificial nest experiments on ground nests, we restricted the data set to bird species classified as ground and near ground nesters (see Appendix 1). Ground nesters have typically a simple nest placed directly on the ground (e.g. francolins, guineafowls, bustards, ostriches or nightjars). Near-ground nesters build more sophisticated structures located up to 30 cm above the ground in a clump of grass or small bushes (e.g. larks, pipits and cisticolas). The differences in clutch size among study sites were tested by analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) test.

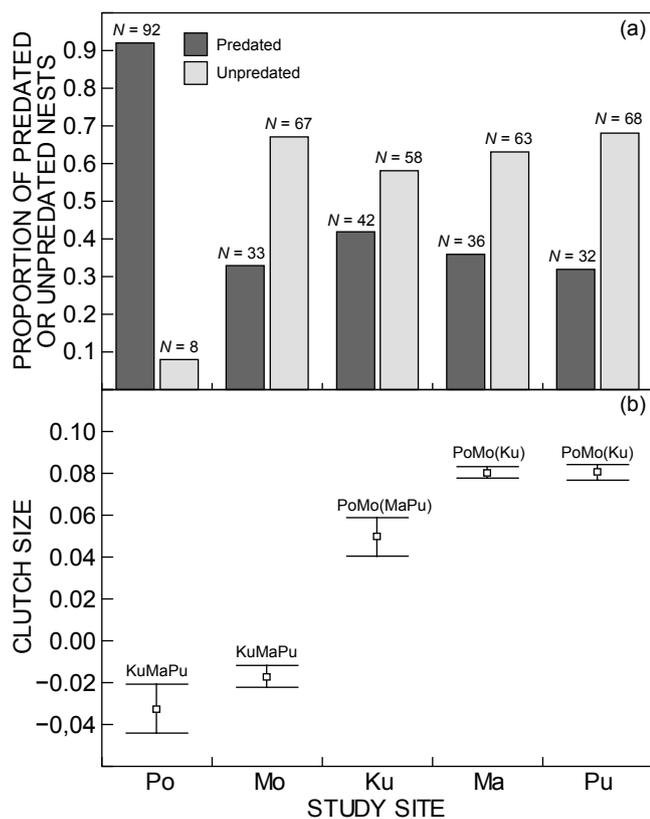
Data processing and the statistical analyses were performed in R 2.12.0 (R Development Core Team 2010), and spatial patterns in clutch size were visualised in SAM software (Rangel et al. 2006). The group data are presented as mean  $\pm$  SE of mean.

## Results

Estimated predation rate differed among study sites being highest in Pofadder (92%), the site with the lowest NDVI. All other study sites showed similar predation rates (Molopo

33%, Kuruman 42%, Marakele 36.4% and Punda Maria 32%). We tested differences in artificial nest predation between pairs of study sites. Our results show that the highest nest predation rate in Pofadder is significantly different from the other sites (all  $p < 0.001$ ; Figure 1a, Table 2). All other comparisons between study sites were insignificant (Table 2). We performed a *post-hoc* analysis and tested the difference between Pofadder and four remaining sites aggregated into one. The analysis revealed again a significant difference ( $\chi^2 = 101.22$ ,  $df = 1$ ,  $p < 0.001$ ).

In addition, we investigated differences in clutch size among study sites. In the first step, we analysed the clutch size variation for ground and near-ground nesters separately. As the analyses revealed a similar pattern, we pooled both groups into one. We also attempted to control for effect of taxonomy in geographical variation in clutch sizes. The inclusion of such an effect did not influence the results. Still, the analyses presented here are based on clutch size data controlled for taxonomy. We found an increasing trend in average clutch size of avian assemblages from sites of low to high productivity: Pofadder  $2.81 \pm 0.10$  ( $n = 21$ ), Molopo  $3.01 \pm 0.05$  ( $n = 25$ ), Kuruman  $3.57 \pm 0.10$  ( $n = 25$ ), Marakele  $3.74 \pm 0.03$  ( $n = 25$ ), and Punda Maria  $3.72 \pm 0.04$  ( $n = 23$ ). The overall differences were statistically significant (ANOVA:  $F_{4,114} = 51.17$ ,  $p < 0.001$ ; Figure 1b). *Post-hoc* comparisons showed that birds living at the two sites with lowest estimates of NDVI (Pofadder and Molopo) had the lowest mean assemblage clutch size that did not differ from each other (Tukey HSD test:  $p = 0.604$ ). However, both sites differed from the three remaining sites with higher NDVI estimates which had significantly larger clutch sizes (Tukey HSD test: all  $p < 0.001$ ; Figure 1b). The two most productive sites did not differ in clutch size from each other but had significantly higher clutch sizes than the site located near Kuruman, which has an intermediate productivity estimate (both  $p < 0.05$ ; Figure 1b). To illustrate clutch size variation at our study sites in geographical context, we provide Figure 2 that visualise the geographical variation in average clutch size of



**Figure 1:** Differences in the proportion of predated (dark bars) and unpredated (pale bars) artificial avian ground nests (a) and in clutch size (b, mean  $\pm$  SE) of ground and near-ground nesting birds at five study sites located along a gradient of environmental productivity in South Africa: Pofadder (Po), Molopo (Mo), Kuruman (Ku), Marakele (Ma) and Punda Maria (Pu). The overall mean was calculated from average clutch sizes of all members of local avian assemblages within 25 grid cells (or less if the site was located close to the South African border) surrounding each study site. The clutch size data were controlled for taxonomy (see Materials and methods for detail). ANOVA:  $F_{4,114} = 51.17$ ,  $p < 0.001$ . Significant differences as revealed by Tukey's HSD test are indicated by study sites abbreviations. The demonstrated differences are at the 0.001 and 0.05 (site abbreviations given in parentheses) levels of significance

ground and near-ground nesters for local bird assemblages across the whole territory of South Africa together with locations of our study sites.

