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Population density and habitat associations of restricted-range bird species at Ruhija, Bwindi Impenetrable Forest, Uganda

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Summary

Bwindi Impenetrable Forest, south-west Uganda, supports 24 of 37 restricted-range bird species of the Albertine Rift Mountains Endemic Bird Area (EBA). In common with other montane forest fragments in the EBA, Bwindi's structure and ecology have been substantially modified by human activities, the impact of which on its birds is difficult to gauge in the absence of quantitative information on their habitat use and abundance. During October 1999, habitat associations of nine restricted-range species and of 12 species with which they were commonly associated, were measured at Ruhija, Bwindi Impenetrable Forest. Logistic regression analysis was used to determine the relationship between habitat, topography, altitude and species occurrence. Population densities of 19 species were estimated using distance sampling, at survey points visited between dawn and midday. Although the detection rate declined during the morning, observations made towards midday helped to improve precision, without lowering density estimates. Eight habitat and topographical features significantly associated with restricted-range species are described. Few of the features measured were significantly associated with more than one species, underlining the importance of maintaining a diverse forest structure. Two restricted-range species were among the commonest birds in the study area, while a further four species were at least as abundant as their more widespread congeners.

Introduction

The Albertine Rift Mountains Endemic Bird Area (EBA) is the second richest in Africa, supporting 37 restricted-range bird species, of which 11 are globally threatened (Stattersfield *et al.* 1998, BirdLife International 2000). The EBA consists of a chain of mainly montane forest fragments running intermittently along both sides of the Rift, and covering a combined area of 56,000 km^2 (Stattersfield *et al.* 1998). Access to many of its constituent forests is limited by their remoteness and by political instability within the region (e.g. Kanyamibwa 2000). Consequently, a high proportion of the EBA's birds are poorly known, and there are few reliable estimates of their population densities. Recent visits to several of the less accessible fragments have shown that extensive forest areas do remain, but are subject to degradation and over-exploitation (Pederson 1997, Omari *et al.* 1999). Also, much of the remaining forest abuts onto land supporting high human population densities. In some parts of the Rift population densities have increased substantially with the arrival of refugees (Gatarabirwa *et al.* 2000), whose use of forest

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resources may be less sustainable than that of long-established communities (Oates 1999).

As a refuge to some 50% of the world's mountain gorilla *Gorilla gorilla beringei* population (McNeilage *et al.* 2001), Bwindi Impenetrable Forest, south-west Uganda, is relatively well protected. Following its designation as a National Park in 1991, its status was further strengthened in 1996 through the establishment of a Global Environment Facility trust fund, supporting community projects, park management, research and ecological monitoring (Hamilton *et al.* 2000). The park is, however, under continuing pressure from the surrounding human population, which averaged 220 people km^{-2} in 1991 (McNeilage *et al.* 2001). Pressures on the park have included pit-sawing, gold panning, hunting, pole cutting, bee-keeping and incursions by rebel groups (Harcourt 1980–81, Hamilton *et al.* 2000). All of these pose a threat to the forest's ecological integrity, its revenue-generating potential and its long-term prospects.

Twenty-four restricted-range bird species occur in Bwindi (Stattersfield *et al.* 1998). Although habitat associations of some of these species have been described (Bennun 1986, Butynski and Kalina 1989, 1993, Dowsett-Lemaire 1990), no quantitative assessment has been made of habitat preferences or population densities at Bwindi. Existing estimates have tended to rely on the assumption that all, or most, of the birds present were detected, and provide no indication of the level of statistical confidence associated with each estimate. In recent years distance sampling has emerged as an efficient, reliable approach to abundance estimation (Buckland *et al.* 1993), performing adequately in dense forest vegetation, where a high proportion of individuals may be missed (Jones *et al.* 1995, Marsden *et al.* 1997, Marsden 1999). This paper describes the habitat associations and population densities of restricted-range birds, and of species with which they are commonly associated, at Ruhija (Ruhizha), Bwindi Impenetrable Forest.

