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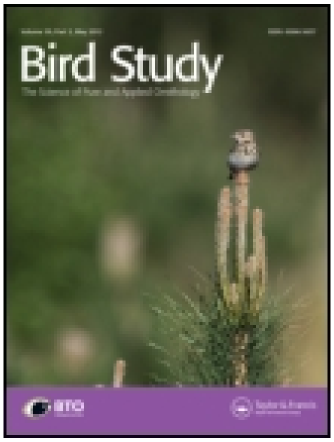

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Avian foraging behaviour in relation to provision of ecosystem services in a highland East African agroecosystem

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Capsule Most birds in a Kenyan highland agroecosystem foraged from the ground, potentially contributing to weed regulation, and invertebrate intake rates by aerial foraging insectivores were high, indicating that birds could contribute to pest regulation.

Aims Bird foraging behaviour and its implications for provision of ecosystem services and crop damage was investigated.

Methods Detailed observations of foraging birds in relation to substrates used and food items consumed were undertaken within cultivated areas during dry and wet seasons.

Results Most birds foraged from the ground, often consuming seeds, fruits and flowers from weeds rather than crop plants. The relatively high rate of invertebrate intake by two aerial foraging species and the high number of insectivorous bird species recorded in the area suggest that invertebrate predation could also be high and potentially contribute to pest regulation. Species-specific differences in the habitats birds used and prey taken were also identified, providing an indication of species likely to contribute to invertebrate and weed pest control and those likely to cause crop damage.

Conclusion The results describe species-specific avian foraging behaviour in African farmland that may be used in informing agricultural management practices to enhance beneficial species and reduce impacts of crop-damaging ones.

The importance and value of biodiversity (species and habitats) in providing key ecosystem services is increasingly recognized (Swift *et al.* 2004, Balvanera *et al.* 2006, Mertz *et al.* 2007). This is particularly well-developed in relation to carbon storage and sequestration and water provision (Daily *et al.* 2000, Heal 2000, Balmford *et al.* 2002, Chan *et al.* 2006, Naidoo *et al.* 2008, Fisher *et al.* 2009). Individual species and species groups, however, can also provide important functions: for example, in habitat restoration, seed dispersal and pest control and pollination. Realizing the value of these species requires quantitative information on distribution, ecology and behaviour (Luck *et al.* 2003, Kremen 2005, Kremen *et al.* 2007, Zhang *et al.* 2007, Whelan *et al.* 2008).

Foraging birds can cause crop damage in agricultural landscapes, but their foraging may also be beneficial in terms of controlling insect pests and weed seed germinations (Wenny *et al.* 2011). Indeed, many avian ecosystem services and functions are a consequence of their consumption of resources (Whelan *et al.* 2008) and understanding how birds forage in different habitats has implications, for example, for habitat conservation and management (Gomes *et al.* 2008). Understanding the foraging behaviour of birds that are natural enemies of pests and weeds could be useful in determining ways of promoting natural pest and weed predators on farms in order to augment non-chemical crop-protection measures. This understanding will both enhance production and conserve birds in agricultural

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landscapes and is especially important in developing countries where access to expensive chemical control may be difficult. In fact, as members of ecosystems, birds play multiple roles and can act as predators, pollinators, scavengers, seed dispersers, seed predators and ecosystem engineers (Sekercioglu 2006). Their preference for certain foraging microhabitats generally determines what type of food is eaten (Gomes *et al.* 2008) and hence the service they may provide. In the case of crop-damaging birds, knowledge of their foraging behaviour could be used to develop more effective damage-mitigation strategies (Herrmann & Anderson 2007).

Nyandarua County is one of the most agriculturally productive administrative regions in Kenya, and it is also rich in bird diversity. Prior to the 1960s it was covered by extensive highland forests and native grasslands, but now over 60% of the area is covered by cultivated farmland. Although there is still high abundance and diversity of birds and other wild taxa in the agricultural landscape, the continued survival of these wild fauna is partly dependent on how farmers perceive the roles they play in the agricultural landscape, especially within productive areas.

The main objective of this study is to provide knowledge of bird foraging behaviour in relation to provision of ecosystem services, in the cultivated areas of Nyandarua. Specifically, the study investigates: (a) the extent to which birds utilize different substrates and food items for foraging, (b) seasonal differences in use of different substrates and food items and (c) the potential contribution of foraging behaviour of common bird species for weed control, crop pest control and crop damage. The information gathered may then enhance the understanding of bird foraging behaviour in farmlands with potential implications for sustainable agriculture and bird conservation in eastern Africa.

METHODS

Study area

The study was conducted in Nyandarua County (0°08′N–0°50′S, 35°13′E–36°42′E) of Central Kenya, East Africa (Fig. 1). Nyandarua County extends over an area of 3528 km^2 (0.6% of the Kenyan land area; Republic of Kenya 1997). Annual rainfall varies between 750 and 1500 mm mainly between March and May (long rains) and again between August and November (short rains). However, in recent years the rainfall pattern has been unpredictable and during the two study years there was no clear break between the long and short rains. The human population density is about 184 people km^{-2}, with a rural density of about 169 and a higher urban one of about 288 people km^{-2} (Kenya National Bureau of Statistics 2010). The main food crops grown in the district are potatoes *Solanum tuberosum*, cabbages *Brassica oleracea* L. var. *capitata*, kales *B. o. acephala*, peas *Pisum sativum*, maize *Zea mays*, beans *Phaseolus vulgaris* L., onions *Allium cepa*, carrots *Daucus carota* and fruits (apples *Malus domestica*, pears *Pyrus* spp. and plums *Prunus salicina*), while cash crops include pyrethrum *Chrysanthemum cinerariaefolium*, wheat *Triticum aestivum* and cut flowers. Livestock production (dairy cattle, sheep, goats and poultry) is widespread in the district.