In spite of our sample size limitations, we attempted to relate average clutch size at each study site to its potential determinants (Figure 3). We found that clutch size increased with increasing NDVI ( $r^2 = 0.86$ ,  $p = 0.024$ ) as well as seasonality in NDVI ( $r^2 = 0.78$ ,  $p = 0.046$ ). Nest predation was related to clutch size rather negatively ( $r^2 = 0.48$ ,  $p = 0.194$ ), but the relationship was statistically insignificant and driven by just one point (Pofadder).

## Discussion

We aimed to describe relationships among artificial nest predation, environmental productivity, and avian clutch size over a large spatial scale. The highest predation rate

**Table 2:** Differences in artificial nest predation rate between pairs of study sites situated along a gradient of environmental productivity in South Africa.  $\chi^2$  statistics of  $2 \times 2$  contingency table and statistical significance (in parentheses) are given for each comparison.  $df = 1$  in all cases

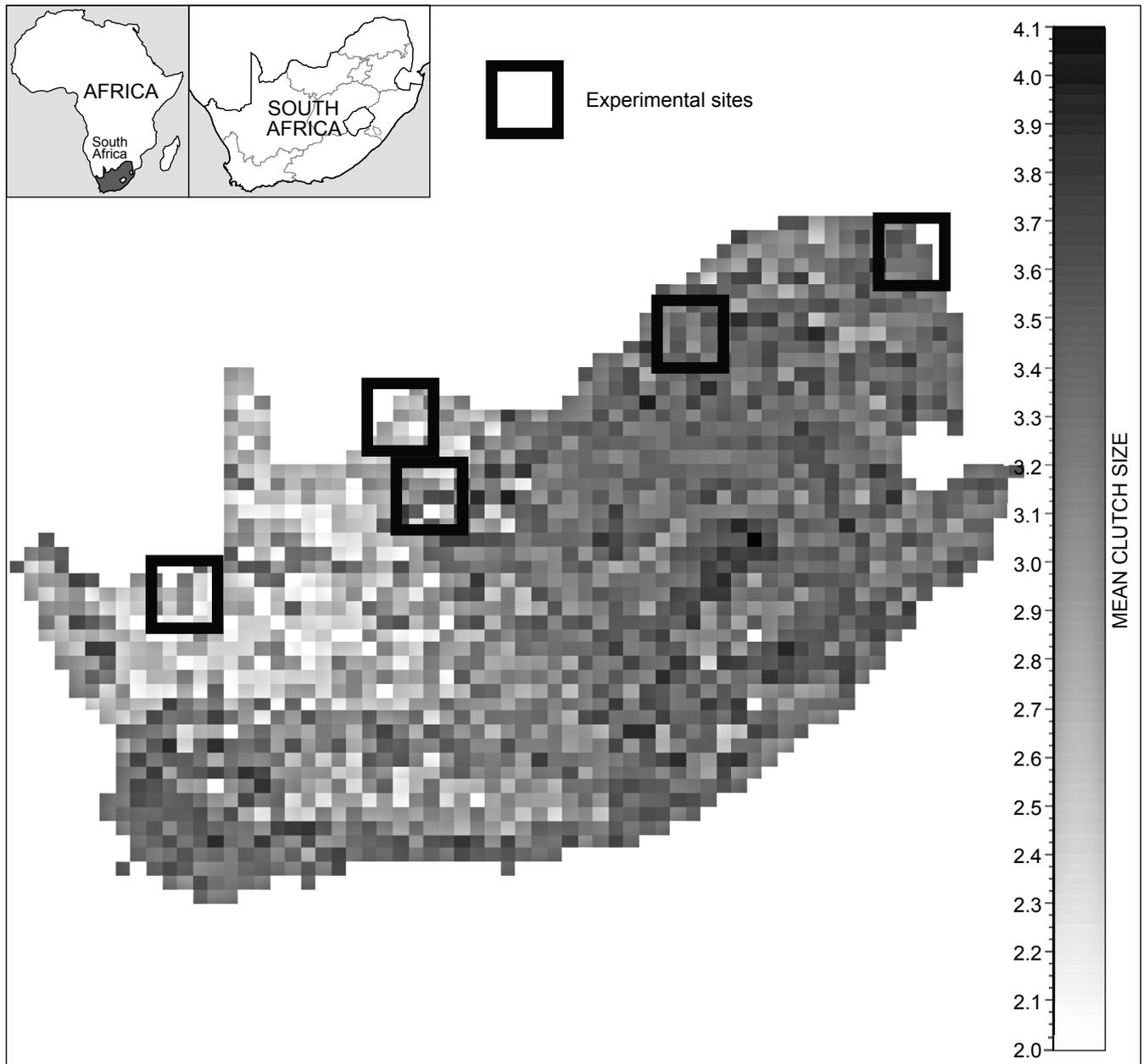
|             | Pofadder | Molopo             | Kuruman            | Marakele           |
|-------------|----------|--------------------|--------------------|--------------------|
| Pofadder    | –        |                    |                    |                    |
| Molopo      | 74.26*** | –                  |                    |                    |
| Kuruman     | 56.54*** | 2.76 <sup>ns</sup> | –                  |                    |
| Marakele    | 67.10*** | 0.25 <sup>ns</sup> | 0.66 <sup>ns</sup> | –                  |
| Punda Maria | 76.40*** | 0.02 <sup>ns</sup> | 2.15 <sup>ns</sup> | 0.42 <sup>ns</sup> |

