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Severe declines of understory birds follow illegal logging in Upper Guinea forests of Ghana, West Africa

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ABSTRACT

We investigated how legal logging history and recent illegal logging affected forest bird community structure in Ghana. Ghanaian forests belong to West Africa's highly fragmented Upper Guinea rain forests, part of a global priority "biodiversity hotspot" under intense pressure from anthropogenic degradation. Between 1995 and 2010, officially-reported legal logging intensities increased up to ~600%, while illegal logging, which now accounts for 80% of timber extraction in Ghana, has driven logging intensities to ~6 times greater than the maximum sustainable rate. We collected data in 2008–2010 and used a comparable dataset collected in 1993–1995 to assess impacts of recent logging on understory bird communities in large forest fragments (100–524 km^2) in southwest Ghana. Forest understory bird species abundance declined by >50% during this period. Species richness also showed declining trends. Whereas analysis based on data collected in 1993–1995 estimated a partial post-logging recovery of the understory bird community at that time, data from 2008–2010 showed no indication of post-logging recovery, likely due to ongoing illegal logging following intensive legal logging operations. Forest generalist species and sallying insectivores declined significantly in logged compared to unlogged forests. These severe declines of Upper Guinea forest understory birds indicate the rapidly deteriorating conservation status of a biodiversity hotspot and could signal collapsing ecosystem processes. Immediate conservation actions are urgently required to protect surviving forest fragments from further degradation and avian declines.

1. Introduction

We present empirical data on the impacts of logging on understory bird communities in West African Upper Guinea rain forest, taking advantage of a unique opportunity to compare findings from two studies conducted 15 years apart in the same study area in Ghana. Logging and other types of anthropogenic forest conversion trigger changes in avian community dynamics, population abundance, and species composition, and may increase extinction rates (Stratford and Robinson, 2005; Sodhi et al., 2011; Thinh et al., 2012; Edwards and Laurance, 2013; Michalski and Peres, 2013; Edwards et al., 2014). Illegal logging is an increasing threat to tropical forests (Laurance, 1999; Curran et al., 2004; Nellemann and INTERPOL, 2012; Finer et al., 2014). However, few datasets allow assessments of the effects of logging history and illegal logging on bird community structure, and no empirical study has quantified the impacts of illegal logging on tropical wildlife.

West Africa's Upper Guinea rain forests form part of a priority global "biodiversity hotspot" where exceptional plant and animal endemism is severely threatened by human activities (Myers et al., 2000; Kouame et al., 2012). Over 80% of Ghana's Upper Guinea forests have been cleared, mainly for agriculture and settlement, and remaining forest is highly fragmented (Hawthorne and Abu-Juam, 1995; Beier et al., 2002). Extant forest fragments have immense conservation value as refuges for endemic birds and other wildlife (Brashares et al., 2001; Cordeiro et al., current issue). A number of priority global Endemic and Important Bird Areas have been designated in these forests (BirdLife, 2013). Ghana's forest avifauna is comprised of ~80% Guinean–Congolian regional endemics and ~14% species restricted to Upper Guinea forests (Dowsett-Lemaire and Dowsett, 2014), making this region important for studies of disturbance effects on bird communities.

Illegal logging is a major driver contributing to tropical forest destruction worldwide, and accounts for 50–90% of timber harvested in many tropical countries (Nellemann and INTERPOL,

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2012; Zimmerman and Kormos, 2012). Illegal logging now comprises 80% of Ghana's annual timber production and in recent years has driven logging intensities up to ~6 times greater than the maximum allowable cut for sustainable forestry (Hansen et al., 2009, 2012). The fact that illegal logging is particularly well studied and documented in Ghana (Hansen and Treue, 2008; Marfo, 2010; Hansen et al., 2009; Hansen et al., 2012; Teye, 2013; Amoah and Boateng, 2014; Franck and Hansen, 2014; Oduro et al., 2014) has set the stage to allow us to examine its impacts on Ghana's Upper Guinea forest understory birds.

Understory birds, especially insectivores, are sensitive to logging damage due to their foraging and habitat specializations, post-logging impoverishment of arthropod fauna, and high site fidelity (Peters et al., 2008; Sodhi et al., 2011; Hamer et al., current issue; Powell et al., current issue-a; Powell et al., current issue-b). Understory birds thus serve as excellent indicators or "sentinels" of forest ecosystem integrity (Corlett and Primack, 2011; Sodhi et al., 2011). Few studies have evaluated avian responses to logging in Guinean–Congolian forests of western and central Africa, and we are aware of only one previous peer-reviewed study that has examined the impacts of logging on Upper Guinea forest birds, based on 1993–1995 data from Ghana (Holbech, 2005). While most empirical studies of tropical logging and birds have been limited to examining short-term impacts (Thinh et al., 2012), we investigated both long-term trends and recent patterns in understory bird dynamics in response to increases of logging intensity in Ghana's remaining Upper Guinea forests. We conducted fieldwork in 2008–2010, and compared our data with findings from fieldwork in 1993–1995 (Holbech 1996, 2005). All data were collected in the same region of southwest Ghana, including several of the same forest fragments. In this paper, we address three main goals: (1) quantifying long-term changes in Ghana's understory birds by comparing sampling data from 1993–1995 (Holbech 2005, 2009) and 2008–2010; (2) quantifying recent trends in forest understory bird communities in response to recent increases in logging intensities, with a particular focus on vulnerable insectivorous guilds and conservation priority species; and (3) examining implications for Upper Guinea forest and understory bird ecology and conservation.

