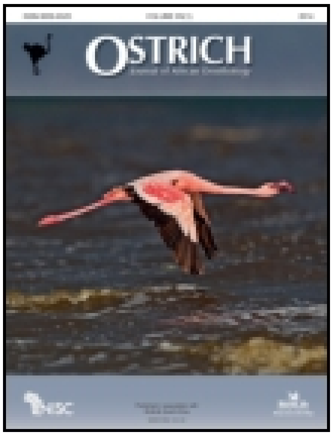

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Movement ecology of five Afrotropical waterfowl species from Malawi, Mali and Nigeria §

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Habitat availability for Afrotropical waterbirds is highly dynamic with unpredictable rainfall patterns and ephemeral wetlands resulting in diverse movement strategies among different species. Movement strategies among waterfowl encompass resident, regional and intercontinental migrants, but little quantitative information exists on their specific movement patterns. We studied the movement ecology of five Afrotropical waterfowl species marked with satellite transmitters in Malawi, Mali and Nigeria. Resident species, including White-faced Whistling Ducks *Dendrocygna viduata*, Fulvous Whistling Ducks *Dendrocygna bicolor* and Spur-winged Geese *Plectropterus gambensis*, remained sedentary during the rainy season and only flew limited distances during other months. In contrast, Knob-billed Ducks *Sarkidiornis melanotos* made short regional movements >50 km in all months and showed little site fidelity to previously used habitats in subsequent years. Garganey *Anas quequedula* followed an intercontinental strategy and made long-distance jumps across the Sahara and Mediterranean to their Eurasian breeding grounds. Most species flew farthest during the dry season, as mean daily movements varied from 1.5 to 14.2 km and was greatest in the winter months (January–March). Total distance moved varied from 9.5 km for White-faced Whistling Ducks (October–December) to 45.6 km for Knob-billed Ducks (April–June). Nomadic behaviour by Knob-billed Ducks was evidenced by long exploratory flights, but small mean daily movements suggested that they were relying on previous experience. Improving our understanding of these movement strategies increases our ability to assess connectivity of wetland resources that support waterfowl throughout their annual cycle and focuses conservation efforts on their most important habitats.

Keywords: migration, nomadism, Sahel, satellite telemetry, sub-Saharan, waterfowl, wetlands

Introduction

The ecology of migratory birds is defined by their movements among habitats spanning vast landscapes. In arid and semi-arid regions, waterbirds are dependent on the availability of food and water in wetlands controlled by rainfall that is unpredictable in both timing and quantity (Petrie and Rogers 1997; Zwarts et al. 2009). Different species exhibit distinct movement strategies to cope with shifting resource availability, but quantitative information documenting the timing and extent of these movements is limited. An understanding of the connectivity of the wetlands that provide breeding habitat, roosting and moulting sites, staging areas, adequate food resources, and protection from exploitation and disease is critical to migratory bird conservation (Dodman and Diagana 2006; Scott and Rose 2006).

Most Afrotropical Anatidae are assumed to make long-distance movements in response to changing water levels at wetlands separated by large areas of unsuitable arid habitats as do nomadic species in Australia (Roshier et al. 2008a,

§ This paper is part of a special memorial issue commemorating the work of the late Philip Hockey

2008b). Waterfowl populations concentrate at permanent wetlands, especially during dry years, but disperse opportunistically with sporadic rainfall events or during wet years to recently flooded ephemeral wetlands (Dodman and Diagana 2007; Cappelle et al. 2010). Temporary wetlands may go unused in some years resulting in underestimation of their importance as critical waterfowl habitat (Dodman and Diagana 2006; Scholte 2006). Consequently, area waterbird counts to track population trends in arid environments are both difficult to conduct and to interpret, especially without movement data that defines the wetland connectivity.

Identifying connectivity of wetland networks is of critical importance for future conservation in the Afrotropics where wetland conversion (Scholte 2006), habitat alteration (Petrie 2000; Li et al. 2007), and threats of climate change (Hulme 2001; Hulme et al. 2001; Delire et al. 2008) are simultaneously affecting wetland hydrology. General movement patterns have been described for Afrotropical waterbirds, including local migrants that move short distances (<50 km) within a network of wetlands; regional migrants and 'rain migrants' that regularly move in response to rainy seasons; 'nomads' that move in response to irregular rainfall events (Dodman and Diagana 2006); and intercontinental migrants that span large distances to reach northern breeding areas. Although ringing returns have been used to describe general waterfowl movements between wetlands (Oatley and Prŷs-Jones 1986; Underhill et al. 1999), little empirical data has been available on the detailed timing and movements of waterfowl using wetland networks in Malawi, Mali and Nigeria. Thus, we conducted a study marking Garganey *Anas querquedula*, Fulvous Ducks *Dendrocygna bicolor*, White-faced Whistling Ducks *D. viduata*, Knob-billed Ducks *Sarkidiornis melanotos* and Spur-winged Geese *Plectropterus gambensis* with satellite transmitters to track their movements and identify the network of key sites they used during different months.

Methods

Study areas

Inner Niger Delta

Located in Mali, the second largest wetland in Africa was designated as a Ramsar Wetland Site of International Importance in 2004. It encompasses over 40 000 km² of low-elevation floodplain including seasonally inundated lakes, ponds and river channels in the Sahel (Figure 1). It is critically important to waterfowl and used during the northern winter by one million migratory ducks that breed in the Palearctic as well as 100 000 Afrotropical ducks (Girard 2006). Seasonal rainfall typically results in flooding from August to December with decreasing water levels in subsequent months leading to large aggregations of

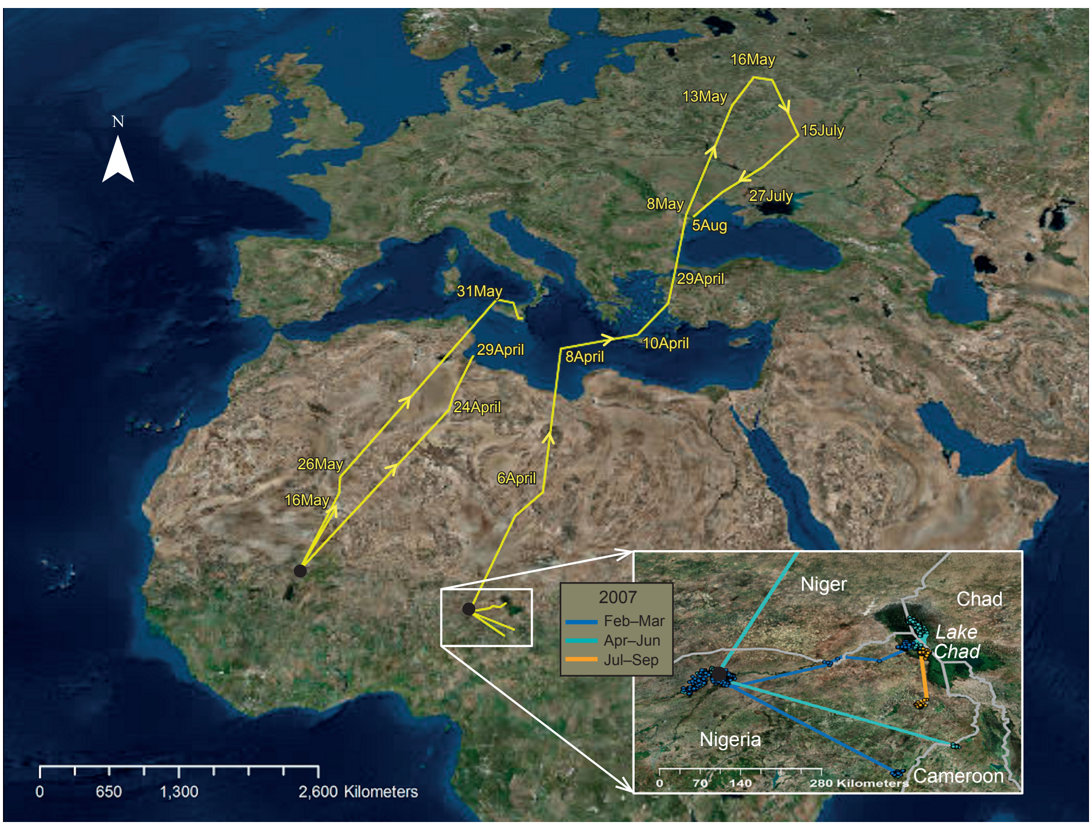

Figure 1: Locations of the Inner Niger Delta of Mali and Hadejia-Nguru wetlands of Nigeria are indicated with black circles, and the inset shows the Hadejia-Nguru wetlands in relation to the Lake Chad Basin. Migration pathways and dates (yellow) are shown for four of the 20 Garganey marked in 2007 and 2009, and the inset shows finer resolution movement patterns of seven Garganey marked in 2007 between Hadejia-Nguru wetlands and the Lake Chad Basin. Samples for each period include (birds, Argos locations, SE): February–March (7, 94.1, 6.2), April–June (3, 91.7, 39.8), and July–September (1, 82, NA)

waterbirds at permanent water bodies as flood levels recede (Dodman and Diagana 2006; Girard 2006). Between 5% and 10% of the floodplains in the southern half of the Inner Delta is used for rice-farming (Zwarts et al. 2009).