\*\*\*  $p < 0.001$ , ns = non-significant

took place in the desert site in Pofadder, with almost all nests depredated within 8 d of exposure. Among our study sites, this location had the lowest estimate of environmental productivity and proportion of vegetation cover (both characteristics are highly correlated; Table 1). This suggests a high nest predation rate in sites with low productivity. However, the relationship between estimates of nest predation and estimates of vegetation cover and NDVI is not linear in our study. Instead, some threshold seems to exist in environmental productivity/vegetation cover, above which the nest predation rate is rather similar across different levels of environmental variables. Accordingly, we can divide the sites into two groups: the desert environment in one and several savanna types in the other. Note that such a division is based on differences found at one site and low predation rate in Pofadder, and thus can be a result of site specificities rather than a general property of desert environments.

Similarly high rates of nest predation in arid environments have been reported also in other studies (e.g. Shekedy and Safriel 1992). Higher nest predation rate in arid environments might result from higher predator activity due to (1) higher predator diversity and abundance within a particular environment or (2) greater predator mobility (determined by large home ranges and/or larger areas searched per unit of time) which increases the probability of finding a nest (cf. Schmidt et al. 2006). Also, nest predation rate is influenced by nest concealment, either in terms of microhabitat characteristics surrounding the nest (Martin 1993b) or the overall complexity and heterogeneity of the environment, which may reduce a predator's ability to locate the nest. Indeed, it has been shown that the probability of nest predation is lower in more complex environments with more potential nest sites (Chalfoun and Martin 2009).

Avian nests are predated mostly by mammals, birds and snakes (especially in tropical regions, but also in South Africa; Lloyd 2006). Although we do not have information about the densities of potential nest predators along our gradient, the overall species richness of mammals and birds increases with increasing productivity in South Africa (Bonn et al. 2004, Ceballos and Ehrlich 2006). Higher predator species and functional diversity and abundance may increase the probability of nest predation. This has been one of the basic explanations for the differential predation rate between the tropics and the temperate zone (Skutch 1949; Ricklefs 1969), with potential consequences on the evolution of avian life histories. However, our results do not

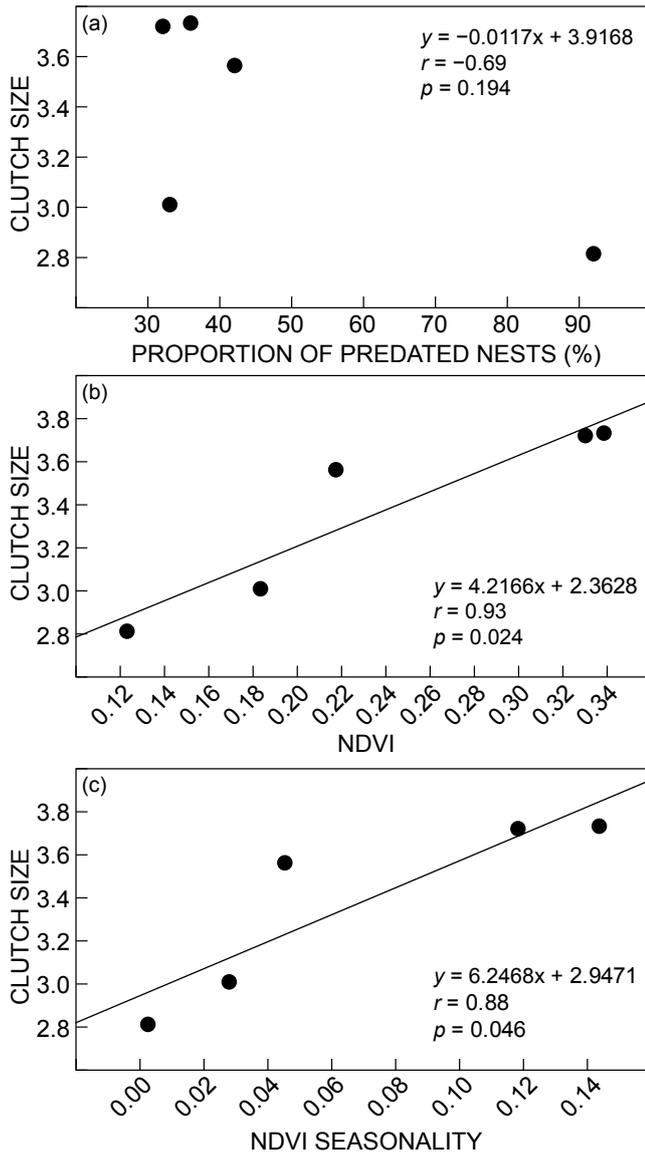


**Figure 2:** Geographic variation in mean clutch sizes of ground and near-ground nesting representatives of avian assemblages in atlas grid squares in South Africa. Locations of experimental sites are in the centre of black squares

support such an explanation, as the environment that is generally species-poor had the highest predation rate.

