Original Research Paper

Prey Abundance and Patch Usage for Foraging by *Buteo augur* in the Afro-alpine Habitats of the Bale Mountains National Park (BMNP), Ethiopia

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SUMMARY

Quantifying diet related responses of species is key for understanding their functional relationship with their environment. Variation in its magnitude reflects differences in the adaptive value of spatial locations within the distributional range of a species. Amongst the key factors that may account for such variation, differences in prey abundance are critical particularly for predatory species. In this paper, the relationship of the use of patches for foraging by *B. augur* with prey abundance in the Afro-alpine habitats of the BMNP was studied. Data on the frequency of usage of patches for foraging by *B. augur* and the abundance of suitable prey species was collected by having samples at three contrasting areas that reflect the overall variation in the Afro-alpine system. Classification of patches using prey abundance predicted their group membership along with the intensity of foraging by *B. augur,* which varied with very high significance. Two latent variates that were computed by linearly combining the abundance of prey species explained significantly *B. augur's* foraging frequency significantly in a quadratic and linear regression models. The first variate that explained most of the group variation in prey abundance predicted the frequency of foraging by *B. augur* significantly in a quadratic model that explained 66 % of the variation. This variate was mainly defined by the abundances of *A. blicki, L. melanonyx* and *O. bottae*. The second variate with a smaller proportion of group variation contributed significantly to the predictive value of a linear regression model that explained 77 % of the variation in the data set. The discriminant scores of this variate were mainly contributed by *A. blicki* and *S. albocaudata*. Interpretation of our results indicated that *A. bilicki* along with *S. albocaudata* and *L. melanonyx* may have played principal role in affecting *B. augur's* foraging decisions across patches. Generally, in this paper we determined the main prey species that affect the foraging behaviour of *B. augur* for the first time and presented a body of information and interpretation essentially laying the foundation for further understanding of the species ecology in the BMNP and also in Ethiopia. The findings also assist the general conservation effort in the NP and also initiatives that may specifically target *B. augur*.

INTRODUCTION

Studies carried out to explain the dynamic relationship of an animal to its environment frequently quantify indirect measures of food use such as the frequency of foraging locations in its behavioural repertoire in order to describe and predict important patterns such as habitat use (Moen 1973, Hutto 1990, Rosenberg & Cooper 1990, Morrison et al. 1998). Through such behavioural studies it has been possible to establish how different species actively utilize particularly the spatial constituents of their environment (Wiens 1989, Ricklefs 1990, Sutherland 1996, Morrison et al. 1998, Krebs 2000). This is so because of the gathering of food shaped by historical and current ecological factors, which play a very important role in the life of an animal (Wiens 1989, Ricklefs 1990, Sutherland 1996, Morrison et al. 1998, Krebs 2000). As a result of the systematic study of aspects of the foraging behaviour of a species, a body of information useful for establishing why its individuals succeed or fail to succeed in a particular environment can be generated (Sutherland 1996).

Diet related responses are particularly essential for understanding how individuals of predatory species such as raptors perceive their immediate environment (Wiens 1989, Ricklefs 1990, Sutherland 1996, Morrison et al. 1998, Krebs 2000). Factors that may cause variations in such responses could explain how individuals of a species may make decisions regarding when and how to use their immediate environment. The quantification of the frequency of foraging substrates such as patches in the behavioural repertoire of an animal is one way of evaluating its dietary responses (Wiens 1989, Ricklefs 1990, Sutherland 1996, Morrison et al. 1998, Krebs 2000). And the frequency at which individuals of a species utilize patches for foraging purposes may vary essentially as a result of the abundance and availability of the food resources that they eat.

Buteo augur is one of the commonest raptor species in the Afro-alpine habitats of the BMNP (Clouet et al. 2000).