Hadejia-Nguru Wetlands
These wetlands in north-eastern Nigeria (Figure 1 inset) are characterised by permanent and seasonal lakes, floodplains, mud flats and marshes that drain into Lake Chad via the Hadejia and Jama'are rivers. The extent of flooded wetlands varies synchronously with the Inner Niger Delta in Mali (Zwarts et al. 2009). Rainfall occurs from May through October and peaks in August (Thompson and Polet 2000) with water levels rising 3–5 m (Zwarts et al. 2009). During the subsequent dry season, water levels gradually decrease, and the Hadejia and Jama'are rivers exhibit little flow. These wetlands are of international importance for resident and migratory waterfowl populations, with the seasonal Garganey population estimated between 70 000 and 150 000 individuals (Cecchi et al. 2008). The wetlands support a dense human population, and land use is dominated by intensive wet-season rice farming and free-range poultry that overlap with waterbirds in the wetlands (Cecchi et al. 2008).

Lake Chad Basin
At the intersection of Niger, Nigeria, Chad and Cameroon, this basin (Figure 1 inset) encompassed 20 000 km^2 prior to 1973 but subsequently declined to <12 000 km^2 due to droughts and irrigation diversion (Zwarts et al. 2009). As a result, the southern extent of Lake Chad has become a small lake surrounded by floodplains while the northern extent has changed from wetlands to woodlands. Rainfall from May to October results in peak lake levels during November–January gradually declining in the dry season, and farmers grow sorghum, millet, maize, beans and rice. The Yaeres floodplains and Logone floodplains of Cameroon provide wetland habitats south of Lake Chad. Aerial surveys indicate that many waterfowl species breed in ephemeral wetlands on the edge of the basin during the rainy season and later move to southern floodplains (October–December) before returning to Lake Chad when the floodplains dry out (December–February) and the lake is at its maximum level (Scholte et al. 2004; Zwarts et al. 2009). After 1979, the Logone floodplains of Cameroon were affected by the construction of an upstream dam that adversely affected hydrology, floodplain vegetation and waterbird populations (Scholte et al. 2000; Scholte 2006).

Lake Chilwa
Lakes and wetlands cover 20% of Malawi and provide a livelihood to over 13 million people (Jamu et al. 2011). Lake Chilwa (Figure 2) is the second largest lake in Malawi and shares a border with Mozambique. It is a shallow (average depth 1.5–2.5 m), endorheic lake comprising 1 500 km^2 of open water surrounded by 1 500 km^2 of seasonal wetlands and floodplains in years of average rainfall (Jamu et al. 2011; Njaya et al. 2011). Classified as a Ramsar site in 1997, it sustains 153 Afrotropical and 30 Palearctic bird species. Rain falls during November–March followed by a lengthy dry season, and peak river flows are during February–March (Njaya et al. 2011). Lake levels vary widely with seasonal changes in precipitation and fluctuate dramatically between years (Kalk et al. 1979), drying out completely every 10–20 years (Njaya et al. 2011). After the lake dried out in 1995, Malawians switched from fish to waterbirds as a source of food and income, trapping an estimated 1.2 million waterbirds in 1996 (van Zegeren and Wilson 1997). The basin is one of the most densely populated and poorest areas in Africa (Njaya et al. 2011).

Capture and marking
Waterfowl were captured with mistnets, nooses or bait traps in Malawi, Mali and Nigeria (Table 1). They were sexed and aged, measured, weighed and marked with a satellite transmitter affixed with a backpack harness in 2007 (see Gaidet et al. 2010; Cappelle et al. 2011), and in 2009 waterfowl in Nigeria were surgically implanted (n = 27). Implantation followed Olsen et al. (1992) with modification for a percutaneous antenna. Specifically, a trochar (an intramedullary pin cut in half with the sharp end dulled) was placed in an aluminum tubing sleeve to penetrate the abdominal wall from inside the coelomic cavity. The trochar was removed from the outside, the antenna was threaded through the sleeve, and the sleeve was removed. The

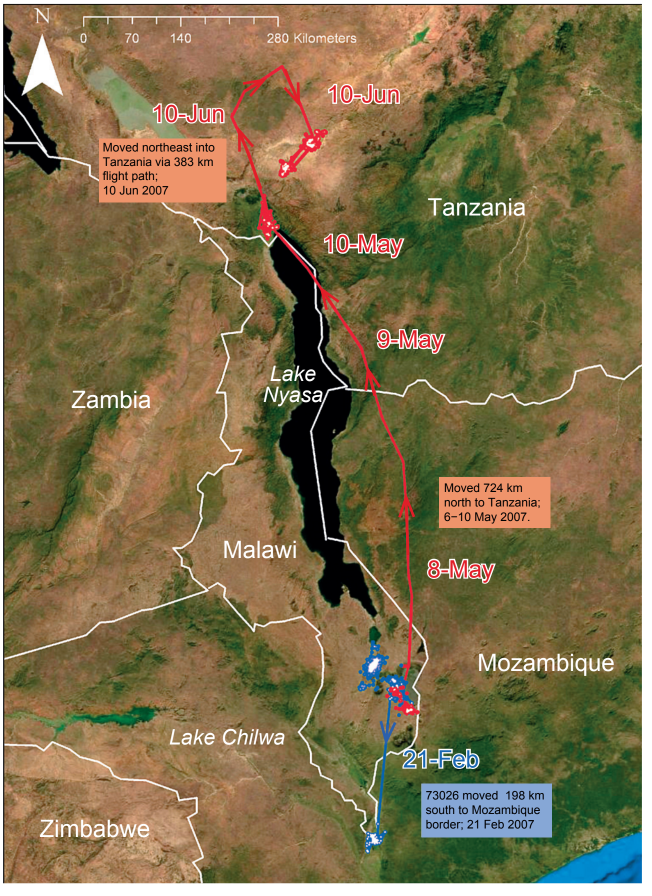

Figure 2: Capture locations (yellow) at Lake Chilwa, Malawi for waterfowl marked with satellite transmitters in 2007. Movement pathways and migration dates are shown for Knob-billed Duck 73295 (red) and White-faced Whistling Ducks 73024 and 73026 (blue)

nylon mesh bag containing the transmitter and antenna cuff was sutured to the internal body wall. Lactated Ringer's solution was administered for fluid resuscitation. Capture, handling and marking procedures were approved by the US Geological Survey Patuxent Wildlife Research Center Animal Care and Use Committee following identical protocols under the University of Maryland Baltimore County Institutional ACUC (Protocol EE070200710).

Movement data

Locations (Table 1) were obtained through the Argos satellite tracking system, and we used locations from GPS transmitters directly or from Argos transmitter location classes LC0–LC3 (>3 transmissions) with an estimated accuracy of <150 m to >1 500 m (see Gaidet et al. 2010; Douglas et al. 2012). We used quantitative and qualitative criteria including implausible flight speeds, angles and rates to remove erroneous locations. For purposes of visualising and summarising data, movements were aggregated by three-month periods (January–March, April–June, July–September and October–December). Data were included if a radio transmitted locations for at least half of a given period. Although locations for most marked individuals ends with signal loss (Cappelle et al. 2011), the cause (radio failure, harness loss, natural or human-caused mortality) was not definitive, so we did not attempt to report their fate. Detailed narratives of movements among wetland networks were provided for individuals whose radios transmitted for >30 d. We used Tracking Analyst in ArcGIS 10.0 (Environmental Systems Research Institute, Inc., Redlands, CA, USA) to describe movement pathways and calculate mean distance and frequency of movements. We used an Argos tracking filter (Douglas et al. 2012) for standard quality locations (LC1–LC3: precision 250–1 500 m) to derive mean and range values for daily movements, total distance travelled, daily travel rate and direction. To visually separate long-distance movements from local utilisation areas in figures, we created fixed kernel home ranges with Hawth's Tools in ArcGIS 10.0 and colour-coded them by three-month periods. However, home-range values were not presented, because we used a mix of Argos and GPS with differing accuracy, and sample sizes to test differences in species, area or time combinations were too small.

