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Methods of studying the distribution, diversity and abundance of birds in East Africa—some quantitative approaches

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Summary

In this paper we compare the use of transect counts with a simpler method of investigating bird diversity and numbers, particularly in terrestrial habitats, both natural and non-natural. Transect Counts (TCs) have long been widely used, whereas Timed Species Counts (TSCs), which estimate relative abundance, are comparatively untried. We find that TSCs give results which are comparable to those from TCs in most respects, except that they can only be used indirectly for estimating population densities, and they give different measures of diversity. However, TSCs generate data on many more species much faster than do TCs and are therefore more cost-effective in most situations. In particular, TSCs are useful for community studies. We show, for example, that in natural habitats bird populations are positively correlated with the amount of woody vegetation, but not with rainfall. Diversity too increases with woody vegetation. Because TSCs are simple, more of them can be made for a given input of time, and hence more distributional data are obtained as an additional benefit.

Key words: bird survey methods, diversity, Kenya, Uganda

Résumé

Nous comparons dans cet article l'emploi des comptages par transects avec un méthode plus simple examinant la diversité et les nombres d'oiseaux, particulèrement dans des habitats terrestres naturels ou non. Les Comptages par Transects (CTs) ont été largement utilisés depuis longtemps, alors que les Comptages par Points d'Ecoute (CPEs), qui estiment l'abondance relative, sont comparativement peu expérimentés. Nous trouvons que les CPEs donnent des résultats comparables à ceux des CTs à bien égards, à part le fait qu'ils ne peuvent être employés qu'indirectement pour estimer les densités de populations et qu'ils donnent des mesures différentes de la diversité. Cependant, les CPEs produisent plus rapidement des données sur beaucoup plus d'espèces par rapport aux CTs, et sont dès lors plus rentables dans la plupart des situations. Les CPEs sont particulièrement utiles pour les communautés d'espèces. Nous montrons, par exemple, que dans des habitats naturels les populations d'oiseaux sont en corrélation positive avec la quantité de végétation forestière. En raison de leur simplicité, on pourrait utiliser plus fréquemment les CPEs dans le cadre d'une investigation ponctuelle, ce qui fournirait comme bénéfice additionel d'avantage de données sur la distribution.

Introduction

It is often asserted that birds are convenient indicators of biodiversity, at least at larger scales (see, for example, ICBP, 1992) and that they are useful for monitoring environmental change (as discussed by Furness & Greenwood, 1993). One reason is that birds have long been popular with naturalists, amateur and professional, and consequently their systematics and distributions are better known than any other comparable group of animals, with the possible exception of the larger mammals.

The abundance of birds and the diversity of their communities are difficult things to measure. In this paper, we evaluate two methods of counting birds which have been widely used in East Africa: transects and timed species counts. Both methods apply primarily to bird communities rather than single species. We shall discuss only land birds, since census methods for water birds often differ; and water birds are the subject of several schemes of regular counts (see, for example, Dodman & Taylor, 1995). In contrast, there are relatively few data sets for land bird numbers in the African tropics; some were summarized by Pomeroy (1991). The acquisition of quantitative data presents many problems, yet such data are becoming more necessary, for example in allocating categories of threat to the rarer species (Mace & Stuart, 1994; Sisk *et al.*, 1994; Bennun & Njoroge, 1996).

Counts of birds at a series of sites provide information on distribution, which is perhaps less well-known for many East African species than is commonly supposed. Britton (1980) gave useful descriptions of the distributions of all birds on the East African list at that time, but most of the drier areas were poorly known and details for them were scant. Perlo (1995) gives maps for almost all East African species, but on a very small scale and often based upon inadequate data. The *Bird Atlas of Kenya* (Lewis & Pomeroy, 1989) mapped the distributions of 871 species in Kenya (there are about 200 more, but they had too few records to be worth mapping). However, at the time of publication, it was estimated that only 40% of the possible records had been obtained, despite the rather large size of the mapping units used (quarters of degree squares). Since then, additional records (Oyugi, 1994) have increased this to about 42%.

