The Auk 115(2):404–411, 1998

ABIOTIC FACTORS AS PREDICTORS OF DISTRIBUTION IN SOUTHERN AFRICAN BULBULS

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ABSTRACT.—The closely related Black-eyed Bulbul (*Pycnonotus barbatus*), Red-eyed Bulbul (*P. nigricans*), and Cape Bulbul (*P. capensis*) occupy parapatric to locally sympatric ranges within southern Africa. We used a multivariate discriminant function analysis to relate the South African distribution of these species at the resolution of a quarter-degree square of latitude and longitude to a suite of six environmental variables extracted from digital models. The analysis correctly classified the distribution of these species for 89% of the 1,426 squares analyzed. Separation on the first discriminant function, which successfully characterized the distribution of *P. nigricans*, was mainly by the coefficient of variation in mean annual rainfall and mean July minimum temperature. Separation on the second discriminant function, which successfully characterized *P. capensis*, was mainly by the "normalized difference green vegetation index" (derived from NOAA satellite scans). Using the standardized coefficients for the first discriminant function, a model generated to predict the distribution of *P. nigricans* at a finer geographic resolution within our Eastern Cape Province study area was 93% successful. The results suggest that the three species occupy distinctly different habitats, as characterized by the suite of six environmental variables that we analyzed.

Received 19 May 1997, accepted 3 November 1997.

TWO LONG-HELD HYPOTHESES in ecology address the question of what shapes biogeographic patterns. One implicates biotic interactions, such as competition, as the main factors controlling these patterns (MacArthur 1958); the other postulates that abiotic factors, such as climate, are the primary forces shaping the biogeographic ranges of species (Andrewartha and Birch 1954). Climate may influence a species' range directly through its influence on physiological processes and/or indirectly (i.e. ecologically) through its influence on vegetation and food availability (Kalela 1949, Hayworth and Weathers 1984, Root 1988a, b, Hall et al. 1992).

For terrestrial birds, vegetation (either floristic composition or spatial structure) has an important effect on the distributions of species, particularly at the local level (MacArthur and MacArthur 1961, Rotenberry 1985, Block and Brennan 1993). The problem in trying to relate the distribution of species directly to this factor is the enormous effort required to quantify the structure and composition of vegetation (e.g. Cody 1968, Folse 1982), particularly when the species involved inhabit a wide variety of different vegetation types. This problem can be circumvented, to some extent, by obtaining indirect indices of vegetation through quantification of a variety of environmental factors that influence vegetation, such as temperature, rainfall and elevation (Palmer 1991a, Gentilli 1992, Palmer and van Staden 1992).

Annual precipitation is an important determinant of vegetation, particularly in semiarid regions, with median annual rainfall providing a better index of aridity than the mean in direct gradient analysis (Gibbs and Maher 1967:3–4, Palmer and van Staden 1992). Elevation is an indirect variable that influences plant growth through correlated changes in direct variables, and it can be used as a location-specific surrogate for a complex set of environmental variables in gradient analysis (Austin et al. 1983).

Large-scale studies are usually required to examine the importance of environmental factors on biogeographic patterns (Root 1988a). Such studies require massive data sets. In this respect, we are fortunate in that South Africa has both a nationwide bird distribution database, that of the Southern African Bird Atlas Project (SABAP; Harrison et al. 1997), and a number of digital databases that model a variety of environmental variables (Dent et al. 1989,

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Palmer 1993). The combination of these models provides the opportunity to relate the distribution of bird species to a complex of environmental variables, and ultimately to prepare a testable model of the relationship between a species' distribution and the environment.

The southern African *Pycnonotus* species complex consists of three closely related bulbuls, the Black-eyed Bulbul (*P. barbatus*), the Red-eyed Bulbul (*P. nigricans*), and the Cape Bulbul (*P. capensis*). These bulbuls occur wherever there is access to drinking water and a sufficient number of fruit-bearing trees or shrubs to satisfy their predominantly frugivorous diet. In South Africa, the three species occupy parapatric to locally sympatric distributions; the transition from one species to another is sharp, usually within 20 km (Lloyd et al. 1998). This makes them ideal subjects for a comparative study of the relationship between distribution and environment.