2. Materials and methods

2.1. Study area and study design

Remaining Upper Guinea forest in Ghana covers ~16 000 km^2 of reserves, representing 20% of extant forest prior to colonization, which were originally designated by the British colonial government for environmental protection and timber production (Hawthorne and Abu-Juam, 1995; Hansen et al., 2012). In the 1970s, ~8% of remaining forest (1261 km^2) was designated as wildlife protected areas (national parks and resource reserves) managed by the Ghana Wildlife Division. The other ~92% is in forest reserves managed as logging concessions by the Ghana Forest Services Division, which leases them to private timber companies. Industrial logging operations are often accompanied and followed by illegal logging, wherein both organized groups and opportunistic individuals use logging roads to penetrate forest interior and further exploit timber (Laurance, 1999; Marfo, 2010; Hansen et al., 2012). Approximately 25% of the total area of forest reserves has been seriously degraded or entirely cleared by human impacts, while 75% (~12 000 km^2) still constitutes dense forest (Norris et al., 2010). Virtually all forest outside of these reserves has been cleared, leaving forest fragments surrounded by a matrix of plantation monocultures interspersed with human settlements (Deikumah et al., 2014).

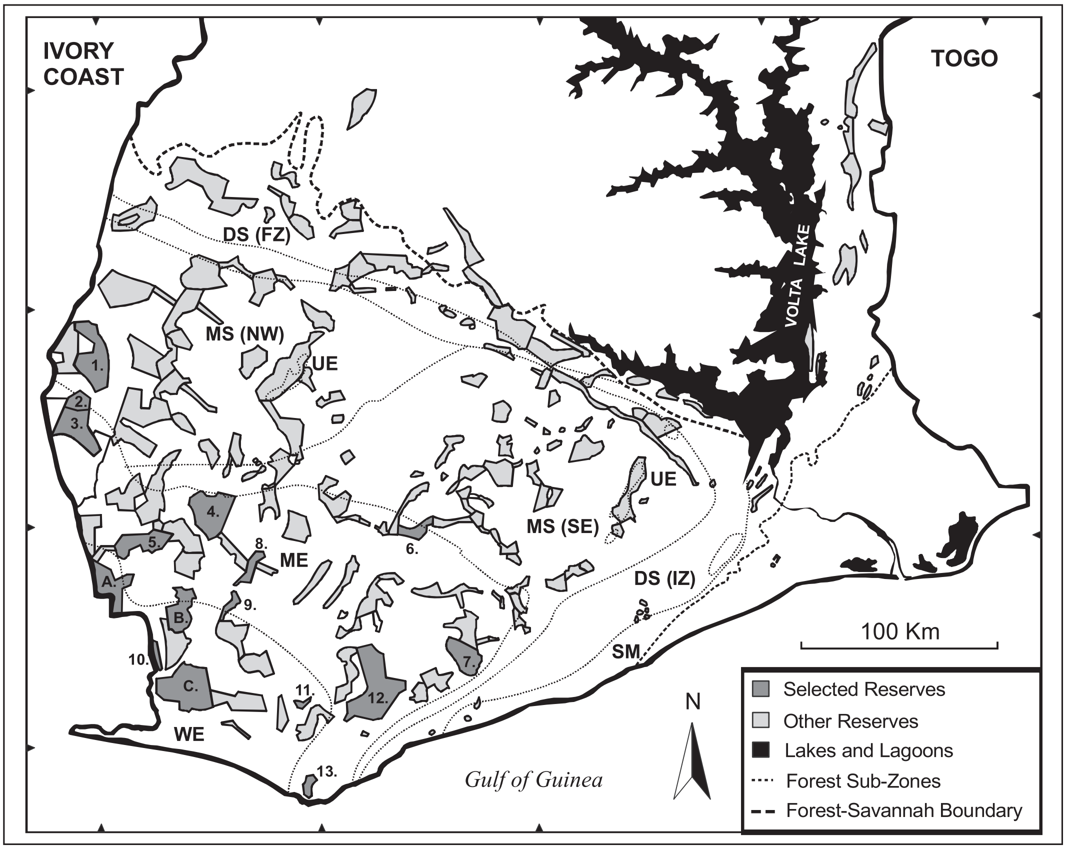
We selected 27 study sites for bird sampling in 2008–2010 and compared our results with sampling data from 1993 to 1995 (Holbech, 1996, 2005) in the same region of southwest Ghana (Table 1 and Fig. 1). Our 2008–2010 sampling took place in 10 protected forests (Fig. 1: 1–7 and A–C) and Holbech's 1993–1995 sampling took place in 9 protected forests (Fig. 1: 8–13; A–C), including 3 of the same reserves, for a total of 16 protected forests (12 forest reserves; 2 resource reserves; 2 national parks) included in this study. We sampled only within large forest fragments (100–524 km^2) in order to focus on logging impacts rather than species-area relationships (Beier et al., 2002; Bregman et al., 2014; Stratford and Robinson, 2005). We sampled evergreen and semi-deciduous forests with approximately equal effort to avoid bias due to habitat type. Sites were assigned as replicates of 1 of 4 treatments: unlogged forest and forest ~2, ~10, and ~20 or more years post-logging. We defined a replicate as a single mist net sampling session of 20–24 h accumulated over 2–3 days (hereafter we refer to a mist net day as a "sampling occasion"). We used at least 3 replicates in each forest type, for a total of 6–9 replicates per treatment. We recorded dates, times, geographic location, and logging history for each forest sampled. We included multiple logging treatments within a single forest fragment wherever possible, but this was sometimes precluded by fragments' specific logging histories.