A characteristically variable climate in the Afro-alpine habitats of the BMNP causes drastic vegetation changes that affect the abundance of avian and mammalian prey species spatially and temporally (Yalden 1992, Sillero et al. 1995, Sillero & Gotelli 1995, Clouet et al. 1999, Clouet et al. 2000). Such variation in prey abundance may affect the intensity at which *B. augur* forages at different locations in the Afro-alpine habitats of the BMNP. In this paper we examined evidence to evaluate the validity of a hypothesis that expects the use of patches for foraging by *B. augur* to vary in space as a result of changes in the abundance of species that may make its prey base. Thus far, a study of the dietary behaviour of the species in the Afro-alpine habitats of the BMNP has not been carried out and this particular work is the first attempt to quantify and explain spatial variation in the foraging behaviour of the species in the study area by focusing on its relationship with prey abundance.

MATERIALS AND METHODS

Study Area

Data were collected at three 100 km^2 areas of BMNP: Kotera, Merabawa and the Sanetti Plateau (Fig. 1). The three study sites differ in altitude and vegetation supporting diverse prey communities (Yalden 1992, Sillero et al. 1995, Sillero-Zuburi & Gotelli 1995, Clouet et al. 1999, Clouet et al. 2000). Additional complexity is created by a strongly seasonal climate with pronounced dry and wet seasons. The general approach was to quantify the frequency of usage of patches for foraging by *B. augur* as a function of variations in prey abundance.

Data Collection

Patch utilization: To quantify the frequency of use of different foraging locations by *B. augur,* six circular patches each with an area of 3.14 km^2 were selected randomly in each study site by separating any two by a minimum distance of 2.5 km. Using instantaneous scan sampling technique the frequency of usage of a patch was measured by counting all the individuals that foraged at three minute intervals for three hours by starting at 9 am (Martin & Bateson 1993, Hall et al. 1997, Morrison et al. 1998).

Prey abundance: Encounters during a prior reconnaissance and ad hoc encounters of foraging by B. *augur* suggested that its prey base may constitute small diurnal rodent and passerine species that were targeted in this study. The abundance of rodents was assessed by setting 60 snap traps at 10 m interval along transect lines (20cm × 10cm) in each patch. Traps were baited and set over a day and night so that an index of abundance calculated as number of animals caught per 60 trap nights.

To assess the abundance of small passerines four 1 km transect lines were set randomly in each scanning patch (Bibby et al. 1992). Birds were counted by setting a 250 m band on both sides of an imaginary central straight line. The total number of individuals sighted in each transect was used to generate mean abundance per transect.

Data Analysis

To measure the importance of prey abundance in affecting the frequency of use of patches by *B. augur* K-means cluster analysis was conducted using the abundances of the small rodent and passerine prey species to predict the group membership of patches (Field 2000). This involved prior determination of the number of groups. Information collected during a reconnaissance indicated that prey species had three general habitat affinities: widespread species, cliff specialists and species with particular preference for the Afro-alpine plains. Using this broad habitat classification of prey species, patches were clustered into a specified number of groups. In order to generate a collective construct of prey abundance and also to determine the importance of each species for the classification of foraging patches, Discriminant Analysis (DFA) was carried out (Morrison et al. 1998, Field 2000). This produced latent variates along which foraging patches were ordinated. These latent variates linearly integrated the abundance of the targeted prey species to generate their function scores. Using the predicted group membership as a fixed factor (Field 2000) in a Univariate ANOVA, the mean abundance of prey species and the frequency of usage of patches for foraging were evaluated. The frequency of patch use for foraging was also regressed against the two latent variates of the DFA to explain its variation in space as a function of the combined abundance of small rodents and passerines.

RESULTS

Prey abundance: Using the abundance of small passerines, rodents patches were clustered into three groups. The resulting two functions separated patches significantly (Fig. 2). As depicted in Table 1, the contribution of prey types for the classification of patches along a foraging resource dimension was different. Most of the spatial variation behind the differentiation value of the first variate was contributed by rodents such as *L. melanonyx* and *A. bilicki*. In the same league was also *O. bottae*. The second function separated the three groups of samples mainly due to the abundances of *S. albocaudata* and *A. bilicki*.