Both transects and timed species counts can yield data on distributions as well as abundance, but they differ considerably in the amount and types of data they produce in relation to the effort put into them. All quantitative methods are relatively time-consuming and cost-effectiveness is thus important.

Methods

Counts

The use of both transect counts (TCs) and Timed Species Counts (TSCs) in East Africa is described by Pomeroy (1992) and, in addition, TCs are discussed in considerable detail by Bibby *et al.* (1992). The latter authors consider that TCs are essentially estimating relative abundance, although they nevertheless lead to density estimates, usually expressed as birds per hectare or a multiple (such as pairs per 100 ha). In contrast, TSCs as used here yield only relative values for each species, on a scale of 0–6.

The TCs used for this paper were 20 or 40 m wide (wider in more open country) and 800–1000 m long, with from 8 to 55 counts of each (Tables 1 and 2). TSCs consist essentially of repeated species lists, on which are indicated the times when each species is first positively identified, by sight or sound. Those recorded within the first 10 minutes of each count are then scored 6, those in the next 10 minutes score 5 and so on to a score of 1 for minutes 51–60. Species with higher mean scores are therefore those observed most frequently: they tend to occur early within a count, as well as in a high proportion of counts.

We have assembled data from 13 sites in which natural vegetation predominates and for which both TC and TSC data exist, thus allowing the methods to be compared (Table 1). Most of these are savannas, ranging from semi-arid to moist, but because of their considerable interest, we have included data from one forest in western Uganda (Kibale), where densities were estimated both from transect counts and by mapping singing males (Dranzoa, 1995). Adjacent to this forest were other, formerly forested sites for which data are also available. Counts from these and several other non-natural sites form a second data set (Table 2). The two data sets include all cases known to us where both TCs and TSCs have been undertaken at the same site.

Diversity

The simplest and least controversial estimate of diversity is the number of species (S, species richness) in a defined area, such as a particular habitat (Magurran, 1988). Species richness can be estimated from TSC data in several ways. Two are discussed here—the mean number of species per one-hour count, and estimates of the total number of species.

The total species richness of a site can only be approximated by exhaustive data collection. Even then, 'new' species can be added after thousands of hours in the field. However, species richness can be extrapolated in various ways from the numbers actually recorded. We used two methods. The first, by regression analysis, is described in Pomeroy & Tengecho (1986; Figs 3 and 4), who also discuss alternatives. This method depends upon the numbers of 'new' species observed in successive counts, which typically decline progressively and are presumed to reach zero when all species have been recorded. A simple regression analysis of new species numbers against the logarithm of the cumulative species number allows the total to be estimated.

Alternatively, a non-parametric method can be applied. We used the first-order jackknife, as reviewed by Palmer (1990, 1991), treating each count as a sample. This leads to reasonable estimates provided that the number of counts is adequate: probably a safe minimum is 10.

All methods have weaknesses, but it is only big differences in species richness which are likely to be useful as indicators of conservation value. However, when considering conservation priorities, species richness should, wherever possible, be combined with other measures, such as the presence of rare or restricted range species (see, for example, Usher, 1986).

As a broader measure of species diversity, we have preferred α of the log series, for the reasons given by Magurran (1988). This could only be calculated from TCs.

Table 1. Data for natural and semi-natural habitats. Those marked with an asterisk are heavily grazed and/or browsed by domestic stock, but the vegetation retains most of its essential characteristics. Data from the authors except where indicated