To investigate the impacts of logging on understory bird communities in 2008–2010, we accumulated a total of 80 sampling occasions. In 1993–1995, Holbech (1996, 2005) used a total effort of 201 sampling occasions, representing a greater range of

Table 1
Upper Guinea forest fragments sampled in Ghana in 2008–2010.

Forest[a]	Area (km^2)	Forest type[e]	Sampling effort (NMH)[f]	Treatment(s) [replication(s)][g]	Governing authority[h]
Ankasa RR[i]	524[b]	WE	2520	L20+(1)	GWD
Bia NP and Bia RR	306	MS	8550	UL(2), L10(1)	GWD
Bia Tributaries North FR	356	MS	5310	L3(1), L20+(1)	GFSD
Boin River FR[i]	278	W/ME	18 970	UL (3), L3(2), L20+(2)	GFSD
Kakum NP	366[c]	MS	2430	L20+(1)	GWD
Nkrabia FR	100	MS	2760	L20+(1)	GFSD
Suhuma FR	360	MS	15 680	UL(1), L3(2), L10(2), L20+(1)	GFSD
Tano Nimiri FR[i]	335[d]	W/ME	5520	L20+(2)	GFSD
Yoyo River FR[i]	236	ME	11 352	L3(1), L10(3)	GFSD

[a] FR = Forest Reserve (active logging concession); NP = National Park, RR = Resource Reserve (including former logging concessions).
[b] Area includes contiguous Nini-Suhien NP.
[c] Area includes contiguous Assin-Atandanso RR.
[d] Area includes contiguous Boi-Tano FR.
[e] Forest habitat type classification (Hall and Swaine, 1976): MS = Moist Semi-deciduous; W/ME = West/Moist Evergreen.
[f] NMH = Net-Meter-Hours.
[g] GWD = Ghana Wildlife Division; GFSD = Ghana Forest Services Division.
[h] UL = unlogged forest; L3 = forest 3 years post-logging; L10 = forest 10 years post-logging; L20+ = forest 20 or more years post-loggng.
[i] Forest fragments also sampled by Holbech 1993–1995 (Holbech 2005, 2009); see Fig. 1 for map and data comparisons.



Forest types (Hall and Swaine 1995): WE = Wet Evergreen; ME = Moist Evergreen; MS = Moist Semi-deciduous; S = Dry Semi-deciduous; NW = North-West; SE = South-East; IZ = Inner Zone; FZ = Fire Zone; UE = Upland Evergreen..

Fig. 1. Map showing the fragmented Upper Guinea forest zone of southwest Ghana, with remaining Forest Reserves (FRs) light-shaded and selected reserves dark-shaded. Reserves selected in 2008–2010 survey only; (1) Bia Tributaries North FR; (2) Bia National Park, (3) Bia Resource Reserve; (4) Suhuma FR; (5) Yoyo River FR; (6) Nkrabia FR; (7) Kakum National Park. Reserves selected in 1993–1995 survey only; (8) Bura River FR; (9) Mamiri FR; (10) Jema-Assemkrom FR; (11) Neung North FR; (12) Subri River FR; (13) Cape Three Points FR. Reserves selected in both survey periods; (A) Boin River FR; (B) Tano Nimiri FR; (C) Ankasa Resource Reserve.

treatments and 2.5 times the effort our 2008–2010 sampling. We resolved this difference in sampling effort by using only a subset of Holbech's 1993–1995 data that matched our 4 treatments (unlogged forest and forest ~2, ~10, and ~20+ years post-logging). This 1993–1995 matched subset represented 72 sampling occasions and 66 528 net-meter-hours (nmh), which was comparable to our 2008–2010 sampling effort of 80 sampling occasions and 72 604 nmh. We used species overlap analysis (beta diversity indices) to test whether sampling data in 2008–2010 were sufficiently congruent with those sampled in 1993–1995 to permit valid comparisons of bird community parameters (Chao et al., 2005; Colwell et al., 2012).

To determine logging history (years of regeneration since the termination of last legal logging operation) and intensity (number of trees removed/ha), we used official reports from collaborating logging companies (Acknowledgments) together with records from the Ghana Forest Services Division. Official figures suggested that logging intensity was 4–6 trees/ha (~40–60 m^3/ha), which was >6 times higher than average logging intensities (~1.0 trees/ha or 10 m^3/ha) calculated 15 years previously in the same study area (Holbech, 2005, 2015). Because illegal logging accounted for 75% of timber extraction in Ghana at the time of our research (Hansen and Treue, 2008), actual logging intensities across the study area were much higher than those officially reported. Illegal logging in the study area was quantified using market data, and logging intensity was calculated across all Ghana's Upper Guinea forest as a whole, rather than for specific forest fragments or locations, due to the clandestine nature of illegal exploitation (Hansen and Treue, 2008; Marfo, 2010). Opportunistic observations in the course of our field sampling suggested that illegal logging was highly variable in time and space across fragments. Overall logging intensity levels thus reflect ongoing unsustainable illegal timber exploitation rather than the legal timber extraction levels in Ghana studied 15 years earlier (Holbech, 1996, 2005).

2.2. Bird sampling

We used constant-effort mist-netting to sample birds, clearing narrow lanes to erect mist nets on a semi-continuous line where permitted by the terrain, or else erected nets along the slopes of hillsides in clusters ~10–20 m apart. Standardized mist-net sampling enables reliable quantitative estimates of several bird community and population parameters, is effective for detecting understory birds, particularly cryptic, shy, and less vocal species, and is repeatable with few observer biases (Ralph and Dunn, 2004). Capture rates vary with birds' territoriality, home range size, flight height and distance, and other factors, so capture data provide indices of relative abundance and levels of activity and mobility (Remsen and Good, 1996).