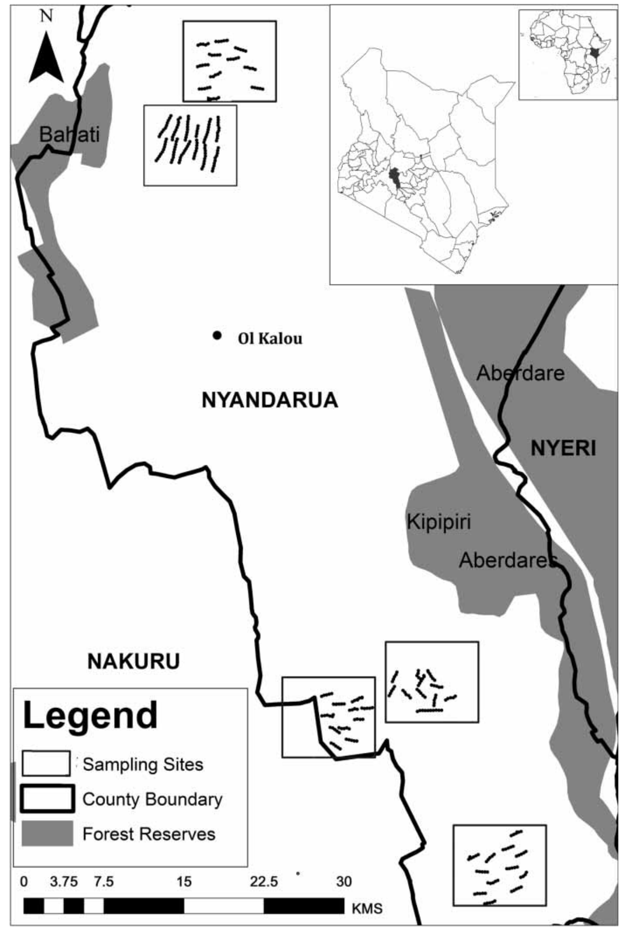

Figure 1. Map of study area In Nyandarua County, the two 5 × 5 km study sites in the North and the three 5 × 5 km study sites in South subdistrict (large boxes) and the five 30-m radius sampling points on each transect (small filled circles).

Pre-1960s, the landscape was almost entirely covered by grassland or forests. Today, native grassland patches, of varying sizes, and indigenous trees are still found in these agricultural landscapes, but 60% of the area is now cultivated farmland. Despite this land use change, the Kinangop Plateau (about 77 000 ha), a largely agricultural area in Nyandarua, is also internationally recognized as an Important Bird Area (IBA) due to the birds inhabiting the grasslands (Bennun & Njoroge 1999).

Apart from the current land use, it is possible that the historical vegetation types affect current bird composition. In areas previously covered by forest, non-crop vegetation is often now dominated by indigenous trees and bushes, whereas in areas originally covered by grassland, non-cropped areas are dominated by grasslands and exotic trees (pers. obs.). Study sites were therefore located in areas that were representative of these two main original vegetation types: Nyandarua South subdistrict, originally covered by highland grasslands and Nyandarua North subdistrict, originally covered by highland forest. Hereafter the two subdistricts are referred to as 'South' and 'North', respectively.

Study design

Within each of the two subdistricts, 5 × 5 km study sites (two in the North and three in the South) were selected from a map to represent varying human population densities (Fig. 1). Within each subdistrict, survey routes were positioned, 1–2 km apart, along access roads or paths. Sets of five 30-m radius plots were located along a transect perpendicular to these routes. The plots were 250 m apart while the transects were 1 km apart and extended from one or both sides of the survey routes. Only plots dominated by cultivation or fallow (> 50%) were selected for bird observations during each of the seasons.

Foraging observations

Foraging observations were conducted during two wet and two dry seasons between June 2010 and April 2012 at randomly located 30-m radius plots (Table 1). Foraging observations were undertaken between dawn and 1100 h, avoiding days of high winds or heavy rains. Each foraging observation session was 0.5 h long and conducted using binoculars (8 × 42) and a telescope (magnification 19–60× zoom) to locate and then make detailed observations of foraging birds following methods modified from Remsen & Robinson (1990). When a foraging bird was seen, its identity (species), foraging substrate and food type (when confirmed) and, where appropriate and possible, the number of foraging birds in a flock, was recorded. To avoid pseudoreplication/double counting, only the first sighting of each bird was recorded. Substrates from which food was taken were categorized as: air, ground, crop plant (including fruit trees), weed plant or tree. At a broader level, food type was recorded as: crop part, weed part, nectar, invertebrate, vertebrate or unconfirmed. More detailed food type recording was done for weed and crop plant parts as: fruit/seed/flower, vegetative (leaf/stem), and nectar. The number of foraging bouts was also recorded for birds that used sallying as a foraging strategy to catch invertebrates.

Table 1. Number of 0.5 h foraging observation sessions undertaken at the North and South subdistricts during wet and dry seasons. Observations were restricted to 30-me radius plots covered by > 50% cultivation or fallow during each season, and because this varied seasonally, the number of suitable plots also varied between seasons.