METHODS

SABAP data (25 August 1993, Phase 3) were used to plot the distributions of the three *Pycnonotus* bulbuls in South Africa. The data were collected by professional and amateur ornithologists from 1986 to 1991. Bird lists on atlas cards at the geographic resolution of a quarter-degree square of latitude and longitude were submitted monthly. This presence/absence data for individual species were then pooled to generate an index of abundance for each species in each square. Value categories V (vagrant), R (rare), 1, and 2 represented cases where the species was recorded on fewer than 1% to 24.9% of the cards. Value categories 3 to 9 represented cases where the species was recorded on 25% to 100% of the cards.

Pycnonotus bulbuls are noisy and conspicuous birds that are well-adapted to human-made habitats, especially gardens. Thus, they have a high profile as far as ease of identification and visibility to birdwatchers are concerned. For this reason, their recorded absence from a locality is more likely to reflect their true absence or rarity rather than their being overlooked by observers. To identify the regions of preferred or "core" habitat, we reasoned that any quarter-degree square that returned a value of less than 25% for a species' abundance represented a "marginal" area for the distribution of that species. We therefore modified the SABAP data for each of the three species by changing the values 3 to 9 to "species present" and the values 2 to vagrant to "species absent." By overlaying the presence/absence data for each species, a single map plotting the "core" distributions of the three species at a quarter-degree resolution was produced (Fig. 1).

Environmental variables for each quarter-degree square were then extracted from grid-based geographical information system models that plot data for the entire South African land surface at a minimum resolution of a one-minute square of latitude and longitude. Variables used were: (1) elevation (Dent et al. 1989), (2) median annual rainfall (Dent et al. 1989), (3) coefficient of variation of mean annual rainfall (Palmer 1993), (4) mean January maximum temperature (Palmer 1993), (5) mean July minimum temperature (Palmer 1993), (6) United States National Oceanic and Atmospheric Administration's (NOAA) NOAA-AVHRR waveband 1 (0.55 to 0.68 μm [visible light] scanned on 29 August 1985 [Palmer 1993]), and (7) NOAA-AVHRR waveband 2 (0.725 to 1.10 μm [near infrared light] scanned on 29 August 1985 [Palmer 1993]).

The two waveband scans, obtained from the advanced high-resolution radiometer (AVHRR) of the NOAA polar-orbiting meteorological satellites, measure the spectral reflectance of the earth's surface. Waveband 1 is characterized by strong chlorophyll absorption of red wavelengths; there is a strong relationship between spectral reflectance in this waveband and the amount of chlorophyll present. Waveband 2 is characterized by high levels of reflectance occurring in the absence of any absorptance; there is a strong relationship between spectral reflectance in this waveband and the amount of green vegetation biomass present (Tucker 1978). Using these two waveband reflectance surfaces, a "normalized difference green vegetation index" (NDVI) surface was produced as:

$$\text{NDVI} = (\text{waveband } 2 - \text{waveband } 1)/(\text{waveband } 2 + \text{waveband } 1). \tag{1}$$

The NDVI is a sensitive indicator of green biomass; the index increases as the vegetation becomes greener or more dense (Tucker 1979, Tucker et al. 1983, Tueller 1989, Grist et al. 1997).

For each quarter-degree square registering the presence of a bulbul, a random point was chosen for which a value for each environmental variable was extracted. Those squares registering the presence of two species simply were recorded twice. A multivariate discriminant function analysis was then used to relate the distributions of the three species to the suite of six environmental variables (nos. 1 to 5 above and the NDVI).