Bird sampling took place over a total of 80 mist-net days ("sampling occasions") from September 2008 through May 2010. We operated 10 nets (12 m × 3 m, 36 mm mesh) simultaneously, which were opened at dawn (generally 06h00) and kept open for up to ~12 h at a time until near dusk (generally 18h00). Nets were closed during periods of rain. We accumulated 20–24 mist-net h per site, usually within 2–3 days. We identified, measured, weighed, photographed, and released birds at the capture site after processing. Birds were not banded because all sampling at a given site occurred within 2–3 consecutive days. Instead, captured birds were marked on the belly feathers with a permanent marker to avoid double-counting (Holbech, 2005, 2009). Recaptured birds were released immediately at capture sites.

2.3. Avian conservation priority status and ecological guilds

To test for impacts on avian habitat and foraging guilds, we assigned species encountered to guilds as follows: forest specialists (forest-dependent species typically restricted to forest interior and which prefer primary forest), forest generalists (forest-dependent species ranging throughout forests and which prefer secondary growth and edge), and forest visitors (species not dependent on forest that occur both outside and inside forests but which prefer non-forest areas), as well as to 3 potentially vulnerable understory insectivore guilds: sallying insectivores, terrestrial insectivores, and ant followers (Bennun et al., 1996; Holbech, 2005, 2009). We used data from this and previous studies to assign conservation priority status to species considered especially vulnerable to extinction due to their rarity, range restrictions, and habitat and/or foraging specializations (Grimes, 1987; Beier et al., 2002; Holbech, 2005, 2009; Dowsett-Lemaire and Dowsett, 2014); this is analogous to "conservation important" species as defined by Holbech (2005, 2009). Nomenclature follows Borrow and Demey (2010).

2.4. Statistical analyses

We standardized relative abundances for all replicate captures per 1000 net-meter-hours (nmh; this is equivalent to 1000/12 = 83 net-hours), and calculated means and standard deviations based on the number of replicates in each treatment (Table 2). As ~88% of bird species are shared between semi-deciduous and evergreen forest in Ghana (Ntiamoa-Baidu et al., 2000), and our sampling effort was equivalent for both forest types, we pooled data from forest types to increase the statistical power of our analyses. We used the mist-net capture rate (birds/10000 nmh) at each site as our unit of comparison. We calculated mean capture rates among sites within each forest category to test for effects of time since logging on bird abundance.

We used EstimateS software v. 9.1 (Colwell, 2013) to generate species accumulation curves (species observed versus individuals for comparable sampling efforts). We compared species richness in the 1993–1995 subsample with that in the 2008–2010 dataset using 95% confidence intervals around mean richness as a conservative statistical test for differences in species richness (Colwell et al., 2012). We extrapolated the 2010 species accumulation curves to match the total bird captures in the 1993–1995 subsample, and also compared asymptotic estimates of total bird species richness between 1995 and 2010 (Abundance Coverage Estimator, ACE: Colwell and Coddington, 1994; Colwell et al., 2012). We used the abundance-based Chao-Jaccard species similarity index to assess whether bird communities were sufficiently congruent across sampling periods to enable accurate comparison; this index represents the probability that a bird randomly chosen from one sample would belong to a species found in the other sample (Chao et al., 2005).

To test for changes in abundance in response to logging, we conducted ANOVAs using general linear models (function lm) in R (R Core Development Team, 2013), testing each of 4 explanatory variables (forest size, forest type, post-logging regeneration time, logged vs. unlogged forest) in turn as a predictor of abundance of each of 6 guilds: forest specialists; forest generalists; conservation priority species; sallying insectivores; terrestrial insectivores; ant-following insectivores. We also compared mean values of overall and conservation priority species abundance between 1995 and 2010 through one-way ANOVAs, using Practistat (Ashcroft and Pereira, 2003; Holbech, 2005).

3. Results

We captured 962 individuals of 46 bird species, of which 32 (70%) were forest specialists, 13 (~28%) were forest generalists, and 35 species (76%) were understory insectivores (Appendix A). We compared this 2008–2010 capture data with the subset of Holbech's 1993–1995 data (1996, 2005) described previously, which resulted in captures of 2293 individuals of 71 bird species. The Chao-Jaccard index for the 1993–1995 (Holbech, 1996, 2005) and 2008–2010 datasets indicated a very high (96.6%) similarity, allowing us to compare bird community parameters between 1995 and 2010 with confidence (Chao et al., 2005).

3.1. Long-term changes in Upper Guinea forest understory bird communities

Following >600% increases in logging intensities in Ghana's Upper Guinea forests between 1995 and 2010, overall empirical abundance (birds/10000 nmh) was 52% lower in 2010 (13.46) than in 1995 (28.07) ($F_{1,28} = 90.52$, $p < 0.001$) and differed in the relationship of abundance with logging treatment (Fig. 2; $F_{3,28} = 6.56$, $p = 0.002$). The greatest differences were in logged forests, which had much higher capture rates in 1995 than in 2010 (Fig. 2). We found no indication of a post-logging bird community recovery by 2010 (Fig. 2). Abundance in all logged treatments in 2008–2010 was significantly lower than in unlogged forest, in contrast to Holbech's (1996, 2005) previous findings of an increase in bird abundance over time following logging in 1993–1995. A separate analysis of the 2008–2010 data also suggested capture rates were significantly higher in unlogged forest but time since logging had no additional effect (Tukey HSD post-hoc test, critical alpha 0.05).