	Subdistrict	
	Nyandarua South	Nyandarua North
Original vegetation type	Grassland	Forest
Timing (season)		
Jun–Sep 2010 (Wet)	53	43
Nov 2010–Feb 2011 (Dry)	61	57
Jun–Sep 2011 (Wet)	57	21
Feb–Apr 2012 (Dry)	60	60

Data analysis

Each of the bird species observed was placed into one of seven foraging guilds based on descriptions of major food items taken by each species (Hockey *et al.* 2005, Kissling *et al.* 2007) and the classifications used in Gray *et al.* (2007). The seven groups were: carnivores (vertebrates), frugivores, granivores, herbivores (vegetable material, e.g. leaves, shoots, roots, flowers and bulbs), insectivores (insects and other invertebrates), nectarivores (nectar) and omnivores (more than one major food item composing of both plant and animal materials). Birds that were not feeding on aerial invertebrates while flying over the observation plots were excluded, as were three outliers caused by large flocks (200, 80 and 60 individuals) of Red-billed Quelea *Quelea quelea* and Jackson's Widowbird *Euplectes jacksoni*. Most observations were of small flocks or were of a few individuals. Data were analysed using R statistical software (R Development Core Team 2012).

Use of foraging substrates

The proportion (%) of the total overall numbers of individual birds and diet-based groups observed foraging on each substrates were calculated to describe the broad patterns of relative use of substrates. A Generalized Linear Model (GLM) with Poisson distribution and a log link (Crawley 2007, Zuur *et al.* 2009) was used to test for effects of substrate types (air, crop, weed or ground), subdistrict (North or South), season (dry versus wet), and the interaction between these factors on numbers of birds foraging in a plot per 0.5 h observation session (foraging birds/session). As overdispersion was detected, the standard errors were corrected using a quasi-GLM model to compensate for overdispersion (Crawley 2007, Zuur *et al.* 2009). Because AIC is not defined in quasi-Poisson GLMs, model selection was done using a hypothesis-testing approach (*F* test) that drops one term in turn (Zuur *et al.* 2009). In this case all explanatory variables were significant at 5% and thus no term was dropped. Between groups comparisons were undertaken by applying Tukey HSD post-hoc test to determine significant (at $P < 0.05$) main effects of substrate type, subdistrict and season.

Use of food items

The proportion (%) of the total number of individual birds of all species confirmed to be taking particular food types from particular substrates was calculated to describe the broad patterns of food item use. Poisson GLMs (as described in above) were used to evaluate the effects of food type, subdistrict and season on numbers of foraging birds. Again, overdispersion was detected and the standard errors were corrected using a quasi-GLM model to compensate for overdispersion and all explanatory variables were significant at 5% and thus no term was dropped. Significant main effects of food type, subdistrict and season were determined by applying Tukey HSD post-hoc tests.

Use of substrate and food items by particular bird species

The importance of particular bird species in terms of their use of different substrates and consumption of different food items was assessed for the most common species (those observed in ≥ 30 observation sessions) and expressed as proportions (%) of total number of observations throughout the study period. This was used as an index to identify species that were particularly important in terms of consumption of weed, crop and invertebrate food types. Analysis of frequency of sallying bouts for invertebrates was only undertaken for Common Fiscal *Lanius collaris* and Common Stonechat *Saxicola torquatus* because these were the species most frequently seen using this foraging strategy.

RESULTS

A total of 5738 individual foraging birds of 82 species were recorded during 233.5 h (467 × 0.5-h sessions) of foraging observations. Of these, 3454 individuals of 60 species were observed in the South subdistrict within 130.5 h, while 2284 individuals of 50 species were observed in the North subdistrict within 103 h. The largest foraging guild was Insectivores, with 32 species. Others were granivores (19), omnivores (13), carnivores (9), nectarivores (5) and frugivores (3).

Use of substrates

Significant differences were observed in the number of birds foraging in different substrates (Table 2). Most birds (54% across both subdistricts) foraged on the ground compared with 24% on crop plants, 17% on weed plants and 4% in the air (sallying or hawking). For 1% of the observations the substrate was unrecorded (Fig. 2). Most of the ground-foraging birds were granivores with the remainder being composed of insectivores and omnivores in almost equal proportions. Species foraging on crop plants were mostly composed of omnivores and granivores to a lesser extent, whereas those feeding on weed plants were almost exclusively granivores (Fig. 3). All birds that took food from the air were insectivores. In the South subdistrict significantly higher numbers of birds foraged from weeds and crops than in the North, whereas in the North subdistrict, significantly more birds foraged from the ground (Table 2).

Food items taken

In terms of overall proportion of all individual birds observed ($n = 5738$) taking different food items (both

Table 2. General linear model of the effects of substrate type (Crop, Ground, Weed or Air), subdistrict (North versus South) and season (Wet versus Dry) on the number of birds foraging from different substrate types. Model: Number of birds per plot = Substrate type + Season + Subdistrict + (Substrate type ×Season) + (Substrate type × Subdistrict) + (Season × Subdistrict), family = quasipoisson (log); (n = 1600 observations made during 400 half-hour long sessions – substrate was not indicated by observer for 67 of 467 sessions in the study).