Study Area

Bwindi Impenetrable Forest is situated in Rukungiri, Kisoro and Kabale Districts of SW Uganda. It covers 331 km^2 and spans an altitude range of 1,160–2,607 m (McNeilage *et al.* 2001), in a continuum between lowland and montane forest (Keith 1980). The vegetation and topography of Bwindi Impenetrable Forest are described by Hamilton (1969), who identified several forest types on the basis of their topography. These included ridgetop, hilltop, hillslope, gully and valley-floor forest. In this study, ridgetop and hilltop forest have been combined into one category (''ridgetop''), as have hillslope and gully (into ''hillside'').

Observations were made within an area of approximately 8×8 km, at between 2,030 and 2,520 m altitude, in the vicinity of the Institute for Tropical Forest Conservation research station at Ruhija (29°46′E, 1°02′S), in the south-east of the Forest. Within the study area, ridgetop forest occurs mainly above 2,200 m, and much of the canopy reaches a height of 10–15 m. Ridgetop and hillside forest in the vicinity of Ruhija has been subject to intermittent logging, leaving gaps in which bracken predominates. Bamboo is evident above 2,330 m, and becomes dominant in a clearly defined zone above 2,420 m. Valley-floor forest occurs at about 2,000–2,200 m, where well-spaced mature trees reach a canopy height of

20–25 m (emergents to 30–35 m). Much of the valley-floor forest surveyed abuts onto Mubwindi, a large, permanent swamp.

Bwindi receives an average annual rainfall of 1,440 mm (Collar and Stuart 1988), most of it falling during October–December and February–April.

Methods

Fieldwork was carried out during 4–15 October 1999, coinciding with the beginning of one of the two main periods of bird breeding activity. The study also coincided with a periodic die-back of the widespread shrub *Mimulopsis*, rendering birds in the field-layer more conspicuous than usual.

Habitat associations of 21 insectivorous passerines and population densities of 19 of these were determined from observations made at 145 survey points. All encounters with these species were recorded for 10 minutes at each survey point, commencing at least two minutes after the observer's arrival at the point. Survey points at which a species was detected are referred to here as ''positive'' points for that species. All observations were made by PS, in dry, calm conditions, between 07h00 and 13h00.

Survey points were located at least 150 m apart, on or near to tracks and paths, and therefore constitute a non-random sample of the habitat. To reduce the level of bias inherent in this approach, alternate points were located at a perpendicular distance of 50 m from either side of the track or path (c.f. Marsden 1999).

Habitat associations

Habitat and topographical variables were recorded at each survey point (Table 1). Since most of the variables recorded were categorical, a logistic regression model was fitted to investigate their relationship with each species' presence or absence at survey points. The model was fitted using SYSTAT 7.0 (Steinberg and Colla 1997). Before fitting the model, categories with small sample sizes were combined with an adjoining category.

A forward, stepwise model was fitted. Variables were retained in the model if the probability associated with their alpha value was less than 0.10. Interactions between retained variables were then added to each model, and these interaction variables were retained or rejected according to the same criterion.

Density estimates

For each encounter, distance of the bird from the observer when first detected was recorded. Distances exceeding 18 m were measured using a Bushnell Lytespeed 400 rangefinder. Shorter distances were estimated or paced. Distances to birds that were only heard, or poorly seen, were estimated by measuring the distance to vegetation immediately in front of and behind the bird. Such detections were assigned to distance bands 5 or 10 m wide for birds less than 50 m from the observer, 10 m wide for distances of 50–100 m, and 20 m wide for distances exceeding 100 m. Distances were measured to each individual, rather than to the estimated centre of each group, except in cases where groups were poorly seen. Group size was then assumed to equal the average group size

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Table 1. Habitat and topographical variables recorded at 145 observation points during a survey at Ruhija, Bwindi Impenetrable Forest, Uganda, October 1999

