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The influence of weather on the migration behaviour of Eurasian Bitterns *Botaurus stellaris*

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ABSTRACT

Capsule: Migration studies of tagged Eurasian Bitterns *Botaurus stellaris* provide information on the behaviour of this secretive species in relation to weather conditions.

Aims: To study if cold spells trigger southward migration in resident Eurasian Bitterns. To describe migratory behaviour including flight routes, altitudes, flight direction in relation to wind speed and direction, and general characteristics of stopping sites.

Methods: Six adult Eurasian Bitterns from Dutch breeding areas were followed for two to five years using ARGOS-PTT/GPS transmitters or GPS trackers.

Results: Four individuals remained at the breeding sites in winter and did not migrate in response to cold spells. Two individuals covered distances of 300 and 1600 km between stopping sites. They migrated predominantly at night, but over the Sahara they extended flights into daylight hours. Depending on wind assistance, flight speeds (groundspeed) varied between 3.6 and 26 ms⁻¹. Flight altitude varied from just above sea level when facing headwinds, to almost 2000 m above sea level under tail wind conditions. Repeatedly tracked individuals showed substantial variation in routes and stopping sites between successive migrations. These flight patterns appeared influenced by the speed and direction of the winds encountered en route.

Conclusions: Eurasian Bitterns were either migratory or resident and the latter individuals did not perform facultative movements at the onset of cold spells. The flight speed, flight altitudes, and routes of migrating birds were influenced by wind conditions. This likely explains the variable use of stopping sites between years.

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Eurasian Bitterns *Botaurus stellaris* (hereafter Bitterns) breed in wetlands from Great Britain in the west to Japan in the east (Cramp & Simmons 1977, Voisin 1991). There is a gradual tendency from residency in the southern part of the breeding range to long-distance migration for those breeding in the north (van der Winden *et al.* 2019, Gu *et al.* 2019). Southern and western European populations, including the Bitterns breeding in the Netherlands, may show seasonal migration or remain resident (White *et al.* 2006). In these temperate climates, males tend to be resident, while the smaller females may either be resident or migratory (van der Winden *et al.* 2019). Male and female Bitterns appear to be highly faithful to the breeding area and winter site fidelity has also been shown to be high (van der Winden *et al.* 2019).

In temperate and warmer European climatic zones, the mixing of northern migrants with residents (van der Winden *et al.* 2019) makes it impossible to tell if individuals wintering in such areas belong to the local breeding population or are migrants. The increase in sightings of Bitterns in December–January in western Europe, especially in periods with ice or snow, led to the idea that Bitterns would perform facultative or weather-induced movements in direct response to cold spells (Bijlsma *et al.* 2001, Toms 2002), in contrast to obligate or ‘calendar’ migrants who migrate at a certain time of year whatever the ambient conditions (Newton 2008). For facultative migrants in western Europe, such as Northern Lapwing *Vanellus vanellus* or Eurasian Skylark *Alauda arvensis*, massive movements have been observed as soon as it starts freezing or snowing (Bijlsma *et al.* 2001, Wernham

et al. 2002). However, such observations of immediate facultative movements are lacking for Bitterns. This might be caused by their secrecy or their nocturnal migratory behaviour; alternatively it may be that they are simply not facultative migrants. As the onset of post-nuptial movements occurs during a fixed period in spring (Puglisi & Baldaccini 2000), and is thus calendar-based, individual Bitterns may be either obligate migrants or residents. Indeed, the timing of trans-Saharan migrations in September–October and March–April is similar to other bird species (Zwarts *et al.* 2009, van der Winden *et al.* 2019). Studies of long-distance migrating Bitterns wintering in China (Gu *et al.* 2019), and of the related American Bittern *B. lentiginosus* (Huschle *et al.* 2013), also point to departures in August to November for southward movements and returns in March to April. But will resident Bitterns breeding in temperate climates move in case of cold spells?