The three sample clusters differed in the abundance of *L. melanonyx* (Fig. 3). The species highest abundance was documented in patches of cluster 3 and its smallest number was observed in patches of category 2. This variation in the abun-

dance of *L. melanonyx* was highly significant (F_2 = 34.5, P < 0.001). *A. bilick*'s abundance was highest in patches of group one and attained its smallest numbers in those samples grouped under cluster 2. The spatial variation in the abundance of *A. bilicki* was highly significant (F_2 = 31.1, P < 0.001). The abundance of *S. albocaudata* in groups 1 and 3 were comparably high while its lowest density was documented in patches of category 2. The overall spatial variation in the abundance of this species was also very high (F_2 = 9.1, P < 0.001). The abundance of small passerines changed only slightly amongst groups of patches and none of these variations were statistically significant (Fig. 4).

Patch difference in foraging use: Along these three classes of samples, the frequency at which *B. augur* used patches for foraging was compared (Fig. 5). The highest patch usage was observed in the first sample cluster and the lowest was reported from patches in the second cluster. This intergroup variation in the intensity of usage of patches for foraging by *B. augur* was significant (F_2 = 12.2, P = 0.003).

To determine the relationship of the availability of foraging resource with the frequency of foraging by *B. augur* discriminant scores were computed using the abundances of the small rodent and passerine prey species. The regression analysis that used the first variate as an explanatory variable generated a quadratic model (Fig. 6) that predicted significantly (F_2 = 8.2, P = 0.009) the utilization of patches by the species after explaining 66 % of the variation in the data set. A linear regression of frequency of usage of patches by *B. augur* against the second variate produced a model that explained 77 % of the variation in the data set significantly (F_1 = 33.7, P < 0.001). The second variate made a highly significant (P < 0.001) contribution to the predictive ability of the model (Fig. 7).

DISCUSSION

In order to understand the dynamic relationships between an animal and its environment one should think of the environment in its functional relation to the animal rather than merely as the geographic area and physical structure of the habitat in which the animal lives (Moen 1973, Morrison et al. 1998). With such a rather broad objective workers that studied ecological relationships focused on indirect measures of food use such as foraging location to describe and predict habitat use (Hutto 1990, Rosenberg & Cooper 1990). Such behavioural studies show how animals actively use their environment (Morrison et al. 1998).

The gathering of food plays a very important role in the life of an animal (Morrison et al. 1998) affecting how organisms select spatial components of their environment such as patches. This reflects their evolutionary history as well as
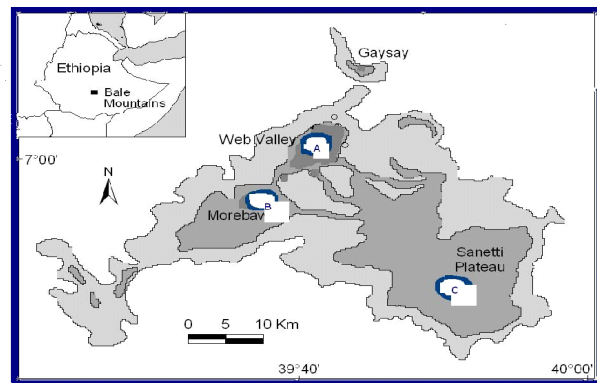

Fig. 1: Map of study sites depicting Kotera (A), Merebawa (B) and Senete (C).

the current ecological conditions of the environment and the influence of other animals (Morrison et al. 1998, Wiens 1989). The manner by which an animal views its environment - namely as, a series of different spatial scales; from the general vegetation type to specific features of the microcosm- is reflected in behaviour of individuals (Morrison et al. 1998). By studying this behaviour in a systematic manner, we can learn much about why animals succeed or fail to succeed in a particular environment (Morrison et al. 1998, Sutherland 1996).

For predatory species such as raptors diet related responses of individuals are critical for understanding of their perception of the immediate environment. After all, most of an organism's relationship to its environment is consequence of its dietary requirements (Wiens 1989, Ricklefs 1990, Sutherland 1996, Morrison et al. 1998, Krebs 2000). Individuals of a species may eat one or more prey types in amounts that may vary both in space and time. The factors that may cause such variation could be the key variables that determine how individuals of a species may make the decision in utilizing the environment in which it lives. Evaluation of dietary responses of species may involve determining the magnitude of use, selection and preference of each prey type and foraging substrate (Morrison 1998).