The success with which the first discriminant function was able to characterize the distribution of *P. nigricans* at the resolution of a quarter-degree square led to the decision to formulate a model to plot the predicted distribution of this species at the finer resolution of a one-minute square. The standardized coefficients for the first discriminant function were used to generate a discriminant function value surface, using the relation:

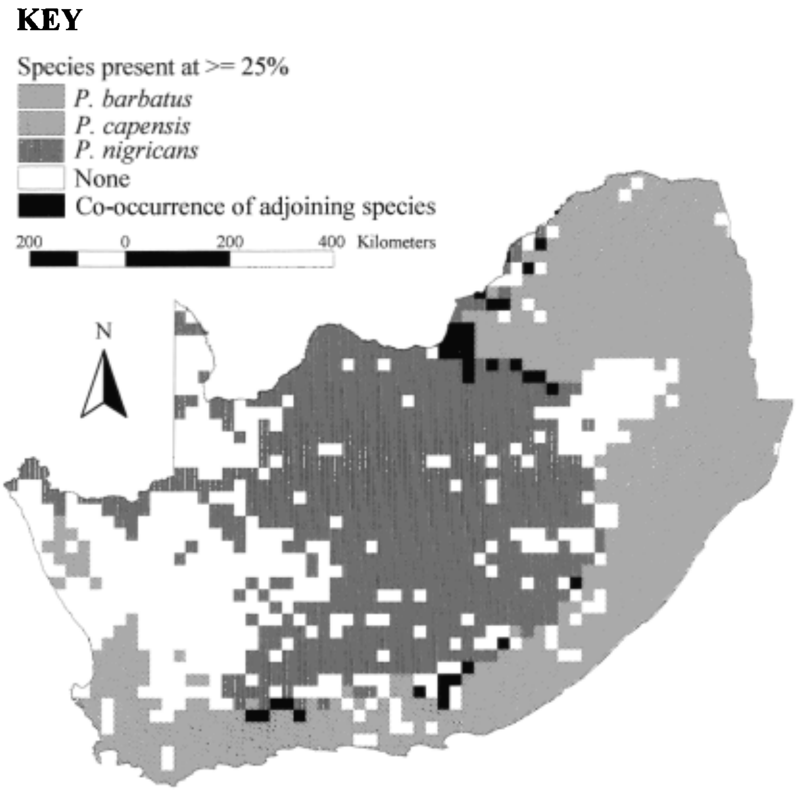

FIG. 1. "Core" distributions of the three *Pycnonotus* bulbuls in South Africa. Modified SABAP data (see text).

$$Z = \lambda_1 X_1 + \lambda_2 X_2 + \ldots + \lambda_6 X_6, \qquad (2)$$

where λ is the standardized discriminant function coefficient and X_i is the value for the environmental variable. The quarter-degree-square Z-values were then ranked in ascending order and grouped into 50-member samples, from which the degree of confidence in predicting the presence of *P. nigricans* was determined. The approximate Z-value delimiting the >95% confidence interval was finally used to categorize the Z-value surface generated for South Africa and to plot the predicted distribution of *P. nigricans* at a resolution of a one-minute square at >95% confidence, within our study area in the Eastern Cape Province (32°00'S, 25°00'E to 34°00'S, 27°00'E).

To evaluate the model, the predicted distribution at the one-minute-square resolution was smoothed to a five-minute-square resolution as follows: if any one-minute pixel predicting the presence of *P. nigricans* with 95% confidence fell within a five-minute square, *P. nigricans* was recorded as "predicted present," otherwise as "predicted absent." The predicted distribution was then visually compared with our five-minute-square resolution distribution plot for the study area (Fig. 2). The latter plot resulted from observations made on a number of surveys throughout the study area (see Lloyd et al. 1998). Finally, the number of squares for which the predicted presence/absence matched the observed presence/absence was counted.