All (82) species captured during both time periods are listed in Table 2, together with their capture rates per 10000 nmh for both time periods and the ratio of their capture rates between time periods. The 2010/1995 capture ratios that as a group also suggest serious declines and highlight changes in empirical individual species abundance between time periods. Of the 3 species captured in greatest numbers, olive sunbird (*Cyanomitra olivacea*) declined by 53%, yellow-whiskered greenbul (*Andropadus latirostris*) declined by 73%, and icterine greenbul (*Phyllastrephus icterinus*) declined by 90% between 1995 and 2010 (Table 2).

Our 1993–1995 data subset displayed an empirical species richness ($S = 71$) that was >50% higher than that in 2008–2010 (71 versus 46 species respectively), even though its sampling effort was 10% lower (66528 vs. 72604 nmh), indicating a declining trend in species richness in logged forests. Because the number of individual birds captured in 2008–2010 was significantly (58%) lower than in 1993–1995, we extrapolated from the 2008–2010 empirical data to simulate a number of captures comparable to that made in 1993–1995. We compared species richness between the two time periods using both empirical and extrapolated data (Fig. 3). Although empirical species richness did not statistically differ between the two sampling periods, species accumulation curves generated by extrapolation indicated declining species richness between 1995 and 2010 (Fig. 3).

Table 2
Upper Guinea forest understory bird species capture rates per 10000 nmh in Ghana in 1993–1995 (for our matched subsample) and 2008–2010. Conservation priority species for Ghana are noted with single asterisks (Holbech, 2005, 2009), of which three red-list species endemic to Upper Guinea forest biome are affixed with double asterisks (IUCN, 2014). Nomenclature follows Borrow and Demey (2010).

Name	Binomial	1995	2010	Ratio 2010/1995
Olive sunbird	*Cyanomitra olivacea*	56.03	26.60	0.47
Yellow-whiskered greenbul	*Andropadus latirostris*	53.76	14.52	0.27
Icterine greenbul	*Phyllastrephus icterinus*	26.01	2.71	0.10
White-tailed alethe	*Alethe diademata*	15.22	13.44	0.88
Grey-headed bristlebill	*Bleda canicapillus*	13.80	13.30	0.96
Red-bellied paradise flycatcher	*Terpsiphone rufiventer*	11.05	4.34	0.39
Forest robin	*Stiphrornis erythrothorax*	9.83	5.16	0.52
Pale-breasted illadopsis	*Illadopsis rufipennis*	8.93	3.80	0.43
Green hylia	*Hylia prasina*	8.03	7.74	0.96
Western bearded greenbul	*Cringer barbatus*	7.93	2.31	0.29
Green-tailed bristlebill**	*Bleda eximius*	7.40	4.61	0.62
Red-tailed bristlebill	*Bleda syndactylus*	7.29	5.16	0.71
White-tailed ant thrush*	*Neocossyphus poensis*	5.71	2.17	0.38
Brown-chested alethe*	*Alethe poliocephala*	4.18	0.81	0.20
Little greenbul	*Andropadus virens*	3.65	3.26	0.89
White-bellied kingfisher	*Aldedo leucogaster*	2.70	3.53	1.31
Yellow-bearded greenbul	*Criniger olivaceus*	2.70	0.00	0.00
African dwarf kingfisher*	*Ceyx lecontei*	2.33	0.27	0.12
Black-throated coucal*	*Centropus leucogaster*	2.27	0.00	0.00
Fraser's sunbird	*Deleornis fraseri*	2.11	0.81	0.39
Red-fronted antpecker**	*Parmoptila rubifrons*	1.74	0.54	0.31
Western bluebill	*Spermophaga haematina*	1.69	1.63	0.96
Blue-billed malimbe	*Malimbus nitens*	1.64	1.09	0.66
Red-tailed greenbul	*Criniger calurus*	1.48	1.09	0.73
Blackcap illadopsis	*Illadopsis cleaveri*	1.27	0.68	0.53
Rufous-sided broadbill	*Smithornis rufolateralis*	1.22	0.68	0.56
Chestnut wattle-eye	*Dyaphorophyia castanea*	1.16	0.14	0.12
Finsch's flycatcher thrush	*Stizorhina finschii*	1.16	1.63	1.40
African goshawk	*Accipiter tachiro*	1.11	0.68	0.61
Buff-spotted woodpecker	*Campethera nivosa*	1.11	0.68	0.61
Spotted honeyguide*	*Indicator maculatus*	1.06	0.27	0.25
Cameroon sombre greenbul	*Andropadus curvirostris*	0.95	0.54	0.57
Tambourine dove	*Turtur tympanistria*	0.95	0.00	0.00
Rufous-winged illadopsis**	*Illadopsis rufescens*	0.90	0.00	0.00
Honeyguide greenbul	*Baeopogon indicator*	0.85	0.14	0.16
Blue-headed crested flycatcher*	*Trochercercus nitens*	0.85	0.68	0.80
Dusky crested flycatcher*	*Elminia nigromitrata*	0.74	0.00	0.00
Shining drongo*	*Dicrurus atripennis*	0.58	0.00	0.00
Green-backed camaroptera	*Camaroptera brachyura*	0.48	0.14	0.29
Red-rumped tinkerbird	*Pogoniulus atroflavus*	0.48	0.14	0.29
Blue-throated brown sunbird	*Cyanomitra cyanolaema*	0.42	0.41	0.96
Speckled tinkerbird	*Pogoniulus scolopaceus*	0.37	0.00	0.00
Blue-headed wood dove	*Turtur brehmeri*	0.37	0.68	1.83
Yellow-spotted barbet	*Buccanodon duchaillui*	0.32	0.00	0.00
Collared sunbird	*Hedydipna collaris*	0.32	0.00	0.00
Velvet-mantled drongo	*Dicrurus modestus*	0.26	0.00	0.00
Chestnut-breasted negrofinch	*Nigrita bicolor*	0.21	0.00	0.00
Western black-headed oriole	*Oriolus brachyrhynchus*	0.21	0.00	0.00
White-throated greenbul	*Phyllastrephus albigularis*	0.21	2.71	12.84
White-crested hornbill	*Tropicranus albocristatus*	0.21	0.27	1.28
Brown-eared woodpecker*	*Campthera caroli*	0.16	0.00	0.00
Olive long-tailed cuckoo*	*Cercococcyx olivinus*	0.16	0.00	0.00
Latham's forest francolin	*Francolinus lathami*	0.16	0.14	0.86
Red-chested owlet*	*Glaucidium tephronotum*	0.16	0.14	0.86
Chocolate-backed kingfisher	*Halcyon badia*	0.16	0.00	0.00
Least honeyguide*	*Indicator exilis*	0.16	0.00	0.00
Lesser honeyguide*	*Indicator minor*	0.16	0.00	0.00
Grey-throated flycatcher	*Myioparus griseigularis*	0.16	0.00	0.00
Grey-headed negrofinch	*Nigrita canicapilla*	0.16	0.00	0.00
Western nicator	*Nicator chloris*	0.16	0.27	1.71
Red-thighed sparrowhawk	*Accipiter erythropus*	0.11	0.14	1.28
Dusky long-tailed cuckoo*	*Cercococcyx mechowi*	0.11	0.00	0.00
Blue-breasted kingfisher	*Halcyon malimbica*	0.11	0.00	0.00
Yellow-billed barbet	*Trachylaemus purpuratus*	0.11	0.00	0.00
Yellow-browed camaroptera	*Camaroptera superciliaris*	0.05	0.00	0.00
Bristle-nosed barbet*	*Gymnobucco peli*	0.05	0.14	2.57
Brown illadopsis	*Illadopsis fulvescens*	0.05	0.00	0.00
Blue-headed bee-eater*	*Merops muelleri*	0.05	0.00	0.00
Olivaceous flycatcher*	*Muscicapa olivascens*	0.05	0.14	2.57
Fraser's forest flycatcher	*Fraseria ocreata*	0.00	0.14	Undefined
Kemp's longbill*	*Macrosphenus kempi*	0.00	0.14	Undefined