Site	Code (Fig. 2)	Country^{a}	District	Habitat^{b}	Rain mm yr^{-1}	WV Σ%	Transect data *n*	Transect data birds ha^{-1}	Diversity α	TSC data *n*	TSC data $\bar{S}$
Olturot*	OL	K	Marsabit	W	200^{c}	35	16	16·4	9·0	8	26·8
Lake Turkana*	LA	K	Marsabit	(G)	200	2	—	1·0^{d}	—	4	5·7
Masalani	MS	K	Machakos	BW	450	145	30	26·2	14·5	35	22·8
Selengei*	SE	K	Kajiado	BW	550	65	14	14·6	6·4	20	23·1
Emali*	EM	K	Machakos	G	600	0	9	5·6	1·4	15	10·0
Ilkerin*	IL	K	Narok	S,t	750	38	8	15·2	10·1	15	26·2
Lake Mburo NP	LM	U	Mbarara	WB, t	800	42	13	12·7	9·6	15	27·2
Queen Elizabeth NP	Q1	U	Kasese	WB, t	850	35	5	10·5	9·6	15	27·3
	Q2	U	Kasese	B, t	850	18	8	6·9	9·6	12	23·2
Kasana Kasambya^{e}	KK	U	Mubende	WB, t	1050	48	10	17·4	21·1	10	41·5
Lusiba^{e}*	LU	U	Mubende	BG, t	1100	6	10	9·4	10·5	10	38·8
Matiri^{e}	MT	U	Kabarole	W, t	1250	193	10	9·9	9·8	10	35·5
Kibale Forest	KI	U	Kabarole	F	1400	184	54	19·3	10·3	55	35·0

WV=woody vegetation summed over four layers; α=measure of diversity in the log-series (Magurran 1988); $\bar{S}$=mean number of species recorded in one hour.
^{a}K–Kenya, U–Uganda; ^{b}B, bushland; G, grassland; S, shrubland; W, woodland; F, forest; the vegetation at the Lake Turkana site is very sparse; t=with thickets; ^{c}vegetation supported by ground water; ^{d}estimate; ^{e}T. Otim (1995).

Table 2. Data for non-natural habitats, either plantations or small-scale farming

Site	Country	District	Habitat[d]	Rain	WV	Transect data		Diversity	TSC data	
				mm yr^{-1}	Σ%	*n*	birds ha^{-1}	α	*n*	$\bar{S}$
Masalani—recent[a]	K	Machakos	DF	450	20[e]	30	22·5	7·5	30	26·2
—older[a]	K	Machakos	DF	450	15[e]	30	21·5	7·6	30	26·6
Kifu[b]	U	Mukono	MF	1250	35	26	14·2	4·9	26	20·7
Mpanga[b]	U	Mpigi	MF	1300	60	26	17·4	4·8	26	23·4
Ziika[b]	U	Mpigi	MF	1400	15	29	23·5	6·2	29	26·0
Kampala[b]	U	Kampala	MF	1200	32	22	23·6	7·1	22	31·2
Kanyawara[c]	U	Kabarole	PP	1400	132[f]	15	2·6	3·5	15	8·3
Kiko[c]	U	Kabarole	EP	1400	93[f]	15	24·0	9·1	15	21·1
Kanyawara[c]	U	Kabarole	MF	1400	25	15	14·8	7·6	15	24·3
Kanyawara[c]	U	Kabarole	TP	1400	92	10	2·8	4·0	10	10·1

Conventions as for Appendix 1.

[a] Recently cleared (less than 5 years prior to data-collection); cf 10–15 years for "older"; [b] These sites are all within 40 km of Kampala; data from Dranzoa (1990); [c] Sites adjacent to Kibale Forest; [d] DF–dry farming (predominantly maize) MF–moist farming (predominantly bananas, beans and cassava); EP, PP, TP–plantations of *Eucalyptus*, pines and tea; [e] Mainly native species; [f] About half native species (mainly undergrowth).