Results

We provide detailed descriptions of the movements for the five waterfowl species marked with satellite transmitters by species and country (Figures 1–5). Monthly movement distances and frequency of movements are presented (Figures 6–7), and we summarise means, standard errors and ranges for daily movements, total distances, daily travel rates and direction of travel (Table 2).

Garganey

The most abundant migratory duck in West Africa (Trolliet and Girard 2006), the population (which breeds in Europe and West Siberia) is currently estimated at 1.8 million birds (Wetlands International 2015). Birds from West Africa are believed to migrate to wintering areas via Spain and Italy, spending little time stopping over in North Africa (Scott and Rose 2006). Garganey are often found in large congregations in shallow freshwater wetlands including floodplains and rice fields.

We marked 21 Garganey (11 male, 10 female), 10 in Mali and 11 in Nigeria between 11 January and 15 February (Table 1). We successfully documented the cross-continental spring migration of a female Garganey 73014 from Nigeria (Figure 1). She first migrated 3 206 km north to Crete, Greece over 5 d beginning on 4 April and stopped over for 17 d (Gaidet et al. 2008). She then flew 618 km north-east to western Turkey (Bosphorus region) on 26 April, 538 km north to Romania (Danube River Delta) on 7 May, and 1 434 km north to breeding areas in Russia on 12 May. She returned to the Danube River Delta on 5 August via stopover sites in southern Russia (near Kastornoye, 15 July) and Ukraine (near Krasnohrad, 22 July and near Nova Odesa, 27 July) where she remained until

Table 1: Waterfowl marked with satellite transmitters by species, country, marking site, marking date, data type, days tracked, locations, transmitter mass and number of birds (*N* = 73). Species included Fulvous Whistling Duck (1 male [M], 2 female [F]), Garganey (11 M, 11 F), Knob-billed Duck (3 M, 14 F, 1 unknown), Spur-winged Goose (2 M, 12 F), and White-faced Whistling Duck (8 M, 6 F, 2 unknown). Data types include Argos or GPS locations, 'Days' reports the range tracked (for birds that moved from the marking area) and 'Locations' presents the range of locations obtained

Species	Country	Marking site	Marking date	Data type	Days	Locations	Mass (g)[a]	No. of birds
Fulvous Whistling Duck	Mali	Inner Niger Delta	Feb 2007	Argos	8–646	1–2 414	18	3
Garganey	Mali	Inner Niger Delta	Feb 2007	Argos	34–494	14–518	12	10
	Nigeria	Hadejia-Nguru Wetland	Feb 2007	Argos	75–564	115–449	12	7
	Nigeria	Hadejia-Nguru Wetland	Jan 2009	Argos	0–362	0–415	9.5, 12	5
Knob-billed Duck	Malawi	Malawi Lakes Region	Feb 2007	GPS	1–283	0–3 580	30	3
	Mali	Inner Niger Delta	Feb 2007	Argos, GPS	15–192	55–1 859	18, 30	8
	Nigeria	Hadejia-Nguru Wetland	Feb 2007	GPS	13–839	169–6 497	30	7
Spur-winged Goose	Nigeria	Hadejia-Nguru Wetland	Jan 2009	Argos	12–353	10–236	26*i*	14
White-faced Whistling Duck	Malawi	Malawi Lakes Region	Feb 2007	Argos	2–486	2–2 236	18	3
	Mali	Inner Niger Delta	Feb 2007	Argos	137	54–68	18	2
	Nigeria	Hadejia-Nguru Wetland	Feb 2007	Argos	24–46	99–162	18	2
	Nigeria	Hadejia-Nguru Wetland	Jan 2009	Argos	6–350	5–226	26*i*	9

[a] *i* = implant

4 November. For other Garganey in Nigeria (Figure 1 inset), we recorded regional movements that either preceded cross-continental migration or indicated that non-breeders were foregoing long-distance migration. A male Garganey 73013 moved 446 km south-east to Waza National Park in northern Cameroon on 8 April where he remained until 17 April. Female Garganey 73009 migrated 375 km south-east to Michika near the Cameroon border on 11 March and remained for 78 d until her signal was lost. Male Garganey 73004 flew 323 km east to the Upper Lake Chad Basin over 4 d beginning 22 February and remained there for 152 d. He then moved south to wetlands in Borno State on 28 July and remained there for 78 d until 14 October. Male Garganey 91217 flew 96 km from his marking location eastward along the Hadejia River, where he remained until 25 July.

In Mali, we recorded the migration movements for three of 10 Garganey (Figure 1). Female Garganey 73018 migrated 2 477 km to the Tunisian coast over a six-day period from 23 April to 6 May. Male Garganey 73019 migrated 607 km into northern Mali 100 km south of the Algeria border on 15 May, but his signal was lost a day later. Female Garganey 73006 migrated 2 961 km to Sicily, Italy over a six-day period on 25 May and remained on the island for the next 97 d. Male Garganey 73002 flew 90 km north to Lake Oro on 24 May, where he remained for 68 d. He made three

Table 2: Season, daily movement, total distance, daily travel rate and direction for five species of waterfowl marked with satellite transmitters in Malawi, Mali and Nigeria. Values in parentheses below the means are (SE, birds, days)