RESULTS

The discriminant function analysis (using the six environmental variables chosen) correctly classified the distribution of the species for 89% of the 1,426 quarter-degree squares analyzed (Table 1). Separation on the first discriminant function, which accounted for 72% of the total variance, was mainly by mean July minimum temperature and the coefficient of variation in mean annual rainfall (Table 2). The first discriminant function was successful in characterizing the distribution of *P. nigricans*. This species occupies regions with a high coefficient of variation in annual rainfall and low July minimum temperatures (Table 2). Separation on the second discriminant function was mainly by the NDVI, with elevation and me-

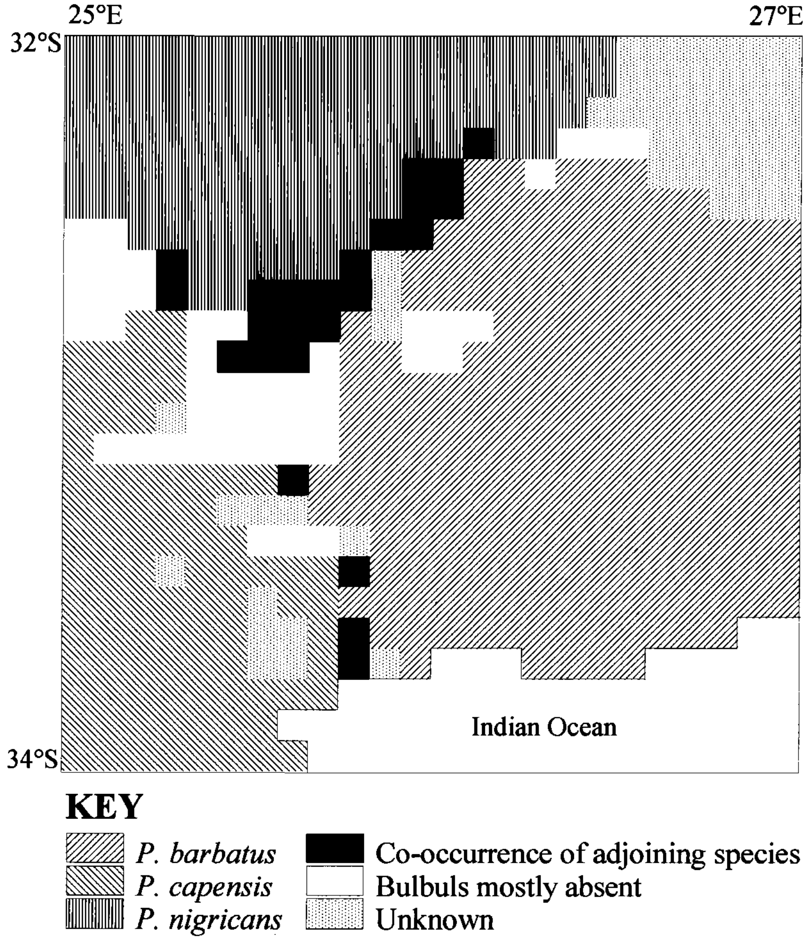

FIG. 2. Observed distributions of the three *Pycnonotus* bulbuls in the Eastern Cape study area (see Lloyd et al. 1998).

dian annual rainfall playing a lesser role (Table 2). Because the satellite scan was conducted in August, toward the end of winter, the parts of the country that experienced winter rains exhibited greener, actively growing vegetation, and therefore higher NDVI values. *Pycnonotus capensis* distribution had a mean NDVI value of 0.15, more than twice that of the other two species (Table 2). The second discriminant function thus served to characterize the distribution of *P. capensis*.

The success of the model in predicting the distribution of *P. nigricans* at the finer resolution of a five-minute square of latitude and longitude was demonstrated by the high percentage of true predictions (93%) as opposed to false

TABLE 1. Discriminant function classification (% of total) of *Pycnonotus* bulbul distributions using six environmental variables. Resolution of squares is a quarter degree of latitude and longitude.

Actual group	Predicted group			Total no. of squares
	P. barbatus	*P. nigricans*	*P. capensis*	
P. barbatus	88	6	6	563
P. nigricans	6	92	2	702
P. capensis	7	14	79	161

TABLE 2. Standardized canonical discriminant function coefficients and mean values for six environmental variables from the distributions of the three *Pycnonotus* bulbuls.