Because climatic features are characteristically variable in the Afro-alpine habitats of the BMNP and cause drastic vegetation changes spatially and temporally, one can expect the likelihood of abundance fluctuations in the populations of the various species in the small mammal and passerine communities that make up the prey base of *B. augur* and other predators in the Afro-alpine sections of the Bale Mountains National Park (Sillero et al. 1995, Sillero & Gotelli 1995, Clouet et al. 1999, Clouet et al. 2000). In fact, past workers reported spatial and temporal variations in densi-
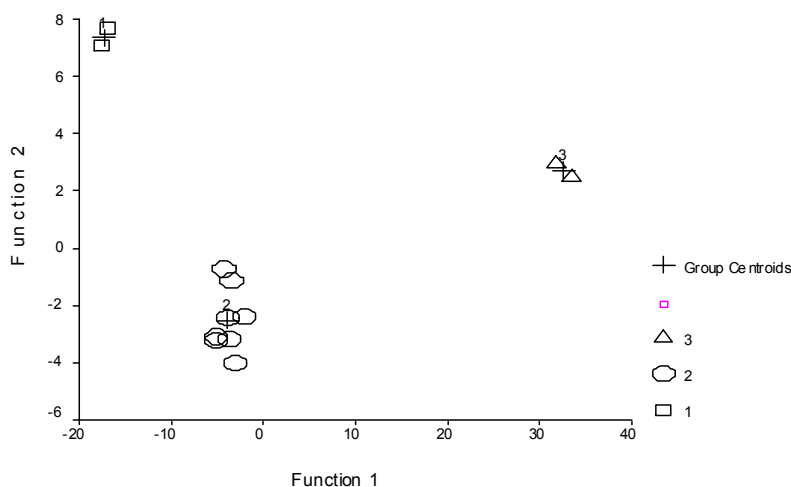
Fig. 2: Clusters of abundances of small rodents and passerines separated significantly along the first (Ch-square = 48.3, P < 0.001) and second functions (Ch-square = 16.6, P = 0.02) of a DFA.

Table 1: Standardized classification coefficients that showed the importance of small rodent and passerine prey species in classifying foraging patches of the *B. augur*.

Prey type	Function 1	Function 2
L. melanonyx	8.1	1.9
A. bilicki	-6.4	3.1
S. albocaudata	0.77	-5.0
C. albitorques	-2.6	2.3
O. bottae	5.1	2.4
A. cervinus	-2.2	-0.9
C. sordida	.065	-0.41
B. cinnamomeus	0.85	-0.73

ties of these prey species in relation to changes in habitat features (Yalden 1988, Sillero et al. 1995). In this paper we examined for the first time the importance of variation in the abundance of small rodent and passerine prey species in explaining variability in the frequency of use of patches for foraging by *B. augur*.

The group membership predicted collectively by the abundances of prey species clustered patches into three groups (Fig. 2) with significant variation in the mean frequency at which they were used for foraging by *B. augur* (Fig. 5). This indicated prey species collectively caused the observed spatial variation in the foraging response of *B. augur*. It is thus important to evaluate the contribution of each species in defining the foraging resource dimension computed linearly (Morrison et al. 1998, Field 2000) to classify patches into groups with different foraging utilization magnitudes by *B. augur*. As indicated in Table 1 the contribution of each prey species in the classification of foraging patches was different (Field 2000, Morrison et al. 1998). This was pointed out by their coefficients weighted as positive

and negative indicating that the differences in the mean abundance of species with opposing signs defined the patch classification gradient as depicted in Fig. 2.