Season	Daily movement (km)		Total distance (km)		Daily travel rate (km h⁻¹)		Direction (°)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Garganey								
Jan–Mar	8.0	0.6–54.4	37.9	0.7–114.2	6.1	0–25.7	206.2	9.3–354.4
	(0.8;15;108)		(2.4;15;108)		(0.6;15;63)		(17.2;15;35)	
Apr–Jun	8.2	0.1–66.9	38.0	0.2–98.3	5.6	0–42.8	176.2	3.6–359.4
	(0.9;8;125)		(1.9;8;125)		(0.6;8;84)		(17.8;8;34)	
Jul–Sep	14.2	0.3–133.4	33.6	0.3–130.6	5.8	0–44.1	183.8	0.9–308.8
	(2.7;5;72)		(3.6;5;72)		(1.4;5;58)		(19.9;5;22)	
Oct–Dec	14.0	1.2–53.4	18.7	1.2–53.4	7.7	0–29.7	167.6	58.7–355.9
	(3.8;2;16)		(4.7;2;16)		(4.8;2;6)		(32.5;2;2)	
White-faced Whistling Duck								
Jan–Mar	9.0	0.2–60.7	12.5	0.3–61.4	2.1	0–17.4	128.0	11.9–338.6
	(1.7;7;49)		(1.9;7;49)		(0.5;7;49)		(25.4;7;13)	
Apr–Jun	7.4	0.2–58.4	12.6	0.2–59.8	2.9	0–46.2	155.5	2.7–357.3
	(1.5;5;47)		(2.1;5;47)		(1.1;5;47)		(29.4;5;9)	
Jul–Sep	6.3	0.4–28.7	9.8	0.6–44.8	5.4	0–72.8	284.8	234.5–347.8
	(1.7;3;23)		(2.6;3;23)		(3.1;3;23)		(24.8;3;4)	
Oct–Dec	5.3	0.2–32.3	9.5	0.2–47.1	4.4	0–51.5	248.4	76.7–346.4
	(1.7;2;22)		(3.1;2;22)		(2.4;2;22)		(45.4;2;5)	
Fulvous Whistling Duck								
Jan–Mar	5.5	0.4–45.9	18.2	0.4–146.7	4.1	0.02–43.3	158.9	17.7–350
	(0.7;1;101)		(2.3;1;101)		(0.6;1;101)		(25.7;1;14)	
Apr–Jun	5.1	0.1–57.1	11.9	0.1–124.3	4.5	0.03–48.1	184.1	17.9–337.5
	(0.6;1;138)		(1.3;1;138)		(0.7;1;137)		(34.3;1;11)	
Jul–Sep	5.4	0.3–61.8	13.8	0.4–152.7	4.5	0.08–55.8	163.0	39.4–293.9
	(0.7;1;146)		(1.6;1;146)		(0.7;1;146)		(20.7;1;18)	
Oct–Dec	5.5	0.3–27.4	16.6	0.5–137.2	4.9	0.01–27.2	184.2	70.1–322.6
	(0.6;1;94)		(2.4;1;94)		(0.7;1;94)		(24.3;1;12)	
Knob-billed Duck								
Jan–Mar	1.5	<0.1–5.6	26.9	0.1–180.8	0.6	<0.1–2.6	174.3	25.2–354.5
	(0.1;12;144)		(2.2;11;144)		(<0.1;11;144)		(12.8;11;32)	
Apr–Jun	1.8	0.5–8.6	45.6	9–162.4	0.7	0.2–3.6	158.2	2.4–356.4
	(0.1;9;91)		(3.2;7;91)		(0.1;7;91)		(16.1;7;37)	
Jul–Sep	1.7	0.3–5.3	34.1	2.3–194	0.6	0.1–2.2	160.0	31.2–347.3
	(0.1;6;92)		(3.9;2;92)		(<0.1;2;92)		(23.2;2;20)	
Oct–Dec	1.9	<0.1–21.6	26.9	0.1–327.6	0.6	<0.1–6.9	172.3	57.4–317.5
	(0.3;2;91)		(6.2;2;91)		(0.1;2;91)		(22.9;2;13)	
Spur-winged Goose								
Jan–Mar	7.1	0.2–76.5	14.7	0.2–76.5	2.8	0–19.9	127.0	8.4–321.1
	(1.6;13;66)		(2.1;13;66)		(0.5;13;66)		(30.1;13;14)	
Apr–Jun	6.8	0.1–56.4	13.0	0.1–66.6	1.7	0–13.1	199.0	17.6–327.4
	(1.3;7;67)		(2;7;67)		(0.3;7;67)		(32.7;7;11)	
Jul–Sep	8.1	0.2–27.8	12.5	0.2–106.5	2.7	0–23.3	164.0	67.2–317.8
	(1.7;2;24)		(4.4;2;24)		(1.1;2;23)		(77.8;2;3)	
Oct–Dec	7.2	0.4–70.8	10.2	0.5–70.8	4.1	0–25.9	213.4	0–288.1
	(2.8;2;28)		(3.1;2;28)		(1.2;2;28)		(68.2;2;3)	

movements exceeding 100 km on 1, 11 and 20 August but remained on the Inner Niger Delta until 9 November.

White-faced Whistling Duck

West African numbers range from 500 000 to 700 000 individuals (Dodman and Diagana 2001; Scott and Rose 2006; Wetlands International 2015). Described as 'semi-nomadic', White-faced Whistling Ducks exploit ephemeral wetlands for part of the year and seasonally congregate at larger water bodies, but undertaking long-distance movements during the wet season (Petrie and Rogers 1997; Scott and Rose 2006). The species prefers floodplains, coastal lagoons and ephemeral wetlands in the tropical forest belt (Dodman and Diagana 2007), but also readily use agricultural fields and ponds (Petrie and Rogers 1997; Petrie 2005; Raeside et al. 2007). They breed during the wet season (May–October) in West Africa, and at the southern extent of their range, they are reported to breed during December–June, peaking in January–February (Johnsgard 1978).

We marked six White-faced Whistling Ducks (3 females, 2 males, 1 unknown) with harnesses between 8 and 14 February: 2 in Nigeria, 2 in Malawi and 2 in Mali (Table 1). We also marked nine individuals (4 males, 5 females) with surgically-implanted transmitters in Nigeria during 21–24 January. Female 73024 remained active within 50 km of the marking location in Malawi for 486 d until its signal was lost (Figure 2), whereas male 73026 moved 198 km south to the border of Malawi and Mozambique on 21 February, where it remained until 24 April. In Nigeria, male 73287 (Figure 3a) flew 515 km eastward along the Hedejia River near its confluence with the Yobe River (near Niger border) over a four-day period beginning on 2 March, then to the upper basin of Lake Chad before returning back to the Hadejia River near the Yobe confluence. On 28 March, he travelled 161 km back to the upper basin until 1 April.

Fulvous Whistling Duck

Population estimates in West Africa have ranged from 85 000 to 100 000 individuals (Delany and Scott 2006; Girard 2006; Scott and Rose 2006), although their current estimate is 20 000 to 50 000 (Wetlands International 2015). They have been described as local residents with 'some quite extensive seasonal movements' (Scott and Rose 2006) and 'nomadic' with movements linked to rainfall events (Dodman and Diagana 2007). There is no evidence of regular migration in West Africa, but periodic appearances of large numbers in some areas suggest that the species is highly mobile with preferred habitats including fringe and emergent vegetation of upland lakes, marshes and rice fields (Scott and Rose 2006). Breeding in West Africa occurs during the drier months (January–April), and adults undergo complete wing moult following breeding when they prefer densely vegetated wetlands.

We tracked three individuals (2 females, 1 male) in Mali from 15 to 18 February. Female 73030 transmitted for 21 months and remained at the marking location for 104 d (Figure 4a) before moving 110 km north on 30 May to Lake Horo. She stayed 85 d before flying 139 km southeast to an area 100 km east of the marking area on 23 August.

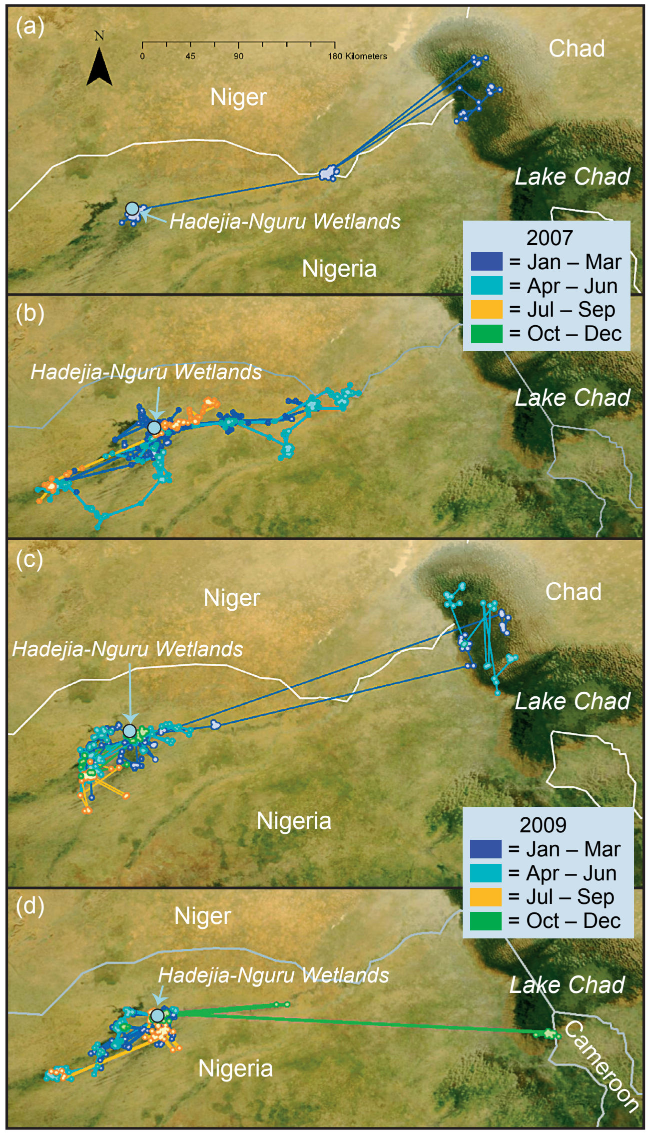

Figure 3: Seasonal movements of a White-faced Whistling Duck (a), four Knob-billed Ducks (b), six White-faced Whistling Ducks (c), and nine Spur-winged Geese (d). Waterbirds were marked at the Hadejia-Nguru wetlands, Nigeria in February 2007 (a, b) and January 2009 (c, d) with capture areas indicated with yellow circles. The single White-faced Whistling Duck 73287 (a) provided 147 total locations, whereas for the other species, locations for three-month periods included (birds, mean locations, SE): Knob-billed Ducks (b) from January–March (4, 471.0, 41.2), April–June (2, 729.0, 248.0), and July–September (1, 445, –); White-faced Whistling Ducks (c) from January–March (6, 41.5, 4.0), April–June (5, 38.8, 7.4), Jul-Sep (1, 54, –), and October–December (1, 48, –); and Spur-winged Geese (d) from January–March (9, 36.6, 3.2), April–June (5, 37.0, 8.3), July–September (2, 37.0, 27.0) and October–December (1, 56, –)

She flew 117 km west near the marking area 56 d later on 18 October and remained there for 121 d. On 16 and 19 February (Figure 4b), she made movements of 60 and 66 km to a lake south-west of Lake Horo before returning back to the marking area. On 13 March, she travelled 86 km north to Lake Horo and remained in the vicinity for 222 d.