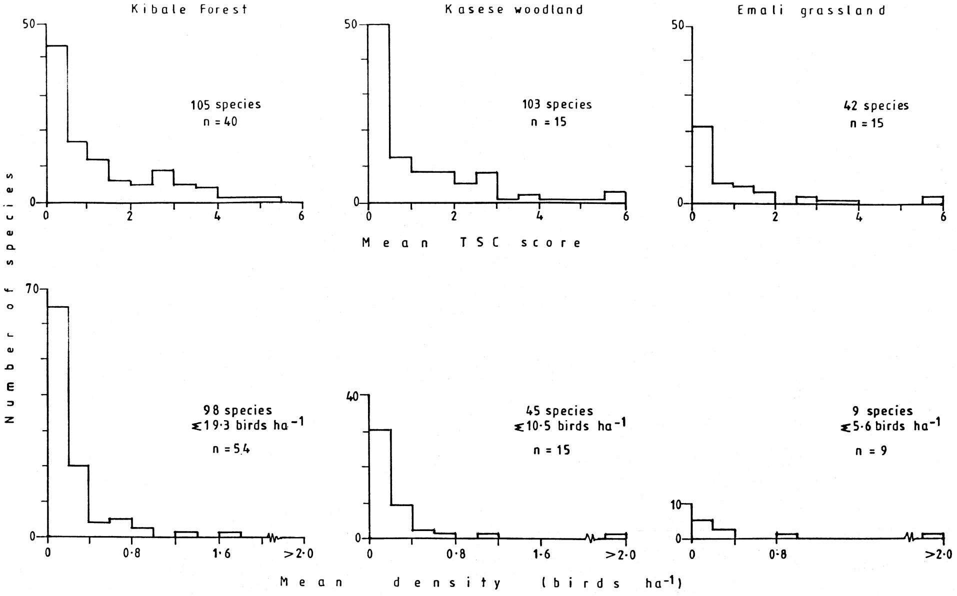

Fig. 1. The frequency distributions for bird abundance in three very different habitats as shown by TSC data (above) and TCs (below).

Habitats

The main characteristics of the study areas are given in Tables 1 and 2. Data for mean annual rainfall are mainly taken from the *Atlas of Kenya* (1970) and the *Atlas of Uganda* (1967). Pomeroy & Tengecho (1986) found a moisture index derived from rainfall to be a useful indicator of productivity but because it is more appropriate for dry areas, it has not been followed in this paper, which deals with both dry and moist areas.

The amounts of woody vegetation at each site are derived from estimated percentage values for each of four layers, averaged over 5–10 representative points at each site, and summed. The four layers are: 0–1, 1–3, 3–8 and >8 m.

Results

Communities

The results obtained from TSCs can be compared with those from TCs in various ways.

Frequency distributions of species abundance are similar for both TSCs and TCs, as seen in Fig. 1, which shows examples from three contrasting habitats. In all cases there are few common species and many uncommon ones. More than half of the species have densities in the lowest category, below 0·2 birds ha^{-1} whilst 2% or less exceed one bird ha^{-1}.

Data for the 13 natural sites in Kenya and Uganda with both TCs and TSCs are shown in Fig. 2, where only the average numbers of species per count are given for TSCs. Both measures show that bird numbers vary with rainfall and the amount and type of woody vegetation. Comparison of the two measures illustrated in Fig. 2 shows that where there are thickets, species richness tends to

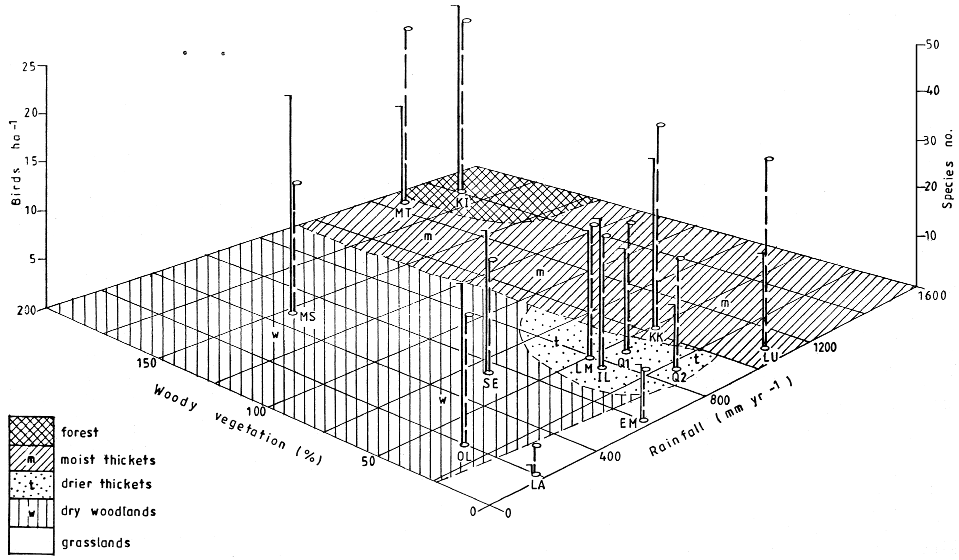

Fig. 2. Bird numbers in relation to rainfall and the amounts of woody vegetation at 13 natural sites. The solid vertical lines ('poles') present density estimates from transects, whilst the broken poles show mean species numbers from TSC scores. A broad classification of vegetation types is given on the base. Further data, including a key to sites, are in Table 1.