Parameters	Coefficients	SE	*t* value	*P**	Interpretation**
(Intercept)	−1.6	0.6	−2.6	**0.009**	
Substrate[Crop]	2.2	0.6	3.5	**< 0.001**	Crop > Air
Substrate[Ground]	4.0	0.6	6.5	**< 0.001**	Ground > Air; Crop; Weed
Substrate[Weed]	1.7	0.7	2.7	**0.007**	Weed > Air
Season[Wet]	−1.2	0.5	−2.6	**0.011**	Dry > Wet
Subdistrict[South]	1.8	0.6	2.8	**0.005**	South > North
Substrate[Crop]:Season[Wet]	1.4	0.5	3.0	**0.002**	Crop [Wet] > Crop [Dry]
Substrate[Ground]:Season[Wet]	0.2	0.5	0.4	0.679	
Substrate[Weed]:Season[Wet]	1.5	0.5	3.1	**0.002**	Weed [Wet] > Weed [Dry]
Substrate[Crop]:Subdistrict[South]	−1.5	0.7	−2.2	**0.027**	Crop [South] > Crop [North]
Substrate[Ground]:Subdistrict[South]	−2.4	0.7	−3.6	**< 0.001**	Ground [North] > Ground [South]
Substrate[Weed]:Subdistrict[South]	−1.4	0.7	−2.0	**0.044**	Weed [South] > Weed [North]
Season[Wet]:Subdistrict[South]	0.6	0.2	2.7	**0.007**	Dry [North] > Wet [North]

*Significant *P*-values are in bold.
**Between-groups comparisons were determined by applying Tukey HSD post-hoc test; only significant differences ($P < 0.05$) are shown.
Null deviance: 12204.7 on 1599 degrees of freedom.
Residual deviance: 8543.5 on 1587 degrees of freedom.

subdistricts combined), 43% of birds took seeds, fruits or flowers, 12% took invertebrates, 1% vegetative parts (stems or leaves), 1% took nectar. Food items taken by 43% of the birds observed could not be confirmed. Only six individuals of three species (Black-shouldered Kite *Elanus axillaris*, Black-headed Heron *Ardea melanocephala* and White Stork *Ciconia ciconia*) were seen taking vertebrates (small mammals, amphibians and reptiles). Significantly more birds were taking seeds/fruits/flowers than any other food items observed whereas significantly fewer birds were taking nectar (Table 3, Fig. 2). Significantly higher numbers of birds

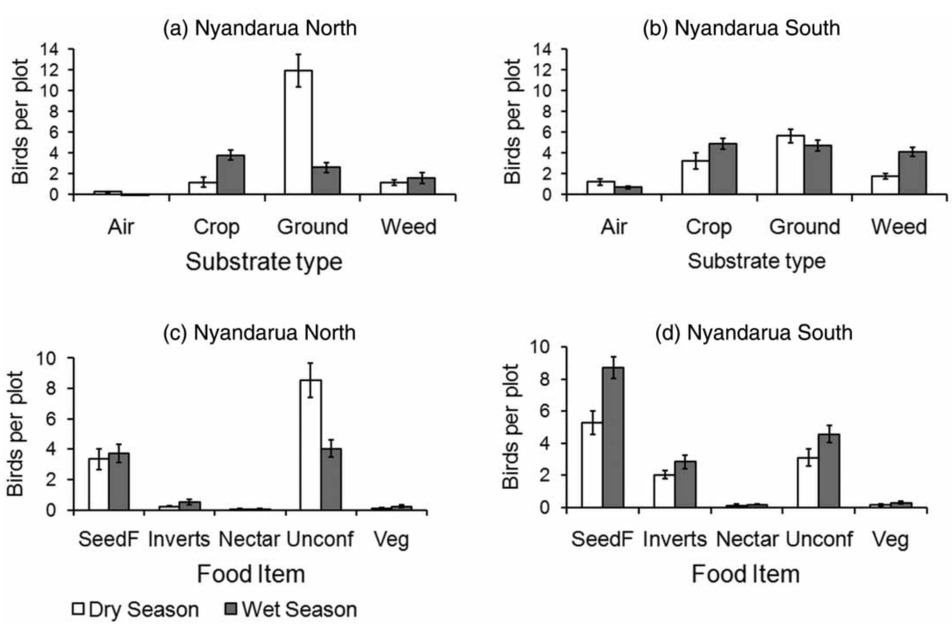

Figure 2. Mean number of birds per plot (± se) foraging on (a, b) different substrate types and (c, d) food item types during wet and dry seasons in Nyandarua North (a & c) and Nyandarua South (b & d) subdistricts. Inverts, invertebrates; Veg, Vegetative (leaves and stems); SeedF, seeds, fruits and flowers; Unconf, unconfirmed.