Instead, greater predator mobility in arid environments might be responsible for the pattern, as home range size has been reported to decrease with increasing environmental productivity (McLoughlin and Ferguson 2000; Nilsen et al. 2005). Larger home ranges and higher nest visibility in sparsely vegetated arid environments might contribute to a greater probability of predators locating avian nests. Although habitat complexity and heterogeneity was related to environmental productivity, the desert study site near Pofadder was distinctly different from all other sites. There was nearly no vegetation cover at this site

(only sparse cover of low bushes and clumps of grass, see Table 1), with consequently more nests being susceptible to predation. Nests were better visible from larger distances and more accessible, and predators thus could scan larger areas than in locations with more vegetation. This could also lie behind the difference in observed nest predation rates between the two least productive sites, Pofadder and Molopo, as the latter one has markedly denser vegetation cover composed of larger bushes. Moreover, arid environments with scarce food resources presumably select for opportunistic feeding strategies (Paltridge 2002), and eggs in avian nests are thus a desirable source of food for a large spectrum of animals.



**Figure 3:** The relationships between mean clutch size of ground and near-ground nesting birds at the five study sites across South Africa and its potential determinants: (a) estimate of nest predation rate; (b) environmental productivity – NDVI estimate in January; and (c) NDVI seasonality – difference between NDVI estimates in January and July

Nest predation is expected to be a strong selective agent in the evolution of avian clutch size (Skutch 1949). In environments with high incidence of nest predation, it is advantageous to limit investment into clutch in order to lower costs of nest failure (Slagsvold 1982) as well as to lower the frequency of nest visits that may attract predators (Skutch 1949). We found that the study site with the highest estimate of nest predation rate (Pofadder) coincided with areas where birds laid the smallest clutches. This suggests a possibility that nest predation is a factor driving evolution of clutch size in South African birds. However, the nest predation rate is not closely related to changes in clutch size across our study sites. Instead, it is constantly low at the majority of them.

By contrast, we found rather gradual increase in clutch size from sites with low to high productivity and, moreover, this increase was relatively tightly correlated with both environmental productivity and its seasonality. Similar results have been reported previously by Lepage and Lloyd (2004) on a subset of South African species. These authors attributed the observed geographical variation in clutch size to environmental stochasticity and seasonality in rainfall (rainfall is considered the most important determinant of environmental productivity in South Africa; Zucchini and Adamson 1984). Their explanations are thus based on unpredictability of food availability in arid environments, which forces birds to employ a bet-hedging strategy and lay small clutches. At our study sites, the differences between environmental productivity corresponded to differences in its seasonality. Therefore, we cannot distinguish between the food limitation hypothesis *sensu stricto* (Lack 1947), according to which the total food abundance during breeding season limits clutch size, and ‘the seasonality in resources hypothesis’ (Ashmole 1963), which states that differences in food availability throughout the year influences clutch sizes of birds via population density effects. Our results suggest that food availability (estimated by NDVI) is most probably responsible for the increase in clutch size of ground-nesting birds along the productivity gradient in South Africa.

We found no statistically significant correlative evidence for the role of nest predation in determining avian clutch size. However, high nest predation rate in a desert location near Pofadder reported by this study may contribute to low clutch sizes of birds observed there. Theoretically, the interaction between low food availability and high nest predation rates may lie behind low clutch sizes of birds in arid environments. Low food availability leading to small clutch size may also enhance nest predation pressure (e.g. by higher frequency of opportunistic feeding strategies of nest predators), which in turn strengthens selection pressure for small clutch size in birds. In such a scenario, one would expect the lowest clutch size in areas with the high nest predation and low food availability. In our study, the two least productive sites (Pofadder and Molopo) differed significantly in predation rate but not in clutch size, although the mean clutch size was slightly lower in Pofadder. This suggests that food availability related to environmental productivity is stronger determinant of clutch size than nest predation at least for our study sites.

**Acknowledgements** — The study was supported by grants of the Czech Academy of Sciences (project no. IAA601970801), Czech Science Foundation (project no. P505/11/1617) and Ministry of Education, Youth and Sports of the Czech Republic (project nos. LC 06073 and MSM 0021620828). The project was performed with the kind assistance of South African National Parks. We are grateful to local farmers who enabled us to carry out field work within their properties. Anonymous referees greatly improved the manuscript and Andrew McKechnie kindly assisted in editing the text. Irena Šimová helped us with compilation of environmental productivity estimates for South Africa. David Hardekopf improved the English.