Variable	Values		Percentage of survey points
Altitude	To the nearest 20 m.	> 2400 m:	28%
		2300–2399 m:	26%
		2200–2299 m:	19%
		< 2200 m:	26%
Forest type		Ridgetop (including hilltop):	62%
		Hillside (including gully):	21%
		Valley floor:	17%
Slope		Shallow (<30°):	33%
		Moderate (30–60°):	50%
		Steep (>60°):	17%
Vegetation	Sparse (<33%), moderate (33–66%), or dense (>66%), recorded at the following levels:		
	Canopy	Sparse:	37%
		Moderate:	44%
		Dense:	19%
	Understorey (>2–3 m)		
		Sparse:	28%
		Moderate:	44%
		Dense:	28%
	Upper field-layer 9< 2– 3)		
		Sparse:	12%
		Moderate:	25%
		Dense:	63%
	Lower field-layer (< 1 m)		
		Sparse:	3%
		Moderate:	9%
		Dense:	88%
Stream or swamp		Present (< 50 m):	9%
		Absent (> 50 m):	91%
Track or path		Point located on (motorable) track:	24%
		On footpath:	29%
		50 m from track or path:	47%
Bamboo		Absent:	81%
		Sparse:	3%
		Dominant:	15%

recorded for that species, based on casual observations. This method will have resulted in the true variance in group size being underestimated, but this is rarely a major component of the variance of the overall population estimate.

Analyses were made using DISTANCE V3.5, Release 5. All detections were grouped into intervals coinciding with one or more distance bands, and containing several detections per interval. Where excessive rounding of detection distances occurred, wider intervals were selected to dampen the effects of rounding.

The full range of models provided by DISTANCE was fitted in each case. Selection of the most appropriate detection function was based on the Akaike Information Criterion. The negative exponential model, regarded as a model of last resort, was only considered if goodness of fit tests suggested that no other model provided a satisfactory fit (Buckland *et al.* 1993). Data for batis *Batis*, tit *Parus* and sunbird *Nectarinia* species, for which sample sizes were small, were pooled with those of their congeners, and a detection function generated for each genus, rather than for each species.

Results

Timing and duration of observations

The mean number of detections made at each survey point declined from 5.6 during 07h00–10h00, to 4.2 during 10h00–13h00. As well as reducing the efficiency of fieldwork towards midday, this decline could, theoretically, have caused the shape of each species' detection function to vary over time, possibly increasing the variance around each estimate.

To investigate whether observations made during the late morning improved or reduced the precision of density estimates, a comparison was made of results obtained from all survey points, with those obtained from points visited up to and including 10h00. The comparison was limited to the six most frequently encountered species. In all cases confidence intervals were narrower when data from the full time period (07h00–13h00) were used. Although in one case the detection function had a smaller variance when only the earlier data were used, this was more than offset by the increased variance in the encounter rate, which is greatly affected by the number of points visited. Hence, based on small sample sizes, it would appear that additional detections made after 10h00, when the birds were less active, were easily sufficient to improve precision, without lowering density estimates.

On average, 43% of detections were made during the second half of each 10-minute observation period, and 8% of detections were made during each of the last two minutes. This indicates that a sizeable proportion of birds remained undetected for much of the observation period, or that new birds were continually moving into the area sampled.

Species recorded

Of the 22 restricted-range species occurring within the altitude range surveyed according to Kalina and Butynski (1996), five were not recorded during this study. One of these was African Green Broadbill *Pseudocalyptomena graueri*, with which PS is familiar. The others were Rwenzori Turaco *Musophaga johnstoni*, Rwenzori Nightjar *Caprimulgus ruwenzorii*, Neumann's Warbler *Hemitesia neumanni* and Purple-breasted Sunbird *Nectarinia purpureiventris*. Seven species seen only during casual observations were: Handsome Francolin *Francolinus nobilis* (at 2,080 m), Dwarf Honeyguide *Indicator pumilio* (c. 2,200 m), Red-throated Alethe

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Alethe poliophrys (2,300 m), Yellow-eyed Black Flycatcher *Melaenornis ardesiacus* (common near Mubwindi Swamp, at 2,080 m), Dusky Crimson-wing *Cryptospiza jacksoni* (2,080–2,300 m) and Shelley's Crimson-wing *Cryptospiza shelleyi* (2,520 m, in the bamboo zone). Grauer's Swamp Warbler *Bradypterus graueri* was present at Mubwindi Swamp (2,080 m), but, being a non-forest species, was excluded from the survey. Strange Weaver *Ploceus alienus* was encountered regularly during casual observations (at 2,070–2,430 m), but was detected at only four survey points, and was also excluded from the analysis.