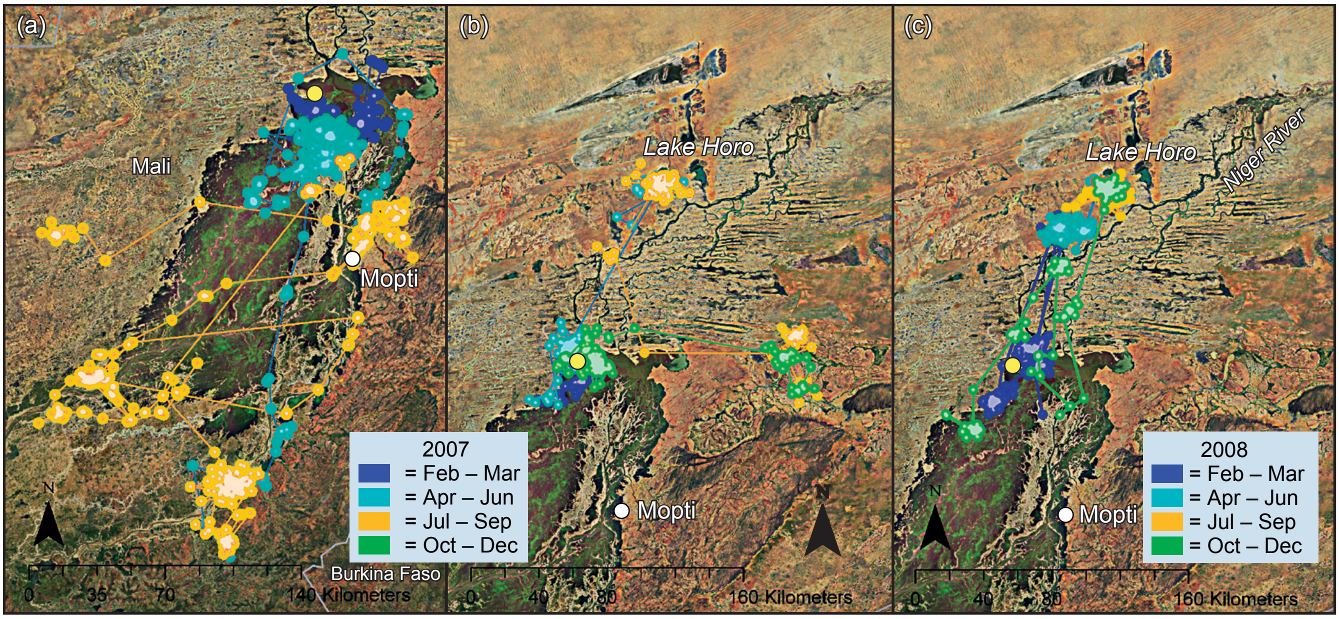

Figure 4: Movement locations of six Knob-billed Ducks in 2007 (a) and Fulvous Whistling Duck female 73030 in 2007 (a) and 2008 (b). Ducks were marked in the Inner Niger Delta of Mali in February 2007. Capture locations are indicated with yellow circles. For each three-month seasonal period in (a), we report the number of marked birds, mean locations , and SE from February–March (5, 348.5, 52.5); April–June (4, 666.3, 147.2); and July–September (3, 321.31, 110.1), respectively. We recorded 2 166 locations from 73030 during 2007 (b) and 2008 (c)

She moved 54 km south on 21 October to the riverine area north of the marking area before flying 171 km south and then back to the same riverine area on 25 October. She remained in this area until her signal was lost on 21 November.

Knob-billed Duck

Populations in West Africa are estimated between 20 000 and 40 000 (Wetlands International 2015) with greatest numbers on the Inner Niger Delta. Described as 'highly migratory' or 'seasonal migrants', they make long-distance movements dictated by rainfall patterns, although sedentary populations are reported (Johnsgard 1978; Delany and Scott 2006; Scott and Rose 2006). They breed during the rainy season in West Africa (May–October) as pairs or groups (harems) occupy tree cavities, but non-breeding may be common in years of poor rainfall (Johnsgard 1978).

We marked 18 Knob-billed Ducks (3 male, 15 female), three in Malawi, eight in Mali and seven in Nigeria (Table 1), during 7–18 February. Female Knob-billed Duck 73295 (Figure 2) remained near her Lake Chilwa, Malawi marking location for 83 d before moving 724 km north to the northern end of Lake Nyasa in Tanzania over a four-day period beginning 6 May and remained there for 32 d. She moved 167 km north on 10 June before turning east for 104 km, finally heading back south 112 km to a wetland south of Ruaha National Park, Tanzania, where she remained for 55 d. She alternated between this location and another wetland 50 km south-west (near Msaka, Tanzania) until 22 November.

In Nigeria, male 73037 (Figure 5a–c) and female 73038 (Figure 5d–f) were marked on 14 February and transmitted for 785 d and 839 d, respectively, during 2007–2009. The male remained near the marking area for 49 d before traveling 180 km eastward along the Hadejia River near its confluence with the Yobe River, Niger over a three-day period beginning 4 April 2007 (Figure 5a). He made five movements that exceeded 50 km, including stops at the Yobe River, the Keffin Haussa River south of Hadejia, wetlands near Gamawa, and multiple stops at Hadejia-Nguru. On 15 July, he moved 299 km north-west into Niger, and 5 d later moved north-west near Zinder, Niger, where he remained for 48 d. He flew back to Hadejia-Nguru on 6 September and stayed until 25 October when he travelled 452 km to upper Lake Chad Basin returning west along the Hadejia River (near confluence with Yobe River) over 3 d and remained there for 25 d. Beginning on 23 November, male 73037 moved 425 km south-east in 2 d to northern Cameroon before settling on the southern shore of Lake Chad where he remained for 153 d until late April 2008 (Figure 5b). From May–June, he made seven movements exceeding 50 km in the Far North Region province, Cameroon and Borno State. He moved 530 km north-west to wetlands east of Zinder, Niger during a six-day period on 27 June where he remained for 31 d. He flew 85 km east towards Goure, Niger on 30 August; 276 km south-east to the Hedjia River near its confluence with the Yobe River at the Niger–Nigeria border on 21 October; 154 km east to the eastern shore of Upper Lake Chad; and back to the Hadejia River 13 d later on 18 January 2009 (Figure 5c). He migrated 207 km west to the Hadejia-Nguru wetlands on 7 February, and during the subsequent two months he made four movements exceeding 50 km along the Hadejia River.