## References

- Albrecht T, Hořák D, Kreisinger J, Weidinger K, Klvaňa P, Michot TC. 2006. Factors determining pochard nest predation along a wetland gradient. *Journal of Wildlife Management* 70: 784–791.

- Ashmole, N P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103: 458–473.
- Batáry P, Báldi A. 2004. Evidence of an edge effect on avian nest success. *Conservation Biology* 18: 389–400.
- Bonn A, Storch D, Gaston KJ. 2004. Structure of the species-energy relationship. *Proceedings of the Royal Society B: Biological Sciences* 271: 1685–1691.
- Carlson A, Hartman G. 2001. Tropical forest fragmentation and nest predation – an experimental study in an Eastern Arc montane forest, Tanzania. *Biodiversity and Conservation* 10: 1077–1085.
- Ceballos G, Ehrlich PR. 2006. Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences of the USA* 103: 19374–19379.
- Chalfoun AD, Martin TE. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. *Journal of Animal Ecology* 78: 497–503.
- Green RE. 2004. Breeding biology. In: Sutherland WJ, Newton I, Green RE (eds), *Bird ecology and conservation: a handbook of techniques*. Oxford: Oxford University Press. pp 57–84.
- DeGraaf RM, Maier TJ. 1996. Effect of egg size on predation by white-footed mice. *Wilson Bulletin* 108: 535–539.
- Hockey PAR, Dean WRJ, Ryan PG (eds). 2005. *Roberts birds of southern Africa* (7th edn). Cape Town: Trustees of the John Voelcker Bird Book Fund.
- Jetz W, Sekercioglu CH, Böhnig-Gaese K. 2008. The worldwide variation in avian clutch size across species and space. *PLoS Biology* 6(12), e303. doi:10.1371/journal.pbio.0060303.
- Kerley GIH. 1992. Ecological correlates of small mammal community structure in the semiarid Karoo, South Africa. *Journal of Zoology* 227: 17–27.
- Kulesza G. 1990. An analysis of clutch-size in New World passerine birds. *Ibis* 132: 407–422.
- Lack D. 1947. The significance of clutch-size. *Ibis* 89: 302–352.
- Lahti DC. 2001. The “edge effect on nest predation” hypothesis after twenty years. *Biological Conservation* 99: 365–374.
- Lepage D, Lloyd P. 2004. Avian clutch size in relation to rainfall seasonality and stochasticity along an aridity gradient across South Africa. *Ostrich* 75: 259–268.
- Lloyd P. 2006. Density-dependent nest predation: a field test. *African Journal of Ecology* 44: 293–295.
- López-Flores V, MacGregor-Fors I, Schondube JE. 2009. Artificial nest predation along a Neotropical urban gradient. *Landscape and Urban Planning* 92: 90–95.
- Martin TE. 1993a. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141: 897–913.
- Martin TE. 1993b. Nest predation and nest sites: new perspectives on old patterns. *BioScience* 43: 523–532.
- Martin TE. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65: 101–127.
- McKinnon L, Smith PA, Nol E, Martin JL, Doyle FI, Abraham KF, Gilchrist HG, Morrison RIG, Bêty J. 2010. Lower predation risk for migratory birds at high latitudes. *Science* 327: 326–327.
- McLoughlin PD, Ferguson SH. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Écoscience* 7: 123–130.
- Nilsen EB, Herfindal I, Linnell JDC. 2005. Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Écoscience* 12: 68–75.
- Paltridge R. 2002. The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research* 29: 389–403.
- R Development Core Team 2010. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.
- Rangel TFLVB, Diniz-Filho JAF, Bini LM. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogeography* 15: 321–327.
- Reif J, Hořák D, Sedláček O, Riegert J, Pešata M, Hrázský Z, Janeček Š, Storch D. 2006. Unusual abundance-range size relationship in an Afrotropical bird community: the effect of geographical isolation? *Journal of Biogeography* 33: 1959–1968.
- Ricklefs RE. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9: 1–48.
- Ricklefs RE. 1980. Geographical variation in clutch size among passerine birds: Ashmole's hypothesis. *Auk* 97: 38–49.
- Schmidt KA, Ostfeld RS, Smyth KN. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. *Oecologia* 148: 22–29.
- Shekedy Y, Safriel UN. 1992. Nest predation and nestling growth rate of two lark species in the Negev Desert, Israel. *Ibis* 134: 268–272.
- Sibley CG, Monroe BL. 1990. *Distribution and taxonomy of birds of the world*. New Haven: Yale University Press.
- Skutch AF. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91: 430–455.
- Skutch AF. 1985. Clutch size, nesting success, and predation on nests of tropical birds, reviewed. In: Buckley PA, Foster MS, Morton ES, Ridgely RS, Buckley FG (eds), *Neotropical ornithology. Ornithological Monographs* vol. 36. Washington, DC: American Ornithologists Union. pp 575–603.
- Slagsvold T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* 54: 159–169.
- Söderström B. 1999. Artificial nest predation rates in tropical and temperate forests: a review of the effects of edge and nest site. *Ecography* 22: 455–463.
- Spanhove T, Lehouck V, Lens L. 2009. Inverse edge effect on nest predation in a Kenyan forest fragment: an experimental case study. *Bird Conservation International* 19: 367–378.
- Yahner RH, Mahan CG. 1996. Effects of egg type on depredation of artificial nests. *Wilson Bulletin* 108: 129–136.
- Zucchini W, Adamson PT. 1984. *The occurrence and severity of droughts in South Africa*. WRC Report no. 91/1/84. Pretoria: Water Research Commission.