	Discriminant coefficients		Species' means		
Variable	Function 1	Function 2	*P. barbatus*	*P. nigricans*	*P. capensis*
Elevation (m)	−0.11	−0.66	946	1,267	503
Median annual rainfall (mm)	+0.23	−0.68	690	380	411
Coefficient of variation in rainfall	−0.65	−0.02	24.3	41.2	32.9
January max. temperature (°C)	−0.06	−0.36	28.1	30.9	29.0
July min. temperature (°C)	+0.66	−0.26	5.1	1.0	5.1
NDVI	−0.08	+0.83	0.07	0.06	0.15
Total variance (%)	72	28			

predictions (Table 3). Furthermore, misclassified pixels were restricted to the borders of the species' distribution (Fig. 3), where a degree of error can be expected due to the coarseness of the geographic resolution.

DISCUSSION

The predicted distribution of *P. nigricans* is closely correlated with its observed distribution in the study area (Table 3). This result provides support for the initial decision to identify "marginal" areas of a species' distribution, at the resolution of a quarter-degree square of latitude and longitude, as those in which the species was recorded on fewer than 25% of atlas cards. This decision considerably reduces the number of squares in which overlap occurs (Fig. 1) and gives a more accurate indication of the degree of geographic overlap and the sharpness of the transition zones between species (see Lloyd et al. 1998).

In southern Africa, annual rainfall decreases from east to west, with an associated increase in the coefficient of variation in mean annual rainfall (Tyson 1986). In addition, the southern and southwestern seaboard of South Africa receives most of its rainfall in the winter months, whereas the rest of the country is a summer-rainfall region. The transition from the more mesic eastern and southern seaboard habitats to the western, inland semidesert habitats generally is associated with a mountainous escarpment. This combination of factors ensures that temperatures in the arid western regions are more extreme (in terms of seasonal maxima and minima) than those of the more mesic eastern and southern regions of the subcontinent.

TABLE 3. Evaluation of model predicting the distribution of *P. nigricans* in the Eastern Cape at a resolution of a five-minute square of latitude and longitude with >95% confidence.

	Predicted present	Predicted absent
True	101 (90%)	336 (93%)
False	11 (10%)	24 (7%)
Total no. squares	112	360

Pycnonotus nigricans inhabits the arid western interior of southern Africa, which explains the success of the discriminant analysis in correlating the distribution of *P. nigricans* with the coefficient of variation in mean annual rainfall and mean minimum July temperature. The distribution limits of *Pycnonotus* bulbuls coincide closely with the −7°C minimum winter isotherm, with *P. nigricans* occupying the region experiencing minimum temperatures lower than this (Lloyd et al. unpubl. data). Several studies have associated the distribution of bird species with temperature (Kalela 1949, Geldenhuys 1981, Root 1988a, Craig and Hulley 1992). Hayworth and Weathers (1984) and Root (1988b, 1989; but see Repansky 1991) found evidence that temperature exerts a direct physiological constraint on distribution. James (1970) and Aldrich and James (1991) noted that continental patterns of intraspecific geographic variation in size corresponded with gradients in temperature and humidity. They suggested that this size variation resulted either from environmentally induced physiological responses or genetically based adaptations to either the physical environment or its correlates. Lloyd et al. (unpubl. data) found no evidence to support the hypothesis that minimum winter temperature limits the distribution of *Pycnonotus* bulbuls through a direct physiological effect. These results suggest that temperature ex-