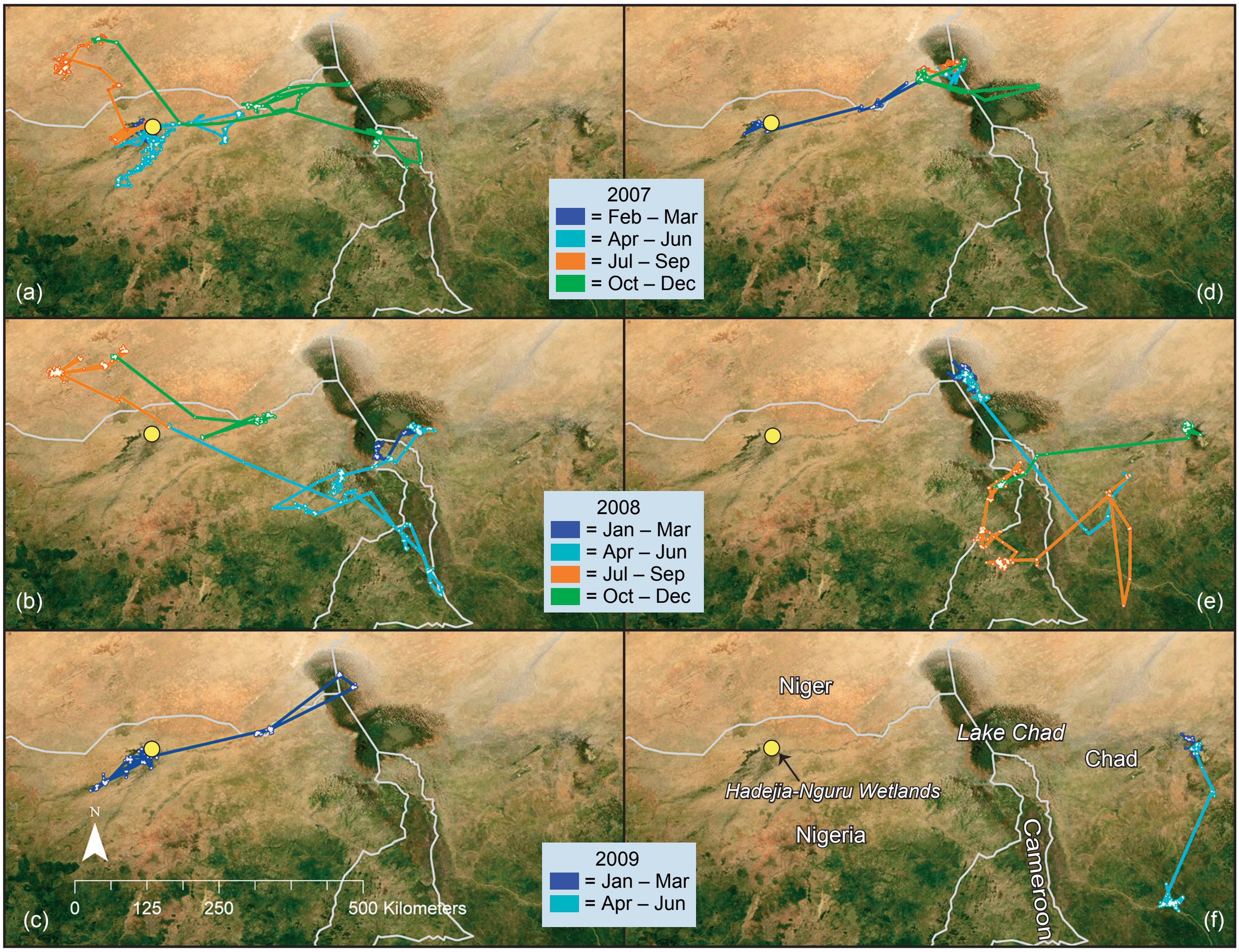

Figure 5: Locations for Knob-billed Duck male 73037 (a–c) and female 73038 (d–f) across three years (2007–2009). Knob-billed Ducks were marked at the Hadejia-Nguru wetlands in Nigeria in 2007, and capture locations are indicated with yellow circles. We recorded 5 365 locations from 73037 and 3 550 locations from 73038

Female 73038 moved 165 km east along the Hadejia River to the Niger–Nigeria border (Yobe River confluence) on 28 February 2007 and remained there for 30 d (Figure 5d). On 31 March, she flew 160 km east to the Upper Lake Chad Basin, where she remained for 122 d. She travelled 20 km west into Niger (Diffa Region) on 31 July and stayed for 118 d; on 26 November, she completed a 410 km exploratory flight eastward to the lower basin and back into Niger. She migrated 66 km west to the eastern shore of the upper basin on 17 December and remained there for six months before returning 334 km south-east into Chad (east of Fauhul Reserve) on 16 June 2008 (Figure 5e) and 83 km north-east to Fadje on 23 June. On 10 July, she flew 409 km in a four-day roundtrip south into the Tandjile Region and back to Fadje. She moved 213 km south-west into the Far North Region of Cameroon over a 22-day period ending on 16 June and flew between Cameroon and Borno State, Nigeria, over the next 81 d. On 18 October, she moved 321 km east from the capture area over a 22-day period into the Batha Region of Chad where she remained for nearly six months. On 15 April 2009 (Figure 5f), she moved 274 km south along the Chari River, Chad, where she remained 44 d until signal loss on 2 June.

Four of the other individuals marked in Nigeria transmitted for >30 d (Figure 3c). Female 73035 remained near Hadejia-Nguru for 24 d before moving 185 km over 23 d beginning on 3 March to settle in an area east along the Hadejia River (between Kariari and Gashua) until its signal was lost 30 d later. Female 73039 remained in the vicinity of the marking area at Hadejia-Nguru for 44 d before moving 56 km east along the Hadejia River (between Kariari and Gashua) on 31 March, where she remained until her signal was lost 56 d later. Male 73040 moved 63 km east along the Hadejia River (between Kariari and Gashua) on 27 February and remained there until 8 April, when he flew 108 km east to the Hadejia River near its confluence with the Yobe River near Niger. Male 73041 made exploratory flights on 24 and 27 February, moving 232 km west (near Jigawa) and 192 km west (near Kirjikasama), respectively, before returning back to the vicinity of the marking area at Hadejia-Nguru on both occasions. On 27 March, he travelled 150 km east along the Hadejia River near its confluence with the Yobe River near the Niger border before moving 50 km south to the Yobe River on 27 April. On 11 May, he moved 247 km over 4 d, flying west towards Hadejia and then east back to Hadejia-Nguru. He moved 127 km south on 28 March and then north-west to the wetlands west of the town of Hadejia, where he remained for 54 d. On 22 July, he flew 111 km north-east back to Hadejia-Nguru, where he remained until his signal was lost 26 d later.

In Mali (Figure 4a), female 73046 remained near the marking area for 105 d before moving 59 km south-west near Sorme on 2 June, 153 km south to Bani River over 3 d beginning on 23 June, and 79 km south-west towards wetlands near Mansara on 29 June, until her signal was lost 10 d later. Female 73048 remained in the vicinity of the marking area for 160 d prior to moving 173 km west on 24 July before signal loss 9 d later. Female 73049 remained near the release area for 129 d before moving 168 km south-east (to the Niger River) over 2 d beginning on 23 June. On 17 July, she moved 167 km south-west over 2 d to the confluence of the Niger and Diaka rivers and flew 124 km over 4 d beginning 23 July returning to the confluence of the Niger and Diaka. Twenty days later on 12 August, she flew east for 296 km over 3 d, returning to the Niger and Diaka river convergence, where she remained until signal loss 12 d later. Female 73291 remained near the release area for 136 d before moving 205 km south to the Bani River (below Djenne) over 3 d beginning 1 July, where she remained for 57 d.

Spur-winged Goose

West Africa numbers are estimated at 50 000–100 000 (Perennou 1991; Delany and Scott 2006; Wetlands International 2015). They are described as partially migratory with seasonal movements up to several hundred kilometres assumed to be associated with fluctuating water levels (Scott and Rose 2006). The species appears to occur in large concentrations during all seasons in West Africa with 22 000 counted at Lac Maga in Cameroon (Delany and Scott 2006). Breeding coincides with the rainy season, and eggs are laid during August–January. During the dry season, they often moult at large permanent water bodies, although they have shifted from a diet of wild foods to agricultural crops for much of the year (Halse 1985).

We marked 14 individuals during 16–21 January at the Dagona Wildlife Sanctuary, Hadeija-Nguru wetland in Lake Chad Basin National Park, Nigeria. Of nine geese with regular movements (Figure 3d), four remained <50 km of the marking area at Hadeija-Nguru until their signal was lost (30 March–7 July). Female 41160 remained at the marking site for 36 d before flying 68 km south-west on 27 February until its signal was lost on 4 March. Male 41144 remained at Hadeija-Nguru for 43 d before moving 50 km south-west on 5 March, where he remained until signal loss on 2 April. Female 40963 remained near the marking site for 96 d before traveling to wetlands 67 km south-west on 26 April, where she remained until 23 July. Female 40931 remained near the marking site for 47 d prior to moving 52 km west on 6 March and remained there until 20 April. Female 40962 transmitted a signal until 29 December and was the only Spur-winged Goose that made several long-distance movements. She flew 50 km to wetlands south-west of the marking area on 10 February before returning back to the marking area 150 d later on 10 July. On 29 October, she moved east along the Hadejia River and then back to the Hadejia-Nguru flying 240 km over a period of 6 d. On 20 November, she flew 376 km east to Lake Chad and remained there until 29 December.