Along the first function the most important species in causing group differences amongst foraging patches were *L. melanonyx*, *A. bilicki* and *O. bottae* (Table 1). Other species, particularly *B. cinnamomus* and *C. sordida* were less important. The difference between *L. melanonyx* and *A. bilicki* was the most important factor that defined the positioning of patch groups along the first function (Figs. 2 & 3). The differences between the two species in groups one and three were almost comparable but their difference in sign put the two groups at the opposing ends of function 1. The contribution of the difference of *O. bottae* with *A. bilicki* was only important for the separation of groups one and two (Figs. 2 & 4). This difference did not separate group three significantly from neither of groups one and two. As a result, *O. bottae* was the least important of the three species that mainly defined the group membership of foraging patches along the first latent variate. The model that resulted from the significant quadratic relationship of the first function with patch usage by *B. Augur* (Fig. 6) explained the variation in the values of the response variable along a patch clustering gradient that progressed from one through two to three (Fig. 2). This pattern was a result of the contributions of the three most important species relative to the classification value of the first function. As was discussed earlier the difference between *L. melanonyx* and *A. bilicki* caused the largest proportion of group differences along the first function. But their mean abundances did not overlap equally with the dependent variable across groups (Figs. 3-5). Of the three species the highest overlap was observed with *A. bilicki*. The mean foraging response of *B. augur* did not vary across groups ex-
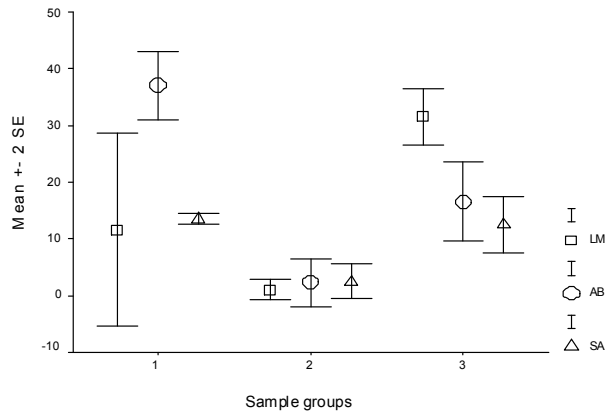
Fig. 3: Variation in the abundance of *L. melanonyx* (LM), *A. bilicki* (AB), and *S. albocaudata* (SA) across patches clustered according to their differences in the abundance of small rodents and passerines.
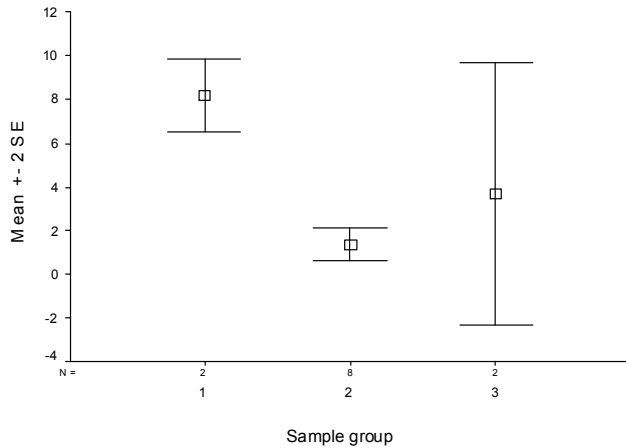

Fig. 4: Variation in the abundance of *B. cinnamomums* (CNBR F_2 = 0.61, P = 0.6), *C. sordida* (HCT, F_2 = 1.8, P = 0.23), *A. cervinus* (RTP, F_2 = 0.6, P = 0.6), *O. bottae* (RBW, F_2 = 1.4, P = 0.3) and *C. albitorques* (WCL, F_2 = 0.6, P = 0.6) across patches clustered according to their differences in the abundance of small rodents and passerines.

Fig. 5: Variation in the mean frequency of usage of patches for foraging by *B. augur* after they were clustered using abundances of small rodents and passerines.

Fig. 6: A quadratic relationship of utilization of patches by *B. augur* with the first discriminant function. Open circles represent observed foraging frequency while the squares stand for the values predicted via the equation UAB = $0.1F_1^2 - 0.25F_1 + 0.36$; where UAB was intensity of patch use for foraging by *B. augur*, F_1 the first variate of prey abundance.