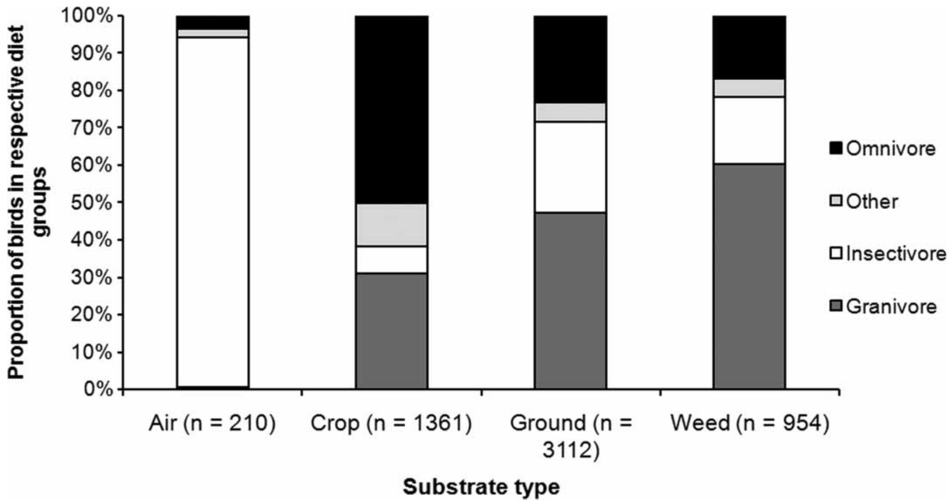

Figure 3. The percentage of birds from the four different diet-based groupings observed foraging on different substrates. Carnivore, frugivore and nectarivore observations were few and are grouped together as 'Other'.

were confirmed to be taking seeds/fruits/flowers in the South subdistrict compared to the North, although significantly more food items were unconfirmed in the latter sub-district (Table 3, Fig. 2). Almost all food items taken aerially were invertebrates (92% confirmed, $n = 210$), whereas most food items taken from crop (81%, $n = 1361$) and weed plants (80%, $n = 954$) were seeds, flowers or fruits. Among ground-foraging birds, it was impossible to confirm the identity of most food items (68% of observations) but when it was confirmed it comprised largely of seeds and invertebrates (19% and 12%, respectively, $n = 3112$).

Effects of season

Significantly higher numbers of birds used crop and weed plants as a foraging substrate during the wet season, but there were no significant seasonal differences in the number of birds using the air and ground as foraging substrate (Table 2, Fig. 2). Birds per plot per session taking seeds/fruits/flowers from the weeds were relatively higher during the wet than the dry season, whereas those taking the same food items from the ground were higher during the dry season (Fig. 4).

Importance of particular bird species in use of substrates and food items

The species most often observed foraging from the respective substrates were as follows (Table 4, including scientific names): (a) ground: Streaky Seedeater, Rufous Sparrow, Ring-necked Dove, Cape Robin-chat, Grassland Pipit, Common Fiscal and Cape Rook; (b) crop plants: Speckled Mousebird, Speke's Weaver, Baglafecht Weaver and Cape Rook; (c) weed plants: Streaky Seedeater, Yellow-crowned Canary and Brimstone Canary; (d) air: Common Fiscal and Common Stonechat.

The species most often observed taking respective types of food items (Table 4) were: (a) crop parts (seeds/flowers/fruits/stems/leaves): Speke's Weaver, Speckled Mousebird and Baglafecht Weaver; (b) invertebrates: Common Fiscal, Grassland Pipit, Common Stonechat and Cape Robin-chat; (c) weed parts (seeds/flowers/fruits/stems/leaves): Streaky Seedeater, Brimstone Canary and Yellow-crowned Canary, (d) nectar: Bronze sunbird; (e) vertebrate consumption by birds was only confirmed in two incidences: taking of a small mammal by a Black-shouldered Kite and an amphibian (frog) by a Black-headed Heron. The identity of food items taken could not be confirmed for large proportions of individuals of several commonly observed species (Table 4), but were predicted from existing literature on diet (Zimmerman *et al.* 1996, Hockey *et al.* 2005, Kissling *et al.* 2007): Baglafecht Weaver (invertebrates and seeds), Ring-necked Dove (seeds), Rufous Sparrow (seeds and invertebrates), Cape Robin-chat (invertebrates and fruits), Grassland Pipit (invertebrates), Streaky Seedeater (seeds) and Hunter's Cisticola (invertebrates and seeds).

There were clear differences between species foraging on crops and weeds. Crop-foraging species were mainly

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Table 3. General linear model of the effects of food item type (note that vegetative refers to stems or leaves), subdistrict (North versus South) and season (Wet versus Dry) on the number of foraging birds. Model: Number of birds per plot = Season + Subdistrict + Food type +(Season × Subdistrict) + (Season × Food type) + (Subdistrict × Food type), family = quasipoisson (log) (n =2335 observations made within 467 half-hour long sessions). Only a few individuals were observed taking vertebrates and therefore this category was not included in the model.

Parameter	Coefficients	SE	t value	P*	Interpretation**
(Intercept)	–1.1	0.3	–3.2	**0.002**	
Season[Wet]	–0.3	0.3	–1.0	0.327	
Sub-district[South]	1.7	0.4	4.9	**<0.001**	South > North
Food[Nectar]	–1.8	0.9	–2.0	**0.046**	Nectar <Inv; Seed/fruit/flower; Unconfirmed
Food[Seed/fruit/flower]	2.3	0.4	6.7	**<0.001**	Seed/fruit/flower > Invertebrate; Nectar; Vegetative
Food[Unconfirmed]	3.2	0.3	9.2	**<0.001**	Unconfirmed > Invertebrate; Nectar; Vegetative
Food[Vegetative]	–0.9	0.6	–1.5	0.146	
Season[Wet]:Sub-district[South]	0.7	0.2	4.0	**<0.001**	Wet [South] > Dry [South]
Season[Wet]:Food[Nectar]	–0.0	0.8	–0.1	0.957	
Season[Wet]:Food[Seed/fruit/flower]	0.2	0.2	0.6	0.528	
Season[Wet]:Food[Unconfirmed]	–0.3	0.3	–1.0	0.307	
Season[Wet]:Food[Vegetative]	0.5	0.7	0.8	0.444	
Sub-district[South]:Food[Nectar]	–1.0	1.0	–1.0	0.332	
Sub-district[South]:Food[Seed/fruit/flower]	–1.4	0.4	–3.7	**<0.001**	South [Seed/fruit/flower] > North [Seed/fruit/flower]
Sub-district[South]:Food[Unconfirmed]	–2.6	0.4	–7.0	**<0.001**	South [Unconfirmed] <North [Unconfirmed]
Sub-district[South]:Food[Vegetative]	–1.9	0.7	–2.6	**<0.001**	South [Vegetative] <South [Unconfirmed] North [Vegetative] <North [Unconfirmed]

*Significant P-values are in bold.