Table 3. Generalized patterns of bird populations in natural habitats of Kenya and Uganda. Based mainly upon data in this paper and in Pomeroy (1991)

Habitat	Rainfall range (mm y^{-1})	Density (birds ha^{-1})	Mean no. of species from TSCs	Notes
Grasslands	<500	1–5	5–10	Species-poor
Dry woodlands	2–500[a]	15–25	≈25	*Acacia tortilis* important
Dry thickets	7–900	5–15	≈25	Density increases with thickets
Moist thickets[b]	>1000	10–20	≈40	Very species-rich
Forest	⩾1000	<20 – >50[c]	≈35[d]	See text

[a]Sometimes dependent upon groundwater; [b]possibly originally forest (see text); [c]the higher figure is from Moyer (1993); lower densities appear to be characteristic of the interior of mature forests, where the figures may be underestimates; [d]probably an underestimate.

be highest—it is noticeable that the species pole is higher than that for density at six of the seven sites. The reverse is true in woodlands (where large flocks of only one or two species, such as some weavers and starlings, can occur). There are insufficient data for such comparisons in grasslands. These results are generalized in Table 3.

Bird densities are normally estimated from actual counts, such as TCs. But they can be predicted in various ways, for example from estimates of woody vegetation (Table 4). In natural habitats, bird densities correlated positively with the amounts of woody vegetation. The converse is true for non-natural habitats, where high levels of woody vegetation equate with plantations. Density can also

Table 4. Regression estimates of density, species numbers and diversity. Data from Tables 1 and 2

Predicted variable	Regression equation	Coefficient of correlation	df	P
Natural and semi-natural vegetation				
Density from woody vegetation	1·73+7·63 (log WV+1·0)	0·7362	11	<0·01
Density from species no.	—	0·4723	11	NS
Density from rainfall[a]	—	0·2223	10	NS
Species numbers from rainfall[a]	4·65+0·026 (rain)	0·8432	10	<0·001
Non-natural vegetation				
Density from woody vegetation	41·2–14·9 (log WV+1·0)	0·5683	8	<0·1
Density from species no.	1·02 ($\bar{S}$)–5·60	0·9083	8	<0·001
Density from rainfall	—	0·3941	8	NS
Species numbers from woody vegetation	51·1 − 17·9 (log WV+1·0)	0·7668	8	<0·01

WV=total woody vegetation (Σ%); rain=mean annual rainfall (mm y^{-1}); $\bar{S}$=mean species numbers from TSCs; df=degrees of freedom.

[a] Excluding Olturot, whose woodland is supported by ground water

be predicted from species numbers, obtained during TSCs, but the correlation is only significant for non-natural habitats. Surprisingly, density is poorly correlated with mean annual rainfall (unlike, for example, large mammals, Coe *et al.*, 1976).

Species numbers, however, are highly correlated with rainfall in natural habitats, and negatively with the amounts of woody vegetation in non-natural habitats (Table 4).

Values for species diversity from TCs varied considerably (Fig. 3). In the natural habitats, they were weakly correlated with the amount of woody vegetation but for non-natural habitats, the correlation is negative. In both types of habitat, one site stood out as being quite different from the others. Kasana Kasambya (KK in Fig. 3) is a vegetation formation described by Langdale-Brown *et al.* (1964) as moist *Acacia* savanna, and although it looks completely natural, they suggest that the area may once have supported forest or evergreen thicket; the present vegetation resulting from 'long-continued cutting, cultivation and burning' (page 56, *loc. cit.*). The exceptional site in the non-natural habitats is the Kiko *Eucalyptus* plantation (EP in Fig. 3). This is adjacent to natural forest and has dense undergrowth of predominantly natural vegetation.