Fig. 7: The linear model that significantly predicted patch use by *B. augur* as UAB = 0.7F2 + 2.9; where UAB was the frequency of usage of patches for foraging by *B. augur* and F2 was the second latent variate that resulted from small rodent and passerine abundances. Open circles represent predicted values while open squares stand for observations made in the field.
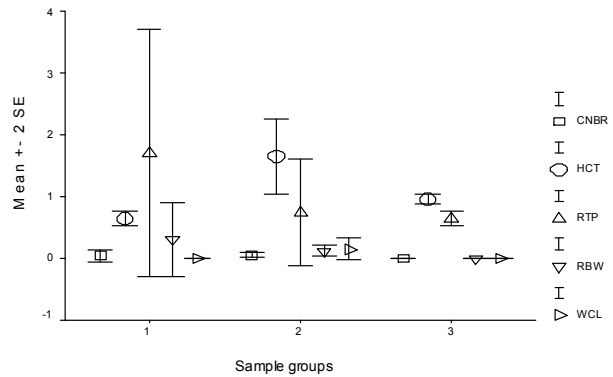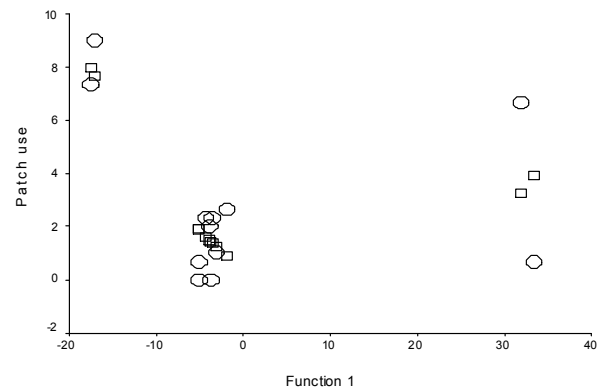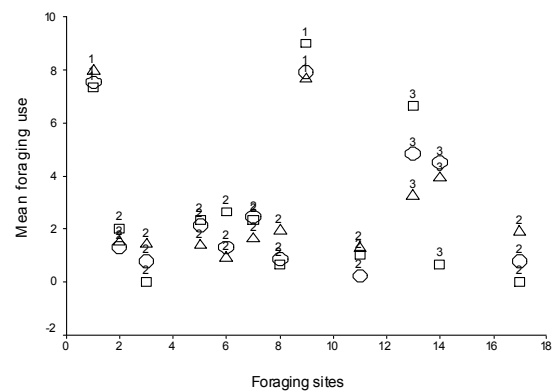

Fig. 8: Similarity in the predictions of the quadratic and the linear models that respectively used the first and the second latent variates as predictors of patch utilization for foraging by *B. augur* (Open squares = observed, Open circles = predictions of the linear model, Open triangles = Predictions of the quadratic model, numbers represent patch categories).

actly as the changes in the mean abundance of *L. melanonyx*. Where, *L. melanonyx's* mean abundance was intermediate, patch usage by *B. augur* was at its highest and where the former attained its maximum the latter foraged at an intermediate level. *O. bottae* had the same minimum mean abundance levels at groups 2 and 3, but the foraging response of *B. augur* at patches in the two groups was noticeably different. It thus can be concluded that in conjunction with the other two species, the predictive value of the first function was mainly the contribution of *A. bilicki*.

The significance of the classification value of the second function was result of the contribution of *S. albocaudata* and *A. bilicki* (Table 1). Due to the difference in their abundances groups 2 and 1 were positioned at the opposing ends of the function (Figs. 2 & 3). The linear model that made use of the second function as a predictor explained significantly the variation in the frequency of foraging by *B. augur* that varied by consistently increasing in magnitude from group 2 to 1 (Fig. 7). Unlike *S. albocaudata* that had comparable abundance levels at groups 1 and 3, the mean abundance of *A. bilicki* increased consistently along the gradient defined by the second latent variate. This suggested that the latter species may have had more to do with the pattern observed in the foraging response of *B. augur* that had significant positive linear relationship with the second factor.