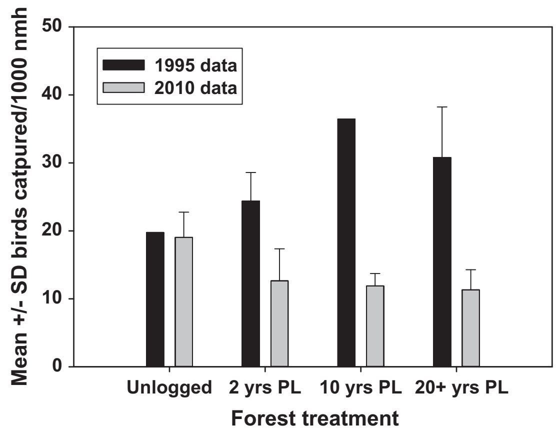


Fig. 2. Upper Guinea forest understory bird abundance in 4 forest treatments (Unlogged, ~2 year post-logging, ~10 years post-logging, ~20+ years post-logging) in southwest Ghana, calculated for both 1993–1995 and 2008–2010. (Error bars do not appear in 1995 subsamples for ~2 year post-logging and ~10 years post-logging treatments because only one replicate of each was used.)

3.2. Recent trends in Ghana's understory bird communities

Sampling data from 2008 to 2010 revealed that across all forest types and fragment sizes, total understory bird abundance was significantly lower in logged forests compared to unlogged forests (Fig. 2 and Table 3). We captured 12 conservation priority (CP) species in 2008–2010 (~26% of total species), of which 6 species were detected on only 1 or 2 occasions (Appendix). In comparison Holbech (2005, 2009) netted 25 CP-species (~37%) in the effort-adjusted subsample matching the 2008–2010 sample, including three IUCN red list species, of which two Upper Guinea endemics, the rufous-winged illadopsis (*Illadopsis rufescens*) and yellow-bearded greenbul (*Criniger olivaceus*) was absent from the 2008–2010 sample. Likewise, forest generalist and sallying insectivore abundance were significantly lower in logged forests compared to unlogged forests (Table 3). In 2008–2010, we classified 75% of conservation priority species and all but two sallying insectivore species as "rare" in this study because they made up <1% of all captures (Appendix).

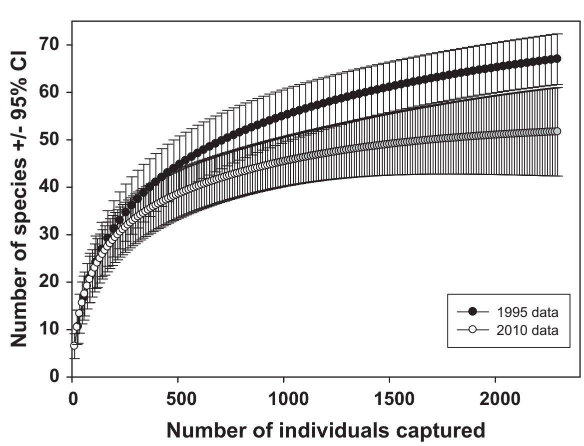


Fig. 3. Upper Guinea forest understory bird species accumulation curves generated by rarefaction showing expected species richness ±95% confidence intervals plotted against number of individuals captured over comparable sampling periods for 1993–1995 (66528 nmh; black line) and 2008–2010 [73604 nmh; white line (empirical data) and gray line (extrapolated data)] in 16 protected forest areas of southwest Ghana.