**Appendix 1:** List of ground and near-ground nesting species included in the clutch size analysis, grouped by study sites and families (following Sibley and Monroe 1990)

### Pofadder

Struthionidae: *Struthio camelus*; Phasianidae: *Pternistis capensis*, *P. afer*, *Coturnix coturnix*; Numididae: *Numida meleagris*; Anatidae: *Alopochen aegyptiaca*, *Anas undulata*, *A. sparsa*, *A. capensis*, *A. erythrorhyncha*, *A. lithii*, *Netta erythrophthalma*, *Plectropterus gambensis*, *Oxyura maccoa*; Strigidae: *Bubo capensis*, *B. Africanus*; Caprimulgidae: *Caprimulgus rufigena*; Otidae: *Ardeotis kori*, *Neotis ludwigii*, *Eupodotis vigorsii*, *Afrotis afra*; Rallidae: *Rallus caerulescens*, *Fulica cristata*; Pteroclididae: *Pterocles namaqua*, *Pterocles bicinctus*; Burhinidae: *Burhinus capensis*; Charadriidae: *Charadrius pallidus*, *C. pecuarius*, *C. tricollaris*, *Vanellus coronatus*, *V. armatus*, *Recurvirostra avosetta*, *Himantopus himantopus*; Glareolidae: *Cursorius rufus*, *Rhinoptilus africanus*; Accipitridae: *Circus maurus*; Podicipedidae: *Tachybaptus ruficollis*; Ardeidae: *Ardea goliath*; Phoenicopteridae: *Phoenicopus ruber*; Muscicapidae: *Oenanthe pileata*, *Cercomela tractrac*, *C. sinuata*, *C. schlegelii*, *Cossypha caffra*, *Cercotrichas coryphaeus*; Cisticolidae: *Euryptila subcinnamomea*, *Cisticola juncidis*, *C. subruficapilla*; Motacillidae: *Motacilla aguimp*, *M. capensis*, *Anthus cinnamomeus*, *A. similis*, *A. crenatus*; Sylviidae: *Eremomela gregalis*; Alaudidae: *Mirafra apiata*, *Calendulauda africanoides*, *C. sabota*, *C. burra*, *Certhilauda curvirostris*, *Chersomanes albofasciata*, *Calandrella cinerea*, *Spizocorys conirostris*, *Spizocorys sclateri*, *Spizocorys starki*, *Galerida magnirostris*, *Eremopterix leucotis*, *E. verticalis*, *E. australis*; Passeridae: *Lagonosticta senegala*, *Estrilda astrild*; Fringillidae: *Emberiza capensis*, *E. impetuani*

### Molopo

Struthionidae: *Struthio camelus*; Phasianidae: *Scleroptila levaillantoides*, *Pternistis adpersus*, *Coturnix coturnix*, *C. delegorguei*; Numididae: *Numida meleagris*; Anatidae: *Alopochen aegyptiaca*, *A. erythrorhyncha*; Strigidae: *Bubo africanus*; Caprimulgidae: *Caprimulgus rufigena*; Otidae: *Ardeotis kori*, *Lophotis ruficrista*, *Afrotis afra*; Rallidae: *Porzana pusilla*, *Fulica cristata*; Pteroclididae: *Pterocles namaqua*, *P. burchelli*, *P. bicinctus*; Burhinidae: *Burhinus capensis*; Charadriidae: *Charadrius pecuarius*, *C. tricollaris*, *Vanellus coronatus*, *V. armatus*, *Himantopus himantopus*, *Glareolidae: Cursorius rufus*, *C. temminckii*, *Rhinoptilus africanus*, Accipitridae: *Circus maurus*; Podicipedidae: *Tachybaptus ruficollis*; Muscicapidae: *Oenanthe pileata*, *Saxicola torquatus*, *Cercotrichas paena*; Cisticolidae: *Cisticola aridulus*, *C. rufilatus*; Alaudidae: *Mirafra passerina*, *M. africana*, *M. apiata*, *Calendulauda africanoides*, *C. sabota*, *Chersomanes albofasciata*, *Calandrella cinerea*, *Spizocorys conirostris*, *Eremopterix leucotis*, *E. verticalis*; Passeridae: *Motacilla capensis*, *Anthus cinnamomeus*, *A. vaalensis*, *Lagonosticta senegala*, *Estrilda astrild*; Fringillidae: *Emberiza tahapisi*, *E. impetuani*