Eight habitat and topographical features were recorded in association with the species surveyed (Table 2). The latter included nine restricted-range species, six of their congeners, and the distinctive, black-headed race of African Hill Babbler *Alcippe abyssinica atriceps*.

The most frequently encountered restricted-range species were Mountain-masked Apalis *Apalis personata* (88 detections) and Rwenzori Apalis *A. ruwenzorii* (78), whose densities exceeded those of their more widespread congeners (Table 3). Four other restricted-range species (Rwenzori Batis *Batis diops*, Stripe-breasted Tit *Parus fasciiventer*, Blue-headed Sunbird *Nectarinia alinae* and Regal Sunbird *N. regia*) were at least as common as their congeners.

Accounts of restricted-range species and their congeners

Archer's Robin-chat *Cossypha archeri*

Of those points at which Archer's Robin-chat was detected (''positive points''), 83% lay above the median altitude of all points surveyed (2,310 m). Logistic regression analysis indicated that Archer's Robin-chat was positively associated with bamboo, a sparse understorey, the absence of tracks and paths, and, as noted in Keith *et al.* (1992), the presence of a watercourse. The species' apparent preference for sparse understorey probably reflects the relative lack of understorey within bamboo thickets, given its association with dense understorey elsewhere (Dowsett-Lemaire 1990). Since Archer's Robin-chat was rarely seen, and difficult to locate accurately by song, no attempt was made to estimate detection distances, and hence population density.

Apalis species

Of six apalis species recorded at Bwindi, five occur within the altitudinal range of the study area. One of these, Grey Apalis *Apalis cinerea*, was not seen, and may be more prevalent at lower altitudes, as is the case in Nyungwe Forest, Rwanda (Dowsett-Lemaire 1990).

Mountain-masked Apalis, which feeds mainly in the understorey and upper field layer (Bennun 1986), was strongly associated with valley-floor forest. By contrast, Rwenzori Apalis, a field-layer specialist (Bennun 1986), was more often encountered in areas with a sparse understorey and in the bamboo zone. As suggested for Archer's Robin-chat, the apparent preference for a sparse understorey may reflect the lack of understorey in dense bamboo thickets. Other field-layer specialists present were Chubb's Cisticola *Cisticola chubbi*, associated with

Table 2. Habitat and topographical associations of species surveyed at Bwindi Impenetrable Forest, Uganda, October 1999