**Between-groups comparisons were determined by applying Tukey HSD post-hoc test; only significant differences ($P < 0.05$) are shown.

Null deviance: 17057.5 on 2334 degrees of freedom.

Residual deviance: 9862.3 on 2319 degrees of freedom.

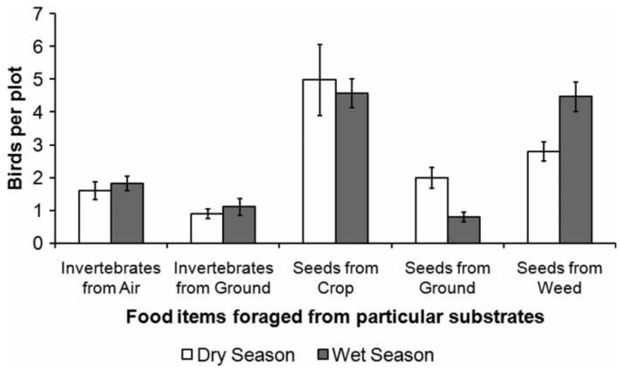

Figure 4. Seasonal comparison of mean numbers of birds per plot (± se) foraging on different confirmed food items from specific substrates types across the study area. Invertebrates from air = invertebrates foraged aerially (n = 113), Invertebrates from ground = ground-foraged invertebrates (n = 375), Seeds from crop = seeds/flowers/fruits foraged from crop plants (n = 232), Seeds from ground = ground-foraged seeds/flowers/fruits (n = 375), Seeds from weed = seeds/flowers/fruits foraged from weed plants (n = 208).

larger granivores (weavers) and mousebirds while weed-foraging species tended to be smaller granivores (seedeaters and canaries). In terms of crop damage, Speckled Mousebird foraged on a wide variety of crop plants, whereas Speke's and Baglafecht Weaver mostly foraged on maize, green peas, wheat and oats. Oats and wheat were taken by most of the granivorous birds in the study area, including the few large flocks of Red-billed Quelea and the Jackson's and Long-tailed Widowbirds that were observed during this study.

Sallying for invertebrates by the Common Fiscal was recorded in 114 (24.5%) of all the 465 half-hour sampling sessions and on average an individual bird would make 2.2 ± 1.3 successful captures (± sd, n = 114). Common Stonechat sallying bouts were recorded in 84 (18.1%) of the same sampling sessions with an average of 2.6 ± 2.6 successful captures (n = 84). This invertebrate capture rate translates to about four to five invertebrates per hour for each individual of the two species. Most of the sallying bouts for the two species were recorded in South (grassland) subdistrict (72% for Common Fiscal and 89% for Common Stonechat).

DISCUSSION

The results of this study provide some of the first quantitative information relating to the foraging resources different species of birds utilize within croplands in East African highland farmland and shows the range of bird species of birds, some in large numbers, obtaining food from the cultivated areas. Because many of the most important ecosystem services that birds provide result from their foraging behaviour (Wenny *et al.* 2011), it is possible that birds provide important services in these farmlands, as has been suggested elsewhere in North and South America (Rodenhouse & Best 1994, Luck & Daily 2003, Jones

Table 4. Percentage observations for most commonly observed bird species (recorded in ≥30 observation sessions throughout the study period) foraging on different substrate and food item types. For each species, the highest and second highest ranked substrate and food items types in terms of frequency of use are highlighted (dark, highest ranking; grey, second highest ranked) except for unconfirmed food items and low frequency (<20%). The species are listed in the order of how common they were starting with the most common. Grd, Ground; Invt, Invertebrates; Nect, Nectar; ?, unconfirmed food item type.

	Substrate					Food item					
Species	n	Air	Crop	Grd	Weed	n	Crop	Invt	Nect	Weed	?
Streaky Seedeater *Serinus striolatus*	672	0	23	39	38	679	18	1	0	48	33
Baglafecht Weaver *Ploceus baglafecht*	478	1	64	27	9	489	51	2	0	12	34
Rufous Sparrow *Passer rufocinctus*	409	0	22	69	9	409	19	7	0	31	43
Common Fiscal *Lanius collaris*	179	40	8	46	6	195	1	67	0	2	30
Common Stonechat *Saxicola torquatus*	174	26	8	37	29	179	0	67	0	1	32
Hunter's Cisticola *Cisticola hunteri*	200	1	19	41	40	204	11	14	0	43	32
Speke's Weaver *Ploceus spekei*	330	0	81	13	6	330	78	2	0	7	13
Cape Robin-chat *Cossypha caffra*	79	5	3	92	0	80	3	21	0	0	76
Yellow-crowned Canary *Serinus flavivertex*	181	0	27	22	51	181	22	4	0	67	7
Grassland Pipit *Anthus richardi*	75	0	0	100	0	75	0	40	0	5	55
Ring-necked Dove *Streptopelia capicola*	65	0	29	68	3	65	29	0	0	20	51
Cape Rook *Corvus capensis*	120	0	47	53	0	120	47	13	0	8	33
Speckled Mousebird *Colius striatus*	109	0	59	17	24	109	57	3	0	29	11
Brimstone Canary *Serinus sulphuratus*	73	0	4	19	77	74	1	0	1	84	14
Bronze Sunbird *Nectarinia kilimensis*	31	3	45	0	52	33	0	6	94	0	0

et al. 2005, Puckett *et al.* 2009) and Europe (Vickery *et al.* 2002).