Movement metrics

We examined the mean distance travelled between wetlands by species and month (Figure 6). We used a distance of >50 km to distinguish between-wetland movements and within-wetland foraging flights, since Argos transmitter errors could be >10 km. Garganey moved farthest during April and May (Figure 6) when flights could exceed 1 000 km and travelled least during the autumn and the summer. White-faced Whistling Ducks made flights in February and March of up to 200 km and continued moving through May but showed little movement for the rest of the year. In contrast, Fulvous Whistling Ducks moved >100 km in spring and autumn, whereas Knob-billed Ducks moved >100 km in most months and especially during October–November. Spur-winged Geese, like many of the ducks, also flew farthest during the dry season (>200 km).

Similarly, the frequency of between-wetland movements varied by species and season (Figure 7). Garganey travelled most frequently during the summer (July–August) and made several short flights during the spring migration (February–May). White-faced Whistling Ducks flew more often among wetlands in winter but made several movements among wetlands during February–May, whereas Fulvous Whistling Ducks moved frequently during February and October. Knob-billed Ducks travelled frequently year-round, whereas Spur-winged Geese moved most in October–November. Generally, Fulvous Whistling Ducks and Knob-billed Ducks moved more frequently than did the other species.

Mean daily movements varied from 1.5 to 14.2 km with a maximum mean value of 133 km (Table 2). Garganey had the greatest mean daily movements in July–September (14.2 km) and October–December (14.0 km), whereas Knob-billed Ducks moved the least (1.5–1.9 km). White-faced Whistling Ducks (9.0 km, January–March) and Spur-winged Geese (8.1 km, July–September) also moved regularly, but across all species the largest mean daily movement was in the winter months (January–March). Mean total distance varied from 9.5 km (White-faced Whistling Ducks, October–December) to 45.6 km (Knob-billed Ducks, April–June), but a Knob-billed Duck had the maximum total distance of 327 km. The mean rate of travel (uncorrected for wind speed) was greatest for Garganey (7.7 km h^{-1}), which is not surprising, but its greatest movements were in autumn (October–December) rather than spring (5.6 km h^{-1}, April–June). A Fulvous Whistling Duck had the greatest individual mean rate of travel (56 km h^{-1}) in summer (July–September). Knob-billed Ducks moved the least, and had the smallest variation in direction travelled (SE = 12.8°) moving southward (174.3°) from January–March.

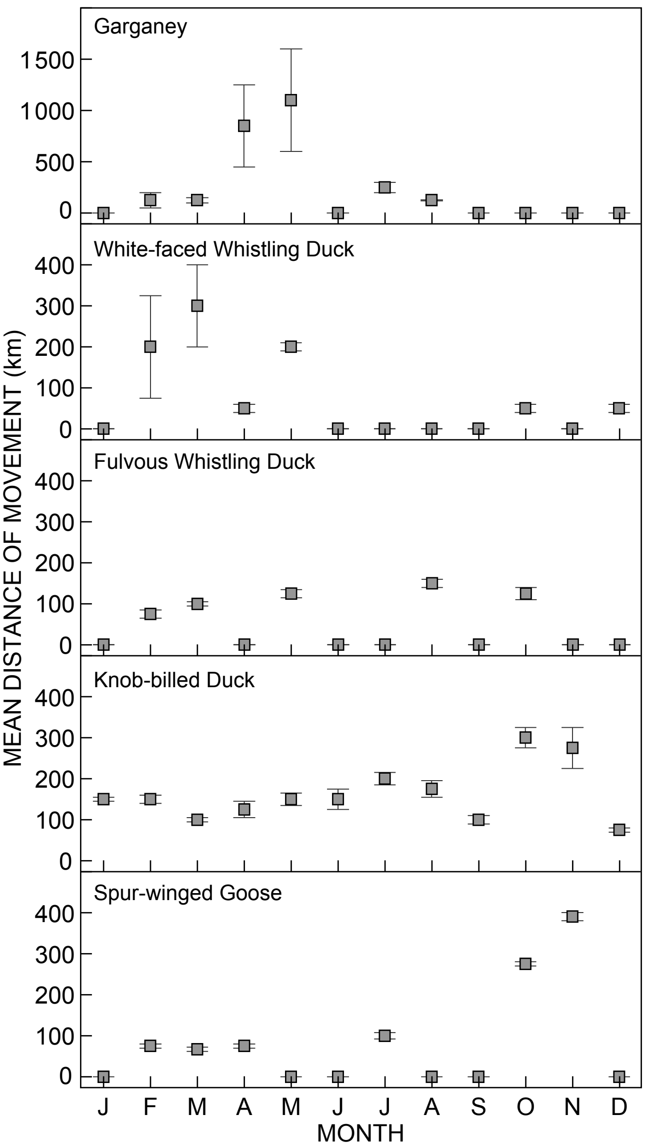

Figure 6: Mean monthly distance of movements >50 km for Garganey (n = 21), White-faced Whistling Ducks (n = 8), Fulvous Whistling Ducks (n = 2), Knob-billed Ducks (n = 16) and Spur-winged Geese (n = 9) from 2007–2009 in Nigeria and Mali. Zeros indicate months during which a species performed no movements >50 km, and vertical bars represent the SE

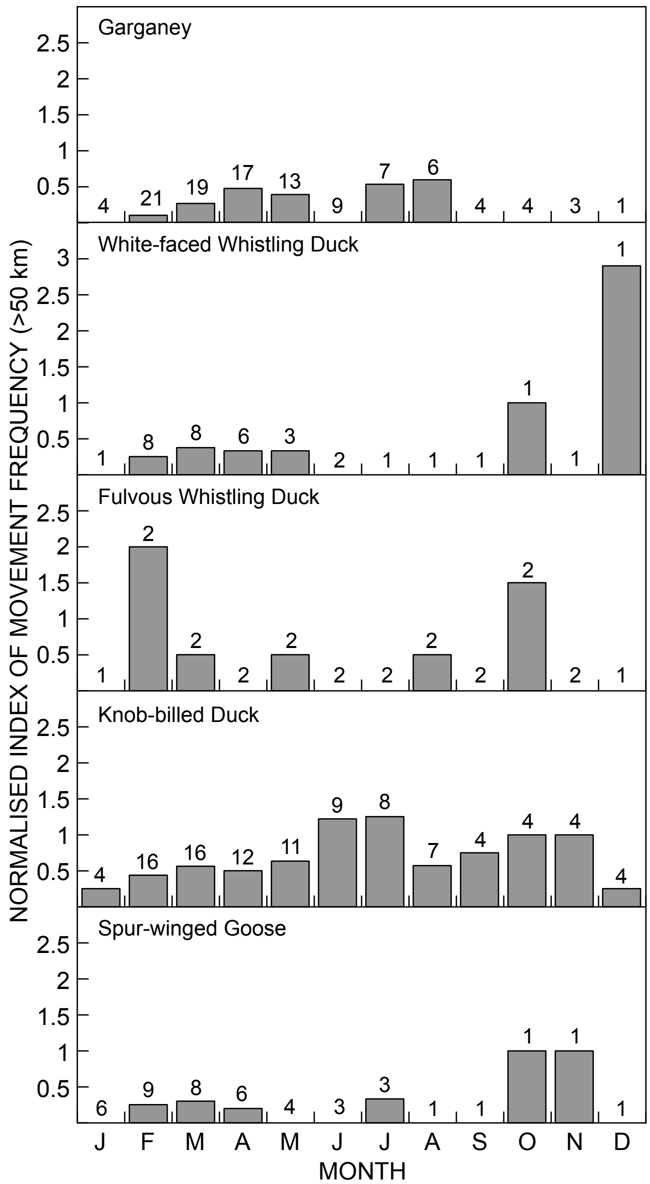

Figure 7: Normalised index of movement frequency of all movements >50 km for Garganey (n = 21), White-faced Whistling Ducks (n = 8), Fulvous Whistling Ducks (n = 2), Knob-billed Ducks (n = 16), and Spur-winged Geese (n = 9) by month from 2007–2009 in Nigeria and Mali. Indices were calculated for each species by dividing the total number of movements >50 km by the number of birds with active satellite transmitters in that month. Values of zero indicate months during which there were no movements >50 km. Numbers above the bars indicate active birds each month and include individuals that had signals for multiple years