Species	Habitat associations	*P*	*n*	Altitude range (m)	% above median altitude
Yellow-rumped Tinkerbird *Pogoniulus bilineatus*	Track present Bamboo sparse or absent	<0.001 0.024	16	2,100–2,430	56%
Archer's Robin-chat ***Cossypha archeri***	Bamboo sparse or dominant Understorey sparse Track and path absent Watercourse or standing water nearby	<0.001 0.002 0.024 0.016	23	2,040–2,520	83%
African Hill Babbler *Alcippe abyssinica atriceps*	Slope moderate or steep Watercourse or standing water nearby Slope moderate or steep, with nearby watercourse	0.048 0.029 0.010	21	2,040–2,490	48%
Chubb's Cisticola *Cisticola chubbi*	Canopy sparse Bamboo sparse or absent Ridgetop	0.021 0.005 0.005	50	2,040–2,490	60%
Banded Prinia *Prinia bairdii*	Valley floor	0.002	48	2,030–2,520	54%
Rwenzori Apalis ***Apalis ruwenzorii***	Understorey sparse Bamboo sparse or dominant	0.016 0.045	62	2,040–2,520	52%
Mountain-masked Apalis ***A. personata***	Valley floor	0.010	65	2,040–2,520	46%
Black-throated Apalis *A. jacksoni*	Watercourse or standing water nearby Slope shallow Bamboo absent Canopy sparse or moderate	<0.001 <0.002 0.020 0.033	23	2,040–2,520	22%
Chestnut-throated Apalis *A. porphyrolaema*	Canopy moderate or dense Hillside or ridgetop Track absent	0.001 0.001 0.044	66	2,040–2,520	45%
Cinnamon Bracken Warbler *Bradypterus cinnamomeus*	Bamboo sparse or dominant Understorey sparse Upper field-layer dense Bamboo sparse/dominant, with sparse understorey	<0.001 0.003 0.007 0.001	21	2,040–2,510	90%
Grauer's Warbler ***Graueria vittata***	Slope steep Bamboo sparse or absent	0.004 0.012	31	2,040–2,490	65%
Red-faced Woodland Warbler ***Phylloscopus laetus***	No significant habitat or topographical associations	—	18	2,070–2,500	61%
Rwenzori Batis ***Batis diops***	Ridgetop Canopy moderate	0.040 0.042	11	2,220–2,520	64%
Chinspot Batis *B. molitor*	Hillside or valley floor	0.002	13	2,070–2,400	23%
Stripe-breasted Tit ***Parus fasciiventer***	Track or path present	0.005	12	2,080–2,520	33%
Dusky Tit *P. funereus*	Hillside or valley floor	0.004	5	2,080–2,250	0%

Table 2. *continued*

Species	Habitat associations	*P*	*n*	Altitude range (m)	% above median altitude
Blue-headed Sunbird ***Nectarinia alinae***	No significant habitat associations	—	6	2,090–2,490	50%
Regal Sunbird ***N. regia***	No significant habitat associations	—	16	2,060–2,520	50%
Collared Sunbird *N. collaris*	No significant habitat associations	—	21	2,080–2,420	43%
Northern Double-collared Sunbird *N. preussi*	No significant habitat associations	—	6	2,120–2,380	50%
Yellow White-eye *Zosterops senegalensis*	Canopy moderate or dense	0.044	38	2,040–2,500	55%

Variables are presented in the order in which they were selected in a logistic regression model. *n*, the number or points at which each species was recorded. The percentage of such points above the median altitude for all survey points (2,310 m) is shown. Restricted-range species are shown in bold.

Table 3. Population density estimates of species surveyed at Bwindi Impenetrable Forest, Uganda, October 1999

Species	Detections	Density (km^{-2})	95% CL
Yellow-rumped Tinkerbird	18	75.2	35.3–159.9
African Hill Babbler	22	39.5	23.5–66.2
Chubb's Cisticola	65	132.2	88.0–198.7
Banded Prinia	78	469.9	261.9–842.9
Rwenzori Apalis	78	271.0	168.9–434.7
Mountain-masked Apalis	88	372.5	209.7–661.7
Black-throated Apalis	27	19.4	9.8–38.4
Chestnut-throated Apalis	99	181.6	130.7–252.3
Cinnamon Bracken Warbler	28	79.7	50.4–126.2
Red-faced Woodland Warbler	19	59.5	30.3–116.7
Rwenzori Batis	15	55.3	36.5–83.8
Chinspot Batis	16	51.6	35.9–74.2
Stripe-breasted Tit	21	45.2	32.9–62.2
Dusky Tit	14	27.5	20.3–37.4
Blue-headed Sunbird	9	22.7	18.5–27.9
Regal Sunbird	27	61.5	44.2–85.7
Collared Sunbird	34	71.0	50.4–100.1
Northern Double-collared Sunbird	9	21.3	18.3–24.8
Yellow-White-eye	74	269.9	174.0–418.6

Restricted-range species are shown in bold.

open areas, particularly in ridgetop forest where bamboo was sparse or absent, and Banded Prinia *Prinia bairdii*, associated with valley-floor forest.