Although Bitterns are known as nocturnal migrants in Europe (Puglisi & Baldaccini 2000), it remains unclear what they do if, at sunrise, they are flying over deserts or other landscapes without feeding possibilities. Do they continue migratory flights just as Purple Herons *Ardea purpurea* do (van der Winden *et al.* 2010)? Bitterns hardly fly during the breeding or wintering periods for feeding or roosting. As ‘reluctant flyers’ we expect wind speed and direction to strongly influence flight behaviour, especially over potentially risky environments.

The use of tracking devices to study migration behaviour can be of particular value for ‘cryptic’ species, like the Bittern, which undertakes nocturnal movements. Six adult Bitterns from the Dutch breeding range were followed over several years in order to examine: (1) whether individuals initiated migration in response to severe winter conditions, such as snow or ice, (2) migration timing, routes, speeds, and altitudes, and (3) the potential impact of wind on heading and flight performance. These tracking data allowed us to check if residents in the Netherlands started moving to wintering areas with milder climates in response to the occurrence of snow and ice. Three severe winter periods occurred during the course of the study period, each with more than 10 days of ice and snow cover. Although the cold spells did not last for more than two weeks, and the intensity varied between years, all cold periods included complete ice coverage and/or snow coverage, creating difficult feeding conditions for Bitterns. Biologging also enabled us to study the timing of migration, flight speeds, and the effect of wind conditions en route. It also presented an opportunity

to determine whether Bitterns continue migration flights in daylight and, if so, under which conditions.

Methods

Catching and tagging the bitterns

Ten adult Bitterns were trapped and fitted with tags between 2010 and 2013 in a breeding area in the Netherlands. Within four months, two of them died: one male collided with a high voltage power line and a female died for unknown reasons in October at the breeding site after raising chicks. Two tags stopped working before September. All remaining tagged Bitterns survived for two to five years, providing multi-annual data for six individuals (three males and three females). We consider four of these individuals as ‘residents’ because they stayed within 100 km of their breeding site and remained within the same climate zone, and the other two as ‘migrants’ as they moved to milder climates (van der Winden *et al.* 2019).

Adult males were captured using walk-in traps in their territories (Huschle *et al.* 2002). The females were captured on their nests with walk-in traps or handheld nets during late incubation (see van der Winden *et al.* 2019). All of the individuals were marked with a metal ring and a coded colour ring.

In springs 2010–2012, two adult males and three females were fitted with a tracking device at Ilperveld (52°26′N 4°55′E) and one male was tagged in spring 2013 near Alkmaar (52°38′N 4°53′E). Thus, all birds belonged to a local breeding population in the province of Noord-Holland. The tags were attached with wing harnesses (Thaxter *et al.* 2014), using lightweight Teflon tubes comparable to Lameris *et al.* (2018) with additional elastic inside the tube to enable flexibility, maximize manoeuvrability and allow for a mass increase. Four individuals (two males and two females) were equipped with a 22 g solar panel Platform Transmitter Terminal global positioning system tag (ARGOS-PTT)/GPS (Microwave Telemetry, USA). Additionally, one male and one female were fitted with an 18 g UvA-BiTS GPS tracking model 5CDLe (University of Amsterdam, Bouten *et al.* 2013). Including the harness, this comprised 1.7–3.1% of the body mass at capture.

The PTT/GPS transmitters provide two types of location fixes. The transmitters provide standard ARGOS (Doppler) fixes with a theoretical accuracy of 100 m to more than 1500 m depending on the quality classes A, B, 1, 2, and 3, where class 3 provides the highest accuracy (see www.argos-system.org). If the battery is charged enough, the additional GPS-device

logs accurate locations (± 15 m). The PTT duty cycle was programmed at 10 h on and 24 h off, while the GPS-transmitter was set at a two-hour interval during the period March–October and at a six-hour interval during the rest of the year. The UvA-BiTS GPS trackers provided information on location, altitude above mean sea level (m), instantaneous ground speed, and instantaneous track direction (Bouten *et al.* 2013). These trackers included a radio transceiver for bidirectional communication with a ground-based antennae network, enabling users to download data and upload new measurement schemes remotely. The positions were measured at an interval of 15–30 min after a Bittern arrived within the detection range of the antennae network (mostly in March). Before expected departure, at the end of September or early October, the interval was set to either 30 min or one hour to account for the shorter daylight period and battery charging times. For accuracy and specifications see Bouten *et al.* (2013).