### Kuruman

Struthionidae: *Struthio camelus*; Phasianidae: *Scleroptila levaillantoides*, *Pternistis adpersus*, *P. swainsonii*, *Coturnix coturnix*; Numididae: *Numida meleagris*; Dendrocygnidae: *Dendrocygna viduata*, *D. bicolor*; Anatidae: *Thalassornis leuconotus*, *Alopochen aegyptiaca*, *A. undulata*, *A. sparsa*, *A. capensis*, *A. hottentota*, *A. erythrorhyncha*, *A. smithii*, *Netta erythrophthalma*, *Plectropterus gambensis*, *Oxyura maccoa*; Turnicidae: *Turnix sylvaticus*; Caprimulgidae: *Caprimulgus rufigena*; Otidae: *Ardeotis kori*, *Neotis ludwigii*, *Lophotis ruficrista*, *Afrotis afra*; Gruidae: *Anthropoides paradiseus*; Rallidae: *Rallus caerulescens*, *Amauornis flavirostris*, *Porphyrio madagascariensis*, *Gallinula chloropus*, *Fulica cristata*; Pteroclididae: *Pterocles namaqua*, *P. burchelli*, *P. bicinctus*; Strigidae: *Bubo africanus*; Scolopacidae: *Gallinago nigripennis*; Burhinidae: *Burhinus capensis*; Charadriidae: *Charadrius pecuarius*, *C. tricollaris*, *Vanellus coronatus*, *V. armatus*, *Recurvirostra avosetta*, *Himantopus himantopus*; Glareolidae: *Cursorius rufus*, *C. temminckii*, *Rhinoptilus africanus*, *R. chalconotus*; Laridae: *Larus cirrocephalus*; Accipitridae: *Circus maurus*, *C. ranivorus*; Podicipedidae: *Podiceps cristatus*, *Tachybaptus ruficollis*; Phoenicopteridae: *Phoenicopus ruber*, *P. minor*; Threskiornithidae: *Plegadis falcinellus*; Muscicapidae: *Oenanthe pileata*, *Saxicola torquatus*, *Cossypha caffra*, *Cercotrichas coryphaeus*, *C. paena*; Cisticolidae: *Cisticola juncidis*, *C. aridulus*, *C. rufilatus*, *C. chiniana*, *C. tinniens*, *C. fluviicapilla*; Alaudidae: *Mirafra passerina*, *M. africana*, *M. apiata*, *Calendulauda africanoides*, *C. sabota*, *Chersomanes albofasciata*, *Calandrella cinerea*, *Spizocorys conirostris*, *Eremopterix verticalis*; Passeridae: *Motacilla aguimp*, *M. capensis*, *Anthus cinnamomeus*, *A. similis*, *A. vaalensis*, *Macronyx capensis*, *Lagonosticta senegala*, *Estrilda astrild*, *Ortygospiza atricollis*, *Euplectes afer*, *E. progne*; Fringillidae: *Emberiza capensis*, *E. tahapisi*, *E. impetuani*

### Marakele

Struthionidae: *Struthio camelus*; Phasianidae: *Peliperdix coqui*, *Dendroperdix sephaena*, *Scleroptila shelleyi*, *Pternistis natalensis*, *Pternistis swainsonii*, *Coturnix coturnix*, *C. Delegorguei*; Numididae: *Numida meleagris*; Dendrocygnidae: *Dendrocygna viduata*; Anatidae: *Thalassornis leuconotus*, *Alopochen aegyptiaca*, *A. undulata*, *A. sparsa*, *A. hottentota*, *A. erythrorhyncha*, *A. smithii*, *Netta erythrophthalma*, *Plectropterus gambensis*, *Oxyura maccoa*; Turnicidae: *Turnix sylvaticus*; Strigidae: *Asio capensis*, *Bubo africanus*; Caprimulgidae: *Caprimulgus pectoralis*, *C. rufigena*; Otidae: *Ardeotis kori*, *Neotis denhami*, *Eupodotis senegalensis*, *Lophotis ruficrista*, *Afrotis afra*; Gruidae: *Anthropoides paradiseus*; Heliornithidae: *Podica senegalensis*; Rallidae: *Rallus caerulescens*, *Crecopsis egregia*, *Amauornis flavirostris*, *Sarothrura rufa*, *Porphyrio madagascariensis*, *Gallinula chloropus*, *Fulica cristata*; Pteroclididae: *Pterocles burchelli*, *P. gutturalis*, *P. bicinctus*; Scolopacidae: *Gallinago nigripennis*; Rostratulidae: *Rostratula benghalensis*; Jacanidae: *Actophilornis africanus*; Burhinidae: *Burhinus capensis*, *B. vermiculatus*; Glareolidae: *Cursorius temminckii*, *Rhinoptilus chalconotus*; Charadriidae: *Charadrius marginatus*, *C. pecuarius*, *C. tricollaris*, *Vanellus coronatus*, *V. armatus*, *V. senegallus*, *Recurvirostra avosetta*, *Himantopus himantopus*; Laridae: *Larus cirrocephalus*, *Chlidonias hybrida*; Accipitridae: *Circus ranivorus*; Podicipedidae: *Podiceps cristatus*, *Tachybaptus ruficollis*; Ardeidae: *Ardea goliath*,