Bennun (1986) observed that two canopy specialists, Black-throated Apalis *A. jacksoni* and Chestnut-throated Apalis *A. porphyrolaema*, tended to occur in different forest types; Black-throated Apalis preferring valley-floor forest, and Chest-

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nut-throated Apalis occurring mainly on hillsides. This is partially borne out by the results of this study (Table 2); Black-throated Apalis was strongly associated with flat or shallow-sloping areas, near watercourses, below the bamboo zone, and with a sparse or moderate canopy cover. Such areas tend to occur in valleys, which are dominated by well-spaced, tall trees, with a more open canopy. At Nyungwe Forest, Black-throated Apalis occurred up to 2,500 m, but was outnumbered by Chestnut-throated Apalis above 2,150–2,200 m (Dowsett-Lemaire 1990). In this study the two species showed similar altitudinal trends; only 22% of positive points for Black-throated Apalis were above the median altitude (2,350 m), compared with 45% for Chestnut-throated Apalis. The latter was positively associated with hillside and ridgetop forest, with a moderate to dense canopy.

In Nyungwe Forest, Mountain-masked Apalis was ''probably the most numerous'' of six apalis species (Dowsett-Lemaire 1990). With an estimated density of 370 birds km^{-2}, it was also the commonest apalis at Ruhija, although confidence limits overlapped broadly with those of Rwenzori Apalis, and moderately with those of Chestnut-throated Apalis. Confidence limits for Rwenzori Apalis (169–435 birds km^{-2}), were similar to the density range estimated by Dowsett-Lemaire (1990) at Nyungwe Forest (200–400 birds km^{-2}).

Black-throated Apalis was the least abundant of the four apalis species at Ruhija, and of the six species at Nyungwe Forest (Dowsett-Lemaire 1990). Although its distinctive song carries further than that of Mountain-masked or Rwenzori Apalis, giving an impression of greater abundance, few Black-throated Apalis were detected close to survey points, and its estimated density was at least one order of magnitude lower than that of its congeners.

Grauer's Warbler *Graueria vittata*

Urban *et al.* (1997) quoted a maximum altitude of 2,300 m for Grauer's Warbler in Uganda, while Kalina and Butynski (1996) placed its upper limit between 2,150 and 2,459 m at Bwindi. In this study the species was recorded at up to 2,490 m, and 65% of positive points occurred above 2,310 m. The species was significantly associated with steeply sloping forest, in areas with little or no bamboo. Its distinctive call was heard at 21% of survey points, but is difficult to locate accurately. Hence, no attempt was made to estimate population density.

Red-faced Woodland Warbler *Phylloscopus laetus*

No significant habitat or topographical associations were selected in the logistic regression model. This species was one of the least abundant of the warblers, occurring at a density of 30–117 birds km^{-2}. It has a wide altitudinal range at Bwindi, and is a relatively unspecialized foliage gleaner, feeding at all levels (Dowsett-Lemaire 1990, Urban *et al.* 1997).

Batis species

Chinspot Batis *Batis molitor* and Rwenzori Batis tended to occur in different forest types; Chinspot Batis being significantly associated with hillside and valley forest, and Rwenzori Batis with ridgetop forest, moderate canopy cover, and a shallow to moderate slope. This is consistent with observations made by Dowsett-Lemaire (1990) at Nyungwe Forest, where ridges with closed forest were considered ''optimal'' habitat for Rwenzori Batis. Although Urban *et al.* (1997) quote an altitude range of 1,600–2,000 m for Rwenzori Batis in Uganda, the species was recorded at up to 2,520 m at Ruhija, and has been recorded at 2,426 m in nearby Echuya Forest Reserve (Gnoske and Marks 1997). Chinspot Batis was recorded up to 2,400 m at Ruhija, but was less common than its congener at this altitude; only 23% of positive points for Chinspot Batis were above 2,310 m, compared with 64% of those for Rwenzori Batis ($\chi^2_1 = 4.59$; $P = 0.03$).