Weather data

Data on wind speed and direction were retrieved from the open access National Centre for Environmental Prediction reanalysis data (NCEP, Kalnay *et al.* 1996) with the R-package RNCEP (see Kemp *et al.* 2012). The NCEP reanalysis data are gridded global datasets of atmospheric variables, with a spatial resolution of 2.5×2.5 degrees and a temporal resolution of six hours (00, 06, 12, 18 UTC). The RNCEP package was used to interpolate the values for the zonal velocity (u) and meridional velocity (v) wind components of wind at the 925 mb (approximately 800 m above sea level) level for each migrating/stopping point for the Bitterns trips (tags 514 and 35218). Based on exploratory analysis of measured flight altitudes and

radar measurements of diverse migratory species, we expected the wind at the 925 mb level to be the most appropriate for exploring bird migration patterns (Bruderer *et al.* 2018). Data on the number and periods of ice and snow days for the station De Bilt ($52^{\circ}06'N$ $5^{\circ}10'E$), 44 km from the Bittern breeding site, were retrieved from the Royal Netherlands Meteorological Institute (KNMI) <https://www.knmi.nl/nederland-nu/klimatologie/gegevens/mowe>. In three winters classified as normal (Hellmann index >73 ; severe >160 , normal 100, mild <40), a significant cold period of more than 10 days with substantial ice and/or snow cover occurred. This included December 2011, the coldest December month in 40 years (Table 1).

Data interpretation and definitions

We used criteria set up by Trierweiler *et al.* (2014) to define wintering area, migration start, and ending. In the light of the large variation in stopping times and the ecological interpretation, following Chan *et al.* (2019), we did not distinguish between ‘stopover sites’ and ‘staging sites’, but used the term ‘stopping sites’ instead. One migration track is the flight path between two stopping sites. The ARGOS-PTT/GPS tags provided locations but no direct measurements of instantaneous ground speed or instantaneous track direction; this meant that ground speed and track direction were instead calculated for these tags using that part of the migration track between subsequent GPS fixes.

The Bitterns with a PTT/GPS tag were assumed to be resting or feeding on the ground if two subsequent GPS fixes were close to each other (mostly less than 50 m). We did not use Doppler signals for this. A simple threshold cannot be given for this, so we manually and approximately used the criteria of subsequent

Table 1. Data from three Bitterns with ARGOS-PTT transmitters wintering in the Netherlands. Presented are the received amount of fixes in the non-breeding season (September to April). Climate source ice/snow days: <http://www.knmi.nl/nederland-nu/klimatologie/maand-en-seizoensoverzichten>. * = signal at a different location than the previous breeding site.

Bird ID/season	2010/2011	2011/2012	2012/2013	2013/2014	2014/2015
Ice/snow days	13/26	13/1	12/18	0/0	1/3
Start cold period	end Nov	Feb	Jan	--	--
Female with PTT tag 49807					
Last autumn fix		13/9	27/9	17/10	9/10
winter fixes		6/2 and 20/2	None	None	None
First spring fix		11/3	23/3	10/3	3/4
Male with PTT tag 35219					
Last autumn fix				June	12/10*
winter fixes				None	None
First spring fix				29/05	unknown
Male with PTT tag 35110					
Last autumn fix	03/10*	12/10*	02/09	31/08	19/08
winter fixes	09/01*	None	None	28/01	None
First spring fix	10/03	21/03	24/04	12/03	None