Phoenicopteridae: *Phoenicopus ruber*, *P. minor*; Threskiornithidae: *Plegadis falcinellus*; Muscicapidae: *Oenanthe pileata*, *O. bifasciata*, *Saxicola torquatus*, *Cossypha caffra*, *C. humeralis*, *Cercotrichas leucophrys*, *C. paena*; Cisticolidae: *Cisticola juncidis*, *C. aridulus*, *C. textrix*, *C. ayresii*, *C. rufilatus*, *C. chiniana*, *C. tinniensi*, *C. aberrans*, *C. fulvicapilla*; Sylviidae: *Camaroptera brachyura*, *Sphenoeacus afer*, *Bradypterus baboecala*; Alaudidae: *Mirafra passerina*, *M. africana*, *M. rufocinnamomea*, *Calendulauda africanoides*, *C. sabota*, *Certhilauda chuana*, *Calandrella cinerea*, *Spizocorys conirostris*, *Eremopterix leucotis*, *E. verticalis*; Passeridae: *Motacilla aguimp*, *M. capensis*, *Anthus cinnamomeus*, *A. similis*, *A. leucophrys*, *A. vaalensis*, *A. lineiventris*, *A. caffer*, *Macronyx capensis*, *Euplectes afer*, *E. albonotatus*, *E. progne*, *Lagonosticta rhodopareia*, *L. senegala*, *Estrilda astrild*, *Ortygospiza atricollis*, *Sporaeginthus subflavus*; Fringillidae: *Emberiza capensis*, *E. tahapisi*, *E. impetuani*

## Punda Maria

Struthionidae: *Struthio camelus*; Phasianidae: *Peliperdix coqui*, *Dendroperdix sephaena*, *Scleroptila shelleyi*, *Pternistis natalensis*, *P. swainsonii*, *Coturnix coturnix*, *C. delegorguei*; Numididae: *Numida meleagris*, *Guttera edouardi*; Turnicidae: *Turnix sylvaticus*; Dendrocygnidae: *Dendrocygna viduata*, *D. bicolor*; Anatidae: *Thalassornis leucanotus*, *Alopochen aegyptiaca*, *A. undulata*, *A. sparsa*, *A. hottentota*, *A. erythrorhyncha*, *Netta erythrophthalma*, *Plectropterus gambensis*; Centropidae: *Centropus grillii*; Strigidae: *Asio capensis*, *Bubo africanus*; Caprimulgidae: *Caprimulgus pectoralis*, *C. rufigena*, *C. fossii*, *Macrodipteryx vexillarius*; Otidae: *Ardeotis kori*, *Lophotis ruficrista*, *Lissotis melanogaster*; Heliornithidae: *Podica senegalensis*; Rallidae: *Crecopsis egregia*, *Amauornis flavirostris*, *Porzana pusilla*, *Sarothrura elegans*, *Porphyrio madagascariensis*, *P. alleni*, *Gallinula chloropus*, *G. angulata*, *Fulica cristata*; Pteroclididae: *Pterocles bicinctus*; Scolopacidae: *Gallinago nigripennis*; Rostratulidae: *Rostratula benghalensis*; Jacanidae: *Actophilornis africanus*, *Microparra capensis*; Burhinidae: *Burhinus capensis*, *B. vermiculatus*; Charadriidae: *Charadrius marginatus*, *C. pallidus*, *C. pecuarius*, *C. tricollaris*, *Vanellus coronatus*, *V. lugubris*, *V. armatus*, *V. albiceps*, *V. senegallus*, *Recurvirostra avosetta*, *Himantopus himantopus*; Glareolidae: *Cursorius temminckii*, *Rhinoptilus chalcopterus*, *Glareola pratincola*; Laridae: *Larus cirrocephalus*, *Sterna caspia*, *Chlidonias hybrida*; Accipitridae: *Circus ranivorus*; Podicipedidae: *Podiceps nigricollis*, *Tachybaptus ruficollis*; Ardeidae: *Ardea goliath*; Phoenicopteridae: *Phoenicopus ruber*, Threskiornithidae: *Plegadis falcinellus*; Pelecanidae: *Pelecanus onocrotalus*; Muscicapidae: *Oenanthe pileata*, *Saxicola torquatus*, *Cossypha caffra*, *C. humeralis*; Pogonocichla: *stellata*, *Cercotrichas leucophrys*, *C. paena*; Megaluridae: *Bradypterus baboecala*; Cisticolidae: *Cisticola juncidis*, *C. aridulus*, *C. ayresii*, *C. lais*, *C. chiniana*, *C. erythropterus*, *C. galactotes*, *C. tinniensi*, *C. natalensis*, *C. aberrans*, *C. fulvicapilla*; Sylviidae: *Phylloscopus ruficapilla*, *Camaroptera brachyura*, *Sphenoeacus afer*; Alaudidae: *Mirafra passerina*, *M. africana*, *M. rufocinnamomea*, *Calendulauda africanoides*, *C. sabota*, *C. cinerea*, *Eremopterix leucotis*; Passeridae: *Motacilla aguimp*, *M. capensis*, *Anthus cinnamomeus*, *A. similis*, *A. leucophrys*, *A. vaalensis*, *A. lineiventris*, *A. caffer*, *Macronyx croceus*, *Euplectes afer*, *E. capensis*, *E. albonotatus*, *Hypargos margaritatus*, *Lagonosticta rhodopareia*, *L. senegala*, *Estrilda astrild*, *Ortygospiza atricollis*, *Sporaeginthus subflavus*; Fringillidae: *Emberiza tahapisi*, *E. impetuani*