Rwenzori Batis occurred at a broadly similar density (36–84 birds km^{-2}) to that attained in optimal habitat in Nyungwe Forest (40–60 birds km^{-2}; Dowsett Lemaire 1990). Confidence limits for Chinspot Batis (36–74 birds km^{-2}) were similar to that of its congener, and were consistent with an estimate for acacia veld (40 birds km^{-2}; Urban *et al.* 1997), but higher than that recorded in broadleaved woodland in the Transvaal (13 birds km^{-2}).

Tit species

Throughout much of their restricted range, Stripe-breasted Tits occur at higher altitudes than the more widespread Dusky Tit *P. funereus*, which is primarily a bird of lowland evergreen forest. In this study, Stripe-breasted Tits were recorded down to 2,080 m and Dusky Tits up to 2,250 m, indicating an overlap zone of at least 170 m. The zone is likely to be more extensive than this, however; Kalina and Butynski (1996) place the lower limit for Stripe-breasted Tits at Bwindi within the range 1,850–2,149 m, and the upper limit for Dusky Tits within 2,150–2,459 m. Also, Stripe-breasted Tits have been recorded down to 1,800 m in the Rwenzoris (Harrap and Quinn 1996) and to *c.* 1,900 m in Nyungwe (Dowsett-Lemaire 1990), where Dusky Tits occur at up to 2,500 m.

In keeping with their generally lower altitude range, Dusky Tits showed a significant association with hillside and valley-floor forest, and with moderate canopy cover. The only significant association shown by Stripe-breasted Tits was with tracks and paths; 8% of detections occurred at points 50 m into the forest, compared with 50% occurring on tracks (Fisher's exact: $P = 0.012$) and 42% on paths (Fisher's exact: $P = 0.017$). This finding is consistent with the observation that the species rarely penetrates closed forest (Dowsett-Lemaire 1990), even though the effects of footpaths on forest structure appear negligible. Alternative explanations are that Stripe-breasted Tits were less easily detected in closed forest, or were disturbed by the observers' approach through dense vegetation. Neither explanation seems likely, however, as the species has a distinctive contact call (Shaw in press), and is normally fairly approachable.

Stripe-breasted Tits are said to be ''generally common, even locally abundant'' in south-west Uganda (Harrap and Quinn 1996). Within the study area they occurred at a density of 33–62 birds km^{-2}, substantially higher than that attained by six woodland tit species in Africa, for which density estimates range from 1 bird km^{-2} (Southern Black Tit *Parus niger*), to 21 km^{-2} (Rufous-bellied Tit *Parus rufiventris*; Alerstam and Ulfstrand 1977). The population density of the Dusky Tit (20–37 birds km^{-2}) was also higher than that of most African woodland tits, but similar to that recorded in lowland forest in Gabon (25–30 birds km^{-2}; Brosset and Erard 1986).

Sunbird species

None of the four sunbird species surveyed was significantly associated with the variables measured, suggesting that their distributions were influenced by more subtle factors. These may include the availability of nectar, as at Nyungwe Forest (Dowsett-Lemaire 1990). Population estimates, obtained by pooling the four species' data to generate a single detection function, indicate that Collared Sunbird *Nectarinia collaris* and Regal Sunbird were approximately three times as abundant as Blue-headed and Northern Doubled-collared Sunbirds *N. preussi* (Table 3). This is consistent with Dowsett-Lemaire's (1990) observation that above 2,200–2,250 m in Nyungwe Forest, Regal Sunbirds were more abundant than Northern Double-collared Sunbirds, considered their most likely ecological competitor.

Discussion

A knowledge of the habitat requirements and population densities of restricted-range birds is a prerequisite for the effective management of key sites within an EBA. However, the general applicability of results presented here is difficult to gauge. Although some of the species–habitat associations described are likely to arise elsewhere, others may be unique to the particular range of conditions sampled at Bwindi.