Discussion

Satellite telemetry provides insights into species-specific behaviours, habitat use and distribution as expressed through diversity and seasonality of movement strategies (Bermingham et al. 1992; Franklin and Miller 2010; Vickery et al. 2014). Our results showed that, although the waterfowl species exhibited a wide range of movement patterns, most had high site fidelity to key wetlands for weeks to months with local movements characterised by relatively short flights. For instance, although Garganey followed a typical pattern for intercontinental migrants increasing pre-migratory local movements in February–March, they congregated in a few major wetlands before flying across the Sahara Desert and Mediterranean Sea to reach their northern breeding areas. Similarly, regional and local migrant White-faced Whistling Ducks, Knob-billed Ducks and Spur-winged Geese concentrated in a few wetlands, but their between-wetland movements were much shorter (300 km) than the Garganey. However, White-faced Whistling Ducks made longer movements between wetlands in February–March, whereas Knob-billed

Ducks and Spur-winged Geese moved farther in October–November (Figure 6, Table 2). Variation in the timing of their movements (Figure 7) may reflect species-specific seasonal resource needs, and that may require targeted conservation efforts for those specific time periods.

Our results also demonstrated some of the difficulties that may be encountered while tracking and marking Afrotropical waterfowl (see Cappelle et al. 2011; Cumming and Ndlovu 2011). Tracking duration was widely variable and, although some individuals were followed for more than a year, many birds were tracked for only a short period. We suspected that the tracking duration was related to high local harvest rates and poor habitat conditions as well as transmitter failures (electronic failure or harness loss). Although adverse transmitter effects on the behaviour of marked birds cannot be ruled out, the transmitters were applied by experienced biologists following standard procedures or by a veterinarian who spent years developing a widely used implant procedure (Olsen et al. 1992), and these techniques have proven successful in many other projects (see Gaidet et al. 2010; Takekawa et al. 2010). Thus, we were confident that the tracks obtained from waterfowl marked with transmitters were representative of general movement patterns for the species.

Longer-term adaptation or learning experience may be influencing their movements, including prior experience with resource distributions that effect dispersal strategies (Roshier et al. 2008b; Cumming et al. 2012; Ndlovu et al. 2013). For example, nomadic behaviour of Knob-billed Ducks was evident from our data. Exploratory flights exceeding 100 km in fewer than 4 d occurred when ducks moved in one direction and then changed course (≥90°) to a different location or returned to the previous location. We documented 15 such exploratory flights in Malawi, Mali and Nigeria, and in nine of these flights (60%) ducks returned to the original area from which they flew. These exploratory flights allow ducks to assess wetland conditions or conspecific activity in surrounding regions before settling. However, their daily movement was only 1.5–1.9 km, in contrast with Australian Grey Teal *Anas gracilis* that moved 2.9–25.2 km daily (Roshier et al. 2006) and Egyptian Geese *Alopochen aegyptiaca* in South Africa for which most daily movements (57%) were 1–10 km (Ndlovu et al. 2013). Thus, Knob-billed Ducks seem to explore far less frequently than those species, which may suggest greater reliance on their experience of the area or environmental cues affecting the frequency of their flights.

We also found that the direction of travel ranged widely across species and seasons (Table 2). For example, the mean direction for Garganey during the spring migration period (206°) seemed inconsistent for an intercontinental north–south migration, but its wide range of movement directions was similar to the finding of directional flexibility in movement patterns of European gadwalls *Anas strepera* (Gehrold et al. 2014). Directionality of long-distance movements for Garganey was likely obscured by numerous within-wetland movements. Greater standard errors suggested more directional flexibility for Spur-winged Geese during autumn (SE = 77.8°) and winter (SE = 68.2°) and for White-faced Whistling Ducks in the winter (SE = 45.4°).

The presence of waterbirds at ephemeral wetland sites and movement between them has been shaped by anthropogenic factors (Dodman and Rose 2000; Herrmann et al. 2004; Hockey et al. 2011) because wetland loss has been exacerbated by degradation through drainage, development, siltation and eutrophication (Petrie 2000). Dam construction has negatively affected the Hadejia-Nguru and the Waza-Logone floodplains (Zwarts et al. 2009) and has highlighted the importance of maintaining water availability. However, waterbirds responded positively to floodplain rehabilitation in these areas (Scholte 2006). Increased grain and rice agriculture and the construction of agricultural water impoundments have resulted in a predictable food supply that is used by some waterfowl species. As a result, waterbirds may be adapting by becoming less nomadic, wintering closer to breeding areas when permanent water bodies and agricultural food sources allow (Petrie and Rogers 1997).

Finally, the ability of migratory species to adapt to climate change may depend on their movement ecology (Arzel et al. 2014). The majority (85%) of precipitation in the Sahel of West Africa falls from July to September (Zwarts et al. 2009), and climate-induced changes to temperatures and the frequency, timing and quantity of rainfall may greatly alter their habitat availability. Climate warming could enhance overwinter survival of both short-distance migrants and resident birds in Eurasia, leaving intercontinental migrants, such as Garganey at a competitive disadvantage (Sanderson et al. 2006). It may be difficult to distinguish changes caused by climate from those related to land-use changes, because the same species may be most responsive to both effects (Hockey and Midgley 2009; Hockey et al. 2011). However, birds that exhibit the greatest flexibility in their movement strategies may be those best able to handle these future global changes.

Conclusions

While structural connectivity of habitats is related to physical adjacency of landscapes (Calabrese and Fagan 2004), functional connectivity depends on the movement characteristics of species (Clobert et al. 2012). Therefore, understanding when, how often and how far different species undertake regional and long-distant movements helps to circumscribe the network of wetlands needed to facilitate efficient conservation (Doerr et al. 2011; Hodgson et al. 2011; Kreakie and Keitt 2012). Our results indicate that travel distances varied widely among the five waterfowl species that we studied, but there were key wetlands to which waterfowl have high site fidelity. Use of focal wetlands may be related to life stages when waterfowl are particularly vulnerable, such as during the moult (Ndlovu et al. 2013).

Changing environmental conditions will shape the future patterns of use for the unique Afrotropical landscape features that are vital to waterbirds across a range of movement strategies (Hockey and Midgley 2009; Cumming et al. 2012; Walther and van Niekerk 2015). Movement ecology information complements available knowledge from site-specific counts in developing long-term conservation strategies that identify wetlands of importance with the context of life history strategies and behaviours (i.e. inter-wetland habitat movements), typical seasonal movements and species requirements for alternative sites with the ability to seek out and utilise (predictability and distance of exploration) in low water years (Morton et al. 2011; Mundava et al. 2012; Iwamura et al. 2014; McIntyre et al. 2014).

Complex seasonal and environmentally influenced movements present difficult challenges for waterbird conservation, especially identifying key sites for different life-cycle stages (Dodman and Diagana 2006). One aim of the former UNEP-GEF African Eurasian Flyways Project was to bring together information on waterbird ecology and habitat use to compile a network of critical waterbird sites for waterbirds in Africa and Western Eurasia (Hagemeijer 2006). In many regions, natural wetland ecosystems have all but disappeared outside of protected areas. It seems likely that within the next two to three decades, many species of waterfowl will become reliant on protected areas where they can find adequate natural food, secure nesting and roosting sites, and freedom from persecution (Scott and Rose 2006).

However, despite >30 years of inter-governmental action, notably the Ramsar Convention on Wetlands and the African–Eurasian Migratory Waterbird Agreement, there remain major gaps in a comprehensive flyway-scale network of sites for waterbirds with less than 25% of key sites designated (Davidson and Stroud 2006). Overall, lack of knowledge of waterbird movements limits our ability to implement conservation programs such as the African–Eurasian Migratory Waterbird Agreement (http://www.unep-aewa.org/). The threat of flyway and population-level external factors, including land-use change, climate change and disease, may lead to further changes in migratory and localised movement patterns (Dodman and Diagana 2007). A better understanding of movement ecology of waterbirds may indicate why some resident and migratory populations are increasing while other populations are in rapid decline in the same flyway (Davidson and Stroud 2006).

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