Species

A study in western Uganda provides an excellent opportunity to compare abundance ratings from the two methods. Four contrasting sites adjacent to Kibale Forest have had TSCs and TCs conducted in them (D.E. Pomeroy,

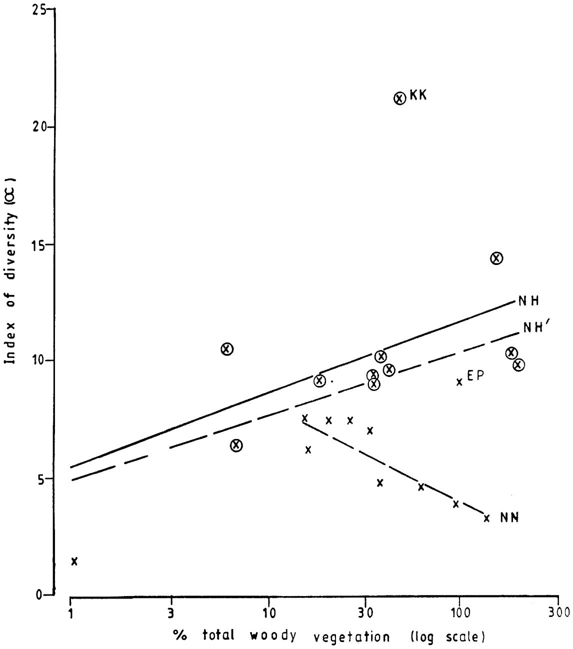

Fig. 3. Regressions of bird species diversity on woody vegetation cover: $\alpha=4{\cdot}40+3{\cdot}67$ (log. WV+1·0), $r=0{\cdot}5114$, $P<0{\cdot}1$ (line NH). The relationship is much stronger if data for Kasana Kasambya (KK) are excluded (see text), and then becomes $\alpha=3{\cdot}97+3{\cdot}33$ (log. WV+1·0), $r=0{\cdot}7027$, $P<0{\cdot}02$ (line NH'). In non-natural habitats, there is a negative correlation, at least where the woody cover is $\geq 15\%$: $\alpha=12{\cdot}45-4{\cdot}22$ (log WV+1·0), $r=0{\cdot}8709$, $P<0{\cdot}01$ (excluding EP, see text) (line NN). ⊗ Natural habitat; x Non-natural habitat.

Table 5. Values of the coefficient of correlation (r) between TSC and TC values for individual species in four formerly forested areas adjacent to Kibale Forest, and for the forest itself

Habitat	*n*	*r*	P	Regression equation
Natural forest	111	0·5980	⩽0·001	$0{\cdot}112\overline{T}-0{\cdot}029$
Eucalyptus plantation	87	0·8355	⩽0·001	$0{\cdot}368\overline{T}-0{\cdot}095$
Pine plantation	34	0·8503	⩽0·001	$0{\cdot}136\overline{T}-0{\cdot}048$
Smallholder farms*	77	0·7500	⩽0·001	$0{\cdot}227\overline{T}-0{\cdot}076$
Tea plantation*	28	0·7000	⩽0·001	$0{\cdot}120\overline{T}-0{\cdot}039$

n=number of species; $\overline{T}$=mean TSC score for each species; *excluding aerial species, which make up a significant part of the TSC scores, but are not included in TCs.

Note that the slopes of the regressions themselves positively correlated with the total population density of each of the non-natural habitats; $r^2=0{\cdot}9850$, $P<0{\cdot}05$.

unpubl.). Inside the natural forest, Dranzoa (1995) carried out TSCs and estimated population densities from TCs and by mapping singing males. The sites outside the forest were plantations of *Eucalyptus, Pinus* and tea, and smallholder cultivations. All had been forested previously.