Collectively, the nine restricted-range species surveyed were associated with a diverse range of micro-habitats and topographical features, none of which emerged as being important for more than one or two species. Important features were: presence of bamboo, streams, moderate canopy cover, a sparse understorey, openings created by tracks or paths, forest cover on ridgetops, steep slopes and valley floor (Table 2). Conversely, some restricted-range species preferred areas from which bamboo, tracks or paths were absent. Faced with these varied requirements, the safest management prescription would be to avoid activities that place pressure on any of these features, and to maintain as rich a mosaic of micro-habitats over as wide an area as possible.

Prior to its designation as a national park, much of Bwindi was subject to selective, manual logging, which has probably influenced the abundance and distribution of the study species. Harcourt (1980–81) estimated that there were 60–65 pitsaws in operation in 1979, affecting 41% of his survey area. Selective logging usually requires the cutting of paths and tracks. More importantly, it has been shown to significantly reduce canopy cover, even at low levels of timber extraction (Struhsaker 1997), leading to an increased growth in the understorey (Harcourt 1980–81). Such changes can have marked affects on forest birds (e.g. Dranzoa 1998). In this study, the distributions of five species (Yellow-rumped Tinkerbird, Black-throated Apalis, Chubb's Cisticola, Cinnamon Bracken Warbler and Stripe-breasted Tit) were positively correlated with features commonly associated with selective logging, suggesting that they may prove more tolerant of low levels of disturbance. Conversely, four species (Archer's Robin-chat, Rwenzori Apalis, Chestnut-throated Apalis and Yellow White-eye) were associated with a dense canopy, a sparse understorey, or the absence of paths, and hence may prove more sensitive to disturbance caused by selective logging. Note, however, that the apparent preference for sparse understorey shown by Archer's Robin-chat and Rwenzori Apalis, probably reflects the relative lack of understorey in bamboo thickets, with which they were positively associated.

The successful application of distance sampling depends on several key assumptions being met (Buckland *et al.* 1993). These include the requirement that the distance between the observer and the bird is measured accurately, particularly when using point transects (Buckland *et al.* 1993). In this study, inaccuracies were minimized through the use of an electronic rangefinder, and by allocating detections to distance bands. A second assumption is that each bird is detected before it makes any movement in response to the observer. This assumption seems likely to have been met on most occasions, but is particularly difficult to ascertain in dense forest undergrowth.

A third assumption is that survey points are located independently of features influencing bird density (Buckland *et al.* 1993). In this study, time and logistical constraints precluded the adoption of a random or grid-based sampling pattern. The placing of alternate survey points some 50 m off-track was therefore a compromise, likely to have eliminated some, but not all of the bias associated with man-made tracks and paths.

In distance sampling it is also assumed that all birds present at zero distance from the observer (i.e. overhead) are detected. In tall, dense vegetation the likelihood of failing to detect birds close to the observer would seem greater than in more open habitats, but may have been partly offset here by the prevailing calm conditions, facilitating species detection, by the adoption of point rather than line transects (e.g. Marsden 1999), and by the length of each survey period. On average, 8% of detections were made during each of the last two minutes of the 10-minute survey period, indicating that a high proportion of birds had remained undetected up to that point, or that new birds were continually moving into the area sampled. Although the former scenario should not have affected the density estimate obtained, the latter would tend to lead to an overestimation of population density.

Field observations for this study were collected over a relatively short period, and were frequently curtailed by rain. In many bird surveys fieldwork is further restricted to those periods in which the study species are most active; typically during the first few hours after sunrise and the last few hours before sunset. In this survey, the detection rate declined between 07h00 and 13h00. Results from a small sample of species and points, however, suggest that observations made during the late morning, when birds were less active, helped to improve precision, without lowering density estimates. Provided that all birds at, or close to the point continue to be detected, distance sampling need not, therefore, be limited to early and late periods, thus extending the time available for survey work during brief visits to remote areas.

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