Substrate use and food items taken

The majority of birds observed foraged on the ground, and most of these were granivores (seedeaters, sparrows, doves). The remaining birds foraged on crops and weeds and were largely insectivores and omnivores. Although the identity of food items taken from the ground was often impossible to confirm, they were almost certainly taking weed rather than crop seeds. The latter tend to be relatively large, often harvested, e.g. maize, and relatively rare on the soil surface compared with weed seeds (pers. obs.). Most of the birds could, therefore, be providing weed control services in these cultivated fields, a finding consistent with studies elsewhere (Howe & Brown 1999, Holmes & Froud-Williams 2005, Booman *et al.* 2009). On the other hand, this provides evidence that weeds play a crucial role in supporting birds and other biodiversity in crop fields (e.g. Moorcroft *et al.* 2002, Marshall *et al.* 2003, Franke *et al.* 2009). Crop damage by birds is likely to be relatively low, as most (>75%) birds forage from non-crop substrates and, even within the crop, foraging omnivorous and insectivorous birds are likely to be taking a large proportion of non-plant materials. These observations could be used to help change the perceptions of birds held by local farmers, most of whom view many bird species as crop pests. Opportunistic discussion with small holders in the area suggests this is the prevailing view in both subdistricts, especially directed towards the Speckled Mousebird and weavers.

Differences between subdistricts, as well as between seasons, may reflect differences in weed cover. For example, higher numbers of birds foraging from weed plants during the wet season in the South compared to the North subdistrict might be due to the fact that, in the latter, weed plants often grow under cover of tall maize crops which are the dominant crops in the subdistrict, whereas in the South weeds were easily visible in the short crop types that dominate the subdistrict, such as potatoes, cabbages and green peas.

There are a number of caveats to the interpretation of these results, particularly in respect to field methodology and the difficulties of undertaking unbiased sampling in habitats where birds differ in their detectability. For example, it was almost certainly easier to detect birds in more open habitats and substrates and the lower numbers of birds and the high proportions of unconfirmed identities of food items recorded in the North subdistrict, where vegetation is more closed, probably reflect this. Similarly, increased weed and crop cover could also result in reduced detectability of birds during the wet compared to the dry season. The high proportion of food items for which identity was unconfirmed also influences interpretation of the results and this was particularly high for ground-foraging birds. However, the general patterns of substrate preference for foraging birds are likely to be valid and, combined with existing knowledge on diet can be used to predict main food items in different substrates.

Contribution of particular bird species

Some bird species commonly found in the Nyandarua agricultural landscape were clearly associated with particular substrates and food items (Table 5). This information along with existing information in the literature allows potential services or disservices within agricultural systems to be identified and provides the basis for management approaches to be designed to attract potentially beneficial species, e.g. natural pest and weed enemies and deter pest species e.g. those that damage crops. (Whelan *et al.* 2008, Jones & Sieving 2006, Table 5).

Many of the apparent affinities for particular habitats reflect preferences for open versus closed habitats (Whelan *et al.* 2008) and at its simplest, knowing whether a bird species is 'cover-dependent' or 'cover-independent' (Lima & Valone 1991) may provide a useful framework for determining where to plant particular crops that could potentially benefit or be damaged by a given species. The Speckled Mousebird, for example, is cover-dependent and is attracted to thick hedges and orchards. This suggests that damage may be reduced by planting horticultural crops away from hedges and orchards especially for dry-season crops, as this is when damage by this species is greatest. Total clearing of native vegetation (e.g. grasslands, forests and bush) for the purpose of growing crops may exacerbate the avian-pest problem by opening habitat for larger granivores, especially doves and ploceids (weavers), while reducing habitat for frugivores and insectivores because they are most sensitive to bush clearance (Maclean 1990).

Implications of foraging behaviour for ecosystem service provision and crop damage

Post-dispersal seed predation is an important mechanism of weed seed loss in agri-ecosystems particularly in

Table 5. Commonly observed bird species (recorded in ≥30 observation sessions throughout the study period) and habitat preference and an indication of their potential role in cultivated areas based their food and substrate preference. Their preferred habitat is described to help in determining what attracts them and possibly help in making farm management decisions.