Table 3
Upper Guinea forest understory bird abundance in response to 3 explanatory variables; forest size (area of fragment in km^2), forest type (Moist Semi-deciduous or Moist Evergreen, as defined by Hawthorne and Abu-Juam, 1995), regeneration time (i.e., logging treatment, designated as post-logging recovery periods of 2, 10, and 20+ years) and unlogged versus (pooled) logged forest. Significant results, of ANOVAS using function lm in R, are indicated with bold and asterisks.

Response variable Abundance	Explanatory variable			
	Forest size	Forest type	Regeneration time	Unlogged vs. logged
All species	$F = 0.2558$, $p = 0.62$	$F = 0.5347$, $p = 0.47$	$\mathbf{F = 6.193}$, $\mathbf{p = 0.02}$	$\mathbf{F = 19.2}$, $\mathbf{p < 0.01}$
Forest specialist (FF) species	$F = 0.0772$, $p = 0.78$	$F = 1.721$, $p = 0.20$	$F = 0.9074$, $p = 0.35$	$F = 1.543$, $p = 0.23$
Forest generalist (F) species	$F = 0.227$, $p = 0.64$	$F = 0.0004$, $p = 0.98$	$\mathbf{F = 6.971}$, $\mathbf{p = 0.01}$	$\mathbf{F = 26.88}$, $\mathbf{p < 0.01}$
Conservation priority species	$F = 0.0597$, $p = 0.81$	$F = 1.356$, $p = 0.26$	$F = 2.022$, $p = 0.17$	$F = 0.1462$, $p = 0.71$
Sallying insectivore	$F = 0.3912$, $p = 0.54$	$F = 0.1244$, $p = 0.73$	$F = 0.911$, $p = 0.34$	$\mathbf{F = 5.976}$, $\mathbf{p = 0.02}$
Terrestrial insectivore	$F = 0.851$, $p = 0.37$	$F = 2.237$, $p = 0.15$	$F = 1.711$, $p = 0.20$	$F = 1.007$, $p = 0.32$
Ant follower	$F = 1.136$, $p = 0.30$	$F = 3.45$, $p = 0.08$	$F = 1.228$, $p = 0.28$	$F = 1.069$, $p = 0.31$

4. Discussion

Several lines of evidence indicate severe declines of Ghana's Upper Guinea forest understory bird communities during the 15 year period between our two datasets. Abundance declines appear to be pervasive across the understory bird community and to be driving declines in species richness over time. Results further indicate that Ghana's forestry management system, which Holbech (1996, 2005) previously deemed to allow post-logging recovery of forest understory bird communities, has seriously deteriorated due to widespread increases in logging intensity coupled with extensive illegal logging, which has decreased or eliminated post-logging forest recovery. The absence of many conservation priority species from 2008 to 2010 field data suggests continuing population declines and increasing rarity of species at risk of extinction. These declining trends are consistent with other recent findings of wildlife declines and extinctions in West Africa (Oates et al., 2000; Brashares et al., 2001; Beier et al., 2002; Thiollay, 2006).

The crucial conservation value of unlogged forest for Ghana's remaining birds is apparent (Fig. 2), although the exceedingly small area of unlogged forest left in Ghana may be insufficient to mitigate the ongoing, overall declines in forest understory birds. The persistence of many species in logged forest demonstrates the importance of regenerating logged forest for understory bird communities. The enormous potential of regenerating logged forest for bird conservation has been demonstrated by Holbech (1996, 2005) in Ghana as well as by other authors elsewhere in the tropics (e.g., Barlow et al., 2007; Michalski and Peres, 2013; Powell et al., 2013; Edwards et al., 2014; Powell et al., current issue-a; Powell et al., current issue-b). For this conservation potential to be realized, urgent measures must be taken to decrease logging intensities and enforce the legally mandated post-logging recovery times, particularly as Ghana's remaining forest consists of fairly small (<200 km^2) and isolated fragments highly vulnerable to biodiversity loss (Holbech, 2005; Beier et al., 2002).

4.1. Long-term changes in Ghana's forest understory bird communities

The greatest difference between the 1993–1995 and 2008–2010 datasets appeared in older regenerating forest treatments (~10 and ~20 years post-logging). In 1993–1995, the understory bird community exhibited increases in abundance following logging (Holbech 1996, 2005; Fig. 2); this led to the conclusion that the forest bird community appeared to be resilient and that post-logging recovery of forest understory bird communities could occur within the legal minimum recovery period in Ghana of 40 years. However, reported logging intensities in Ghana have increased over 600% since 1995, well beyond the threshold of sustainability for timber production (Hansen et al., 2009, 2012). Over the same period, repeated incursions by illegal logging operations have inhibited forest recovery. In response, our findings indicate that by 2008–2010, understory bird communities declined >50% in abundance and did not show any indication of recovery. Empirical species richness declined by 35% (from 71 to 46 species), and extrapolation indicated this decline is significant (Fig. 3). The fact that the 1993–1995 dataset represents a smaller sampling effort underlines that these results are conservative and reflects grave implications for conservation.