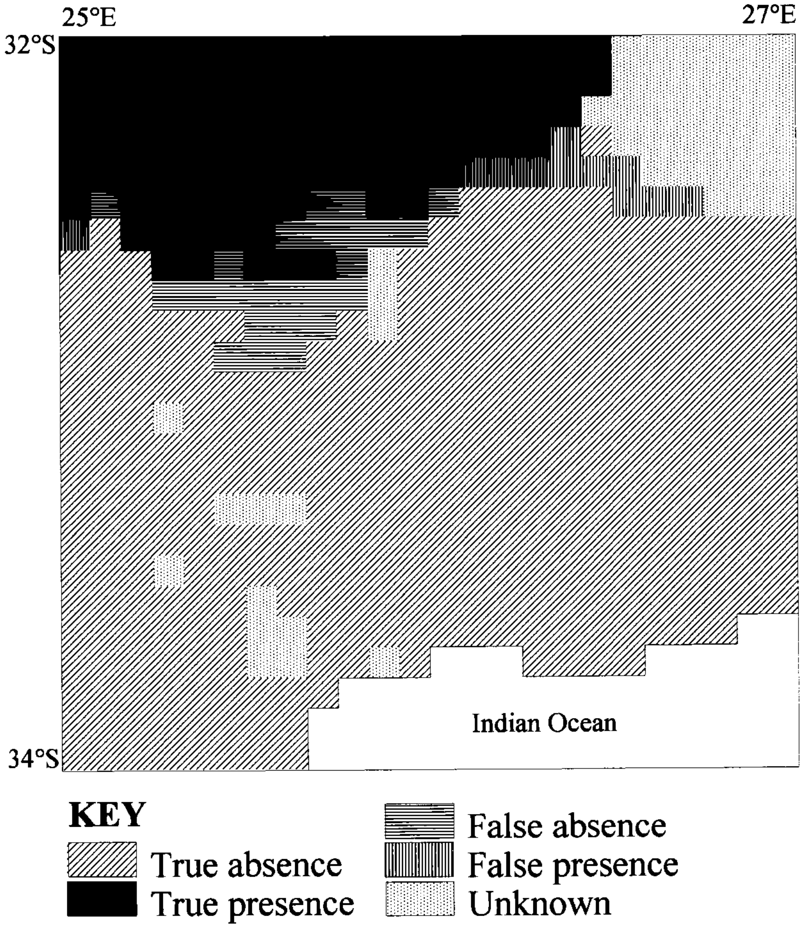

FIG. 3. Graphical evaluation of the model predicting the distribution of *P. nigricans.*

erts an indirect influence on the distributions of *Pycnonotus* bulbuls through its effect on, for example, vegetation, or that it is an integral component of a complex suite of environmental variables (see Hall et al. 1992).

The distribution of *P. capensis* mirrors that of the Fynbos and Succulent Karoo biomes (Rutherford and Westfall 1986). These two biotic provinces receive most of their rainfall during the winter months (Tyson 1986), which explains why the NDVI (based on late winter satellite scans) was so successful in characterizing the distribution of *P. capensis. Pycnonotus capensis* occupies the predominantly winter-rainfall region, whereas *P. barbatus* and *P. nigricans* occupy predominantly summer-rainfall regions.

With their parapatric distributions, each *Pycnonotus* species occupies its own range within a region experiencing broad gradients in a variety of climatic and geographic variables. The success of the discriminant analysis in characterizing the distributions of the three *Pycnonotus* species (Table 1) could be expected simply because the gradients differentiate the species at the extremes. However, the clustering of the misclassified pixels along the border of the distribution of *P. nigricans* (Fig. 3) suggests that the complex of six environmental variables chosen serves as a good predictor of distribution in this group. These results add to a growing body of literature on the use of models that integrate a variety of environmental variables to map the potential distributions of plants and animals. Palmer (1991a, b) and Palmer and van Staden (1992) found that a combination of elevation and rainfall models was useful in predicting the distribution of plant communities. Austin et al. (1990) used generalized linear modeling incorporating rainfall, temperature, solar radiation, and rock type to predict the distributions of several species of *Eucalyptus* and to determine the shape of the species' responses to these environmental variables. Lindenmayer et al. (1991) and Carpenter et al. (1993) describe additional modeling procedures for determining the climatic profile of a species' distribution. Such models are becoming useful tools for quantifying habitats, and they have a variety of applications in wildlife surveys, conservation, and management.

Acknowledgments

We thank the Southern African Bird Atlas Project for distribution data, and the Computing Centre for Water Research, Pietermaritzburg, for access to the XGRID data base. Adrian Craig, Pat Hulley, Townsend Peterson, Robert Zink, and two anonymous reviewers gave constructive comments on earlier drafts of the manuscript. Charlotte Heijnis' assistance with the production of the figures is much appreciated.

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Associate Editor: R. M. Zink