Comparisons of TSC and density data over the five sites are given in Table 5, which shows that the densities of individual species can be estimated from

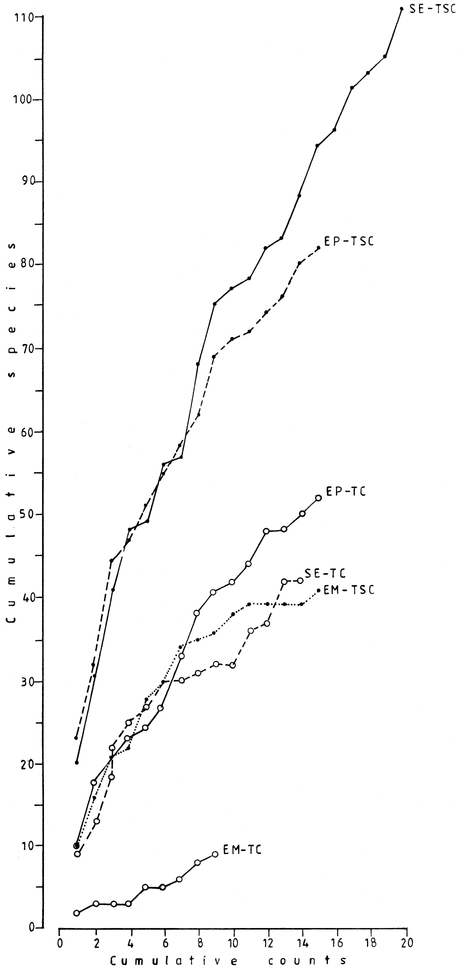

Fig. 4. Species accumulation curves for three contrasting sites, with TSC (small dot) and TC (open circle) data in each case. Selengei (SE) is a well-wooded savanna, Emali (EM) a natural grassland devoid of any woody vegetation, and the *Eucalyptus* plantation (EP) has a dense understorey, mainly of native shrubs and herbs. Estimates of total species numbers at these sites are given in Table 6.

their TSC scores. But because the regression constants vary widely, separate regressions are needed for each site.

Estimates of total species richness

Figure 4 shows species accumulation curves based upon TC and TSC data for three contrasting sites. The species accumulation rate during TCs is substantially lower and this is presumably why estimates of total species richness from TCs are much lower than from TSCs (Table 6). The more open the site, the poorer seems to be the estimate derived from transect data. Jackknife estimates were lower than those from regressions at TSC sites where species are more numerous. Although regressions themselves underestimate actual species numbers in most savanna ecosystems by 10% or so (Table 6; Pomeroy & Tengecho, 1986), they are nevertheless the better method for those habitats. Many forest species are difficult to detect, especially those of the understorey. It appears that neither of these methods is satisfactory for estimating species numbers in forests, both giving very low figures (Table 6).

Table 6. Estimates of total species numbers from representative sites by various methods. The TC data for Emali were too few to allow estimates to be made and those for Kibale Forest were unsuitable. Figures in the two final columns are given when extensive studies and opportunistic records over several years have reached the point where most (although probably still not quite all) recordable species (S) have, in fact, been recorded

		From TSC data by		From TC data by		Probable actual no. of species	Ratio:
	Habitat[b]	Jackknife	Regression (R)	Jackknife	Regression	(S)	R/S
Selengei[a]	BW	142	161	63	54	186	0·87
Emali[a]	G	56	53	—	—	—	—
Ilkerin[a]	S	147	159	56	58	—	—
Kasana—Kasambya[a]	WB	167	196	93	89	216[c]	0·91
Kibale Forest	F	135	131	—	—	218[d]	0·60
Kiko	EP	114	103	67	115	—	—

[a]Regression estimates for these savanna sites involved separating residents from other species, as described in Pomeroy & Tengecho (1986); [b]Key as in Table 1; [c]T Otim, 1995; D.E. Pomeroy (unpubl); [d]Dranzoa, 1994: forest species only.