Substantial increases in logging intensities together with decreased post-logging recovery times appear to be driving severe declines that are manifest throughout the entire bird community, rather than restricted to any single group or species. Of the 3 species captured in greatest numbers, yellow-whiskered greenbul (*A. latirostris*) declined by 73% and icterine greenbul (*P. icterinus*) declined by 90% between 1995 and 2010 (Table 2). These provide examples of 2 species with distinctly different life histories, despite belonging to the same family. Yellow-whiskered greenbul is a forest generalist that occupies both interior and edge of all types of primary and secondary forest, feeding on fruit and arthropods; it is generally solitary and has variable reproductive strategies; in some areas it uses leks for breeding and is polygamous and nomadic, whereas in others it may be resident and monogamous (Fishpool and Tobias, 2005b). Icterine greenbul is a forest specialist that prefers interior to edge habitats, often forages in mixed-species flocks, sometimes as the leader, and is monogamous and territorial (Fishpool and Tobias, 2005a). One feature they both share is foraging by gleaning and sallying as well as attendance of *Dorylus* ant swarms in order to capture insects fleeing the ants (Fishpool and Tobias, 2005a; Fishpool and Tobias, 2005b). Logging and fragmentation is known to negatively affect *Dorylus* ants, which in turn could affect their avian associates (Peters et al., 2008).

The 15 year period between our 2 datasets should represent at least 1–2 generation lengths for many small-bodied birds, and thus potentially sufficient time to reflect differences in reproductive success influenced by logging and related disturbance patterns. Green-tailed bristlebill (*Bleda eximius*; vulnerable) is an example of a red list species endemic to Upper Guinea that has declined (by 38%) but remains sufficiently abundant to be a feasible candidate for follow up demographic study. Many other species (e.g., 25 species detected in 1993–1995 but not in 2008–2010; Table 2) should be monitored in future study, but were captured in such small numbers that population-level responses to logging would be difficult to quantify. As is typical in tropical forests with high species richness, most species are relatively rare, and Ghana is no exception; in 2008–2010, more than 90% of species were captured at a rate of less than 10 per 10000 nmh (Table 2), highlighting their vulnerability to local extinction. In contrast to some other tropical and temperate contexts, no edge, pioneer, or invasive species have moved into replace the understory birds disappearing from this system, resulting in many fewer birds and species in Ghana's increasingly disturbed and degraded forests.

4.2. Recent trends in Ghana's forest understory bird communities

Overall understory bird abundance and conservation priority species declined significantly in logged compared to unlogged forest (Table 3). Forest generalist and sallying insectivores were the guilds hardest hit by logging (Table 3). Typically we would expect forest specialists rather than generalists to be more greatly affected by forest disturbance (Fimbel et al., 2001; Sodhi et al., 2011). The fact that the opposite appears to apply in this case is provides an example of the difficulty predicting specific impacts of logging in any particular system or region *a priori*, without collecting empirical data (Weber et al., 2001; Edwards et al., 2014). Forest generalist declines may be related to declines in forest quality that interface with life history traits of individual species in this group.

Salliers may respond negatively to logging due to the post-logging emergence of denser understory vegetation and changes in light conditions and lower strata aerial arthropod abundance (Sodhi et al., 2011). Both or either group may be particularly adversely affected by the interaction of logging with foraging, nesting, predation, competition, and/or other factors (Sigel et al., 2006). However, further studies, particularly demographic and population studies, will be necessary to reveal the precise mechanisms and processes that may have led to significant declines of this and other groups or species, particularly as baseline ecological data for many West African bird species are lacking (Thiollay, 2006; BirdLife, 2013). High variation in guilds' responses to forest treatments was evident, likely due to high variation in forest destruction, degradation and disturbance associated with illegal exploitation. Our data reflect this unevenness in avian distributions, with large capture values as well as zeros (Appendix).

4.3. Conservation and management implications for Ghana's Upper Guinea forests and avifauna

Previous studies have demonstrated that illegal logging is the main driver of forest destruction and degradation in Ghana's protected forests (Hansen and Treue, 2008; Marfo, 2010; Hansen et al., 2012). Here, we show that excessive logging intensities, driven both by increases in legal and illegal logging in Ghana's protected forests since 1995, have resulted in precipitous declines of Ghana's forest understory bird communities. Recent and current levels of timber extraction Ghana not only appear to be unsustainable in terms of timber production but also with respect to birds, and likely other forest wildlife. Other wildlife conservation failures that have already been documented in Ghana provide an ominous picture of the fates that await forest wildlife without substantial intervention to change their current trajectory (Oates, 1999; Oates et al., 2000; Brashares et al., 2001).

Previous reports and publications (e.g., Oates, 1999; Oates et al., 2000; Holbech, 2005; Oates, 2006; Jachmann, 2008; Holbech, 2009; Marfo, 2010; Hansen et al., 2012; Franck and Hansen, 2014) have made extensive forest conservation and management recommendations for Ghana. Measures should include installing road blocks in logging concessions (to prevent entry by illegal operators) and establishing and maintaining a patrol presence in areas where vulnerable species persist. Conservation priority species as well as avian guilds and species that have exhibited exceptional declines since 1995 (e.g., forest generalists, sallying insectivores; Tables 2 and 3, Appendix), should be targeted for special protection and monitoring. Such actions should be accompanied by follow up studies, including demographic and/or other population research investigating potential mechanisms of species declines and/or resilience (Sigel et al., 2006; Hamer et al., current issue; Powell et al., current issue-a; Powell et al., current issue-b) and the values of regenerating forest (Barlow et al., 2007; Michalski and Peres, 2013; Edwards et al., 2014) for understory birds.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.02.010.

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