Species	Major foods (Hockey *et al.* 2005, Kissling *et al.* 2007)	Major substrates used (this study)	Potential role in cultivated areas	Preferred habitat (Zimmerman *et al.* 1996, Hockey *et al.* 2005)
Streaky Seedeater	Seeds, insects and invertebrates	Ground, weed plant	Weed control	Cultivation, woodland edges, scrub, gardens
Baglafecht Weaver	Insects and invertebrates, seeds and plant matter	Crop plant, ground	Crop damage, pest control	Cultivation, open woods, forest margins
Rufous Sparrow	Seeds	Ground	Weed control	Cultivation, open woods, non-forest
Common Fiscal	Insects and invertebrates, some vertebrates	Air, ground	Pest control	Shrub with scattered trees, grassland with scattered bushes and trees
Common Stonechat	Insects and invertebrates	Ground, weed plant	Pest control	Grassland with scattered scrub and low bushes, forest edges, marshy areas, cultivation
Hunter's Cisticola	Insects and invertebrates	Weed plant, ground		Shrub, overgrown gardens
Speke's Weaver	Seeds, insects and invertebrates	Crop plant	Crop damage, pest control	Cultivation, bush, urban
Cape Robin-chat	Insects and invertebrates, fruits, seeds	Ground	Pest control, weed control	Dense low cover, trees, shrubs, wooded drainage lines, gardens, orchards
Yellow-crowned Canary	Seeds and vegetable materials	Weed plant	Weed control	Forest edges, clearings, cultivation, pastures, gardens
Grassland Pipit	Insects and invertebrates	Ground	Pest control	Grasslands, fallow agricultural fields, areas enriched by droppings of cattle, sheep and game
Ring-necked Dove	Seeds	Ground, crop plant	Weed control, crop damage	Woodland, open farmlands with scattered trees, parks and gardens
Cape Rook	Insects and invertebrates, vertebrates, plant matter	Ground, crop plant	Crop damage, pest control	Grassland with scattered trees, grasslands, alien plantations, cultivation
Speckled Mousebird	Fruits and other plant matter	Crop plant, weed plant, ground	Crop damage, Weed control	Forest edges, thickets, gardens, orchards, fruiting alien plants
Brimstone Canary	Seeds, fruits	Ground, weed plant	Weed control	Forest, thickets, forest edges, shrub, old croplands, gardens, edges of alien plantations
Bronze Sunbird	Nectar and insects	Weed and crop plants	Pollination, pest control	Forest edges, clearings, cultivation, bushed grassland, gardens

no-tillage systems (Holmes & Froud-Williams 2005). In Nyandarua large numbers of granivorous birds were observed foraging from the ground and on weed plants, and weed seed predation could be one of the key beneficial roles that birds play particularly species such as Streaky Seedeater, Yellow-crowned Canary, Brimstone Canary, Ring-necked Dove and Rufous Sparrow. Apart from cultivated areas, these species prefer heterogeneous habitats with a mix of wood, shrubs and thickets (Table 5) and these may be the elements needed in the landscape in order to attract them.

Insectivorous species composed the highest proportion (40%) of foraging species recorded and most of the confirmed invertebrate consumption was from aerial captures above vegetation- and ground-foraging in cultivated areas, by species such as Common Fiscal, Common Stonechat, Grassland Pipit and Cape Robin-chat. However, these birds may also consume beneficial invertebrates (e.g. bees, spiders, ladybirds, lacewings, hoverflies, predatory bugs, praying mantis, ants, etc.) from crops, making their role difficult to confirm.

Several bird species foraged from crop plants and took seeds, fruits, flowers, stems and leaves. The species mostly associated with crop damage were Speke's Weaver, Baglafecht Weaver and Speckled Mousebird, particularly where farmers grew monocultures of wheat, oat, maize and *Brassica* vegetables (kale and cabbages). Although this small number of bird species does cause economic damage at the local scale, most studies suggest that, at the ecosystem level, the services provided by birds are overwhelmingly positive (Sekercioglu 2006, Whelan *et al.* 2008) and that some birds that cause crop damage can, at other stages of crop growth serve to control pests (Dolbeer 1990, Wenny *et al.* 2011). In this study, for example, Baglafecht and Speke's Weavers also take invertebrate prey (Hockey *et al.* 2005, Kissling *et al.* 2007) and Speckled Mousebirds were also observed taking weed plant parts. During two seminars held with farmers in the study area, the Speckled Mousebird was cited as a major pest of horticultural crops. Further work is required to develop environmentally friendly measures to manage crop damage by species such as this one. Examples of such measures may include 'push–pull' strategies whereby stimuli are integrated that act to make the protected resource (crops) unattractive or unsuitable to the pests (push) while luring them toward an attractive source (pull) from where the pests are subsequently removed (Cook *et al.* 2007) and by manipulating habitat to exploit the habitat preference of pest and beneficial bird species (Tracey *et al.* 2007).

CONCLUSIONS

This study contributes to understanding the foraging behaviour of birds in East African highland farmlands and its implication for predation of pests, weed seeds and crop damage. The work suggests that many of the granivorous birds foraging on the ground and on weed plants may predate weed seeds, thus potentially contributing to natural weed control. Although most of the species that forage in the farmlands are insectivorous, confirming prey identity was extremely difficult with the exception of 'hawking'/'sallying' insectivores that appear very active predators of insects in farmland. Birds foraging in crops were particularly abundant in the wet season, when crop growth is at its highest, and crop damage at this time, especially for crops grown as monocultures, may be significant. The species that are most likely to contribute to crop damage were identified as Speke's Weaver, Speckled Mousebird and Baglafecht Weaver. The knowledge provided by this study regarding species-specific preference of diet, substrate and habitat for the common species foraging in the farmlands may inform recommendations with respect to managing farmland to enhance beneficial species and/or reduce impacts of damaging ones. However, it is recommended that further detailed species-specific studies be undertaken to develop clear management strategies. Experimental research on the benefits offered by birds in terms of weed and insect pest control are also needed to confirm the correlations noted in this study.

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