Discussion

Choice of methods

Where the main purpose of counting birds is to estimate the population densities of particular species, the choice of method should be dependent upon the abundance of the species and the openness of its habitats. Transects can give reliable data for reasonably common species in relatively open habitats; for example, shrikes in bushed grasslands or doves in woodlands. However, they are less suitable for uncommon birds or in other habitats. Mapping singing males seems more likely than transect counts to give repeatable results in tropical forests (eg, Terborgh *et al.*, 1990; Moyer 1993). It also gives higher estimates of population density (Dranzoa 1995). Raptors, swamp birds and many others require specialized methods of counting.

Timed Species Counts have much wider applicability than transects, being suitable for bird communities in almost all habitats. Although they only estimate relative abundance, this is sufficient for many purposes, including those concerned with conservation. Their chief merit is that they yield data on more species and in less time than most traditional quantitative methods, thus giving substantially greater benefits for a given cost. Further, results from TSCs can also be used to estimate abundance and the frequencies of common and rare species (Fig. 1). However, because the scores obtained from TSCs reflect detectability as well as abundance, they cannot be used to compare even relative abundance of species which differ widely in their detectability.

Some measures of species diversity, such as α of the log series, require estimates of the numbers of both species and individuals. To the extent that α is a better measure of diversity than species richness, which is usually the case for smaller samples (Rosenzweig 1995), then TCs provide suitable data.

Using TSC data

Species richness, as the most widely used method for measuring diversity, can be assessed by TSCs either from species accumulation curves or from regression estimates. Patterns of species numbers and diversity can be determined satisfactorily from TSCs alone in many habitats. They can also be used to compare habitats, or subsets of species, such as forest specialists. Further, they generate records of uncommon species which rarely feature in TCs and can include aerial species which are impracticable to count in transects.

The data presented in this paper reveal several interesting patterns and trends. In natural habitats, species richness increases with rainfall, a trend also observed over a continental scale by Pomeroy & Lewis (1987). Diversity tends to be correlated with the amount of woody vegetation (Fig. 3) and the numbers of bird species and woody plant species are also correlated (Otim, 1995).

We would therefore predict that reducing the woody cover—deforestation—will lead to loss of bird species diversity. That would conform to the classic predictions of MacArthur & MacArthur (1961), since foliage height diversity obviously decreases with deforestation. However, not all researchers have confirmed this relationship (Weins, 1989) and in the case of our data set, the relationship is certainly not simple (see Fig. 3). Replacing natural woody vegetation with plantations of exotic trees is another form of habitat loss for forest birds, and has the same effect as deforestation. On the other hand, small-holder farms, despite having relatively few trees, support many more species.

Both $\bar{S}$ from TSCs, and α, from TCs, give good measures of diversity and indeed are quite closely correlated ($r_{10}=0{\cdot}7156$, $P<0{\cdot}01$ for natural habitats; $r_8=0{\cdot}6925$, $P<0{\cdot}05$ for non-natural habitats). Our site at Kasana Kasambya had a remarkably high value of α (Fig. 3) as well as the highest value of $\bar{S}$ (41·5) so far recorded from any site in East Africa (D.E. Pomeroy, unpubl. data). Although, as mentioned earlier, the present vegetation at KK is believed to be a result of human activity over long periods of time, all the plant species there are native to the area. A number of studies have found high species diversities in savannas (see, for example, Fry, 1983). But whilst the number of species in savannas may be high, few of them are rare, at least in the case of KK, where almost all are widespread species. This contrasts with forests, where many species are rare, even allowing for the difficulty of recording them (Thiollay, 1994; note also the low value of R/S in Table 6).

This brings us to our final point, the question of species *quality*—the notion that rare species, or those with restricted distributions, have higher conservation value than those which are common or widespread. Forest species provide an interesting example. Moderate amounts of forest degradation may increase species numbers (Dranzoa, 1995; Ulfstrand, 1994), but often by the invasion of generalists which are typically widespread species of low conservation significance. Forest specialist species are, as a group, species of limited distributions (Bennun *et al.* (in press)) and therefore include a high proportion of birds of conservation concern. TSCs are as efficient as TCs in demonstrating the absence of forest interior birds from altered habitats, and they record species much faster (Fig. 4).

Overall therefore TSCs are usually more suitable than TCs for bird survey work, especially in the field of conservation.

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