As depicted in Fig. 8, the predictions of both the quadratic (r = 0.8, P = 0.002) and linear (r = 0.88, P < 0.001) models coincided highly with the observed values of the response variable about which they made very similar predictions (r = 0.95, P < 0.001). But the variability in the response variable explained by the second function that contained the smallest percentage of group difference (Field 2000) was larger. This suggested the prey species that were important relative to the second variate had more value in explaining the foraging response of *B. augur* spatially.

Our evaluation of the foraging utilization of patches as a function of spatial variability in prey abundance provided an insight for the first time regarding which prey species in the Afro-alpine habitats of the BMNP played important role in explaining food related behaviour of *B. augur*. The findings indicated that the foraging response of *B. augur* may be affected mainly by changes in the abundance of *A. bilicki* that may be its most preferred prey and the other key species may form the alternative prey base of the species.

The results in this paper also form a body of information that elaborately pointed towards expectations of future research that may intensively study aspects of *B. augur*'s ecology basing their premises on its dietary behaviour. As there is generally shortage of literature on the food habits of most species of animals in the world that is useful in describing and especially predicting their pattern of habitat use (Morrison et al. 1998, Rosenberg & Copper 1990), our work contributes significantly to the current body of knowledge and forms the baseline for any conservation initiative that particularly targets the species in the BMNP (Morrison et al. 1998, Ash et al. 1996).

REFERENCES

Ash, A., Coughenour, M., Fryxell, J., Getz, W., Hearne, J., Owen-Smith, N., Ward, D. and Laca, E.A. 1996. Second International foraging behaviour workshop. Bulletin of the Ecological Society of America 77: 36-38.

Bibby, J.C., Burgess, D.N. and Hill, A.D. 1992. Bird Census Techniques. Academic Press, London.

Clouet, M., Barrau, C. and Goar, J. 1999. The golden eagle (*Aquila chrysaestos*) in the Bale Mountains. J. Raptor Res., 33: 102-109.

Clouet, M., Barrau, C. and Goar, J. 2000. The diurnal Afro-alpine raptor community of the Ethiopian Bale highlands. Ostrich, 71: 380-384.

Field, A. 2000. Discovering Statistics. London, Andy Field.

Hall, L.S., Krausman, P.R. and Morrison, M.L. 1997. The habitat concept and a plea for standard terminology. Wildlife Society Bulletin, 25: 173-182.

Hutto, R. L. 1990. On measuring the variability of food resources. Studies in Avian Biology, 13: 20-28.

Krebs, C. J. 2000. Ecology. New York, Longmans.

Martin, P. and Bateson, P. 1993. Measuring Behaviour. 2d ed., Cambridge, Cambridge University Press.

Moen, A. N. 1973. Wildlife Ecology. San Francisco, W.H. Freeman

Morison, M. L., Marcot, B. G. and Manna, R. W. 1998. Wildlife-Habitat Relationship. Concepts and Applications. The University Wisconsin Press.

Ricklefs, E. R. 1990. Ecology. W. H. Freeman and Company, US.

Rosenverg, K. V. and Cooper, R.J. 1990. Approaches to avian diet analysis. Studies in Avian Biology, 13: 80-90.

Sillero, C.Z., Tattersal, F.H. and Macdonald, D.W. 1995. Bale Mountains rodent communities and their relevance to the Ethiopian wolf. Afr. J. Ecol., 33: 301-320.

Sillero, C.Z. and Gottelli, D. 1995. Spatial organization in the Ethiopian wolf *Canis simensis*. J. Zool., 237: 65-81.

Sutherland, W.J. 1996. From Individual Behaviour to Population Ecology. Oxford University Press, Oxford.

Wiens, A.J. 1989. The Ecology of Bird Communities. Cambridge University Press, Cambridge.

Yalden, W.D. and Largen, J.M. 1992. The endemic mammals of Ethiopia. Mamm. Rev., 22: 115-150.