GPS locations within the range of a few metres up to a maximum of a few hundred metres. Bitterns in active migration flight move at least 30 km in one hour, so our approach was unlikely to have incorrectly classified migrational movements as resting or feeding bouts. As the UvA-BiTS tags provide instantaneous measurements of ground speed, altitude, and track direction, it was evident if Bitterns were flying or resting; higher instantaneous ground speeds indicate flight (range 5.1–24.0 ms⁻¹). To determine migration routes, GPS fixes were preferred and, in some cases, complemented with eight high-quality ARGOS fixes (location classes 1,2,3). As the latter can show larger errors compared to GPS locations, fixes just before and after possible outliers were visually inspected. In total eight high-quality (1,2,3) doppler fixes were used and 47 GPS fixes for the autumn track of tag 35218.

Bitterns do not fly much when not actively migrating. With a home range size between 20 and 150 ha, females sometimes perform foraging flights up to 500 m (White *et al.* 2006, Gilbert *et al.* 2005, Adamo *et al.* 2004). We therefore conservatively assumed the onset of migration as the moment at which a Bittern left the breeding or wintering area and started flying for at least 5 km in a single direction, continuing to its wintering site afterwards. For migrants, a wintering area was defined following Trierweiler *et al.* (2014) as the location where a bird was present during November–February before returning to the breeding site. Stopping sites were defined as locations where Bitterns checked their migration for at least one daylight period during July–November and February–April.

To analyse migration characteristics such as flight speed, track direction, and altitude above mean sea level, only the GPS fixes of migrants were used. ARGOS fixes were just used to confirm locations of stopping sites in periods with very few GPS recordings. GPS data were available for the Bittern with tag 514 from autumn 2010 up to spring 2015. For the bird with tag 35218 enough GPS data were available to analyse migration characteristics for spring 2011.

Flight speed is either the instantaneous ground speed measured by the UvA-BiTS GPS tag or that calculated for the PTT-GPS tags if at least two subsequent GPS locations were available, in which case flight speed was calculated at the distance between consecutive fixes divided by the duration. Both methods provide enough detail to compare with general patterns of encountered wind direction and speed. Travel speed (ms⁻¹) was calculated between stopping sites as the

cumulative daily travel distance (km), calculated as the shortest path between subsequent locations (great circle distance), divided by the time elapsed between these locations. For the ARGOS-PTT/GPS transmitters this only provides an estimate of the travel time because of the programmed sampling interval, but for the UvA-BiTS trackers the measurement of travel time is precise to the nearest few hours.

We tested if Bitterns experienced tailwinds along the route more often than headwinds. We compared the proportion of track segments with headwinds to the proportion of segments with tailwinds for Bitterns 514 and 35218. We tested if wind direction between 0° and 90° (tail wind component) occurred more often than between 90° and 180° (headwind component). Additionally, using a linear regression model (R Core Team 2020, R package version 1.0.10), for Bittern 514 we tested if tailwind assistance incorporating wind speed (see tailwind equation in Kemp *et al.* 2012), as well as season and a seasonal interaction with tailwind assistance, influenced flight speed. The response variable was flight speed, and the predictors were tailwind assistance, season, and an interaction with season.

Due to cloud cover, short daylight periods, low solar radiation, and the tendency of the birds to stay in dense vegetation, transmitter signals of birds wintering in the Netherlands were scarce or absent in the period October–March (Table 1). This was especially the case for the PTTs. All of the Bitterns were fitted with a yellow colour ring, which gave birdwatchers a possibility to check for their presence during winter. General landscape characteristics were qualitatively checked on images provided on Google Earth (DigitalGlobe 2012. <http://www.earth.google.com> [May 15, 2018]).

Results

No indication for cold spell-induced movements

Two Bitterns migrated to milder climates and four Bitterns wintered in the Netherlands. Extensive cold spells occurred during three winters in the study period (Table 1). Despite sparse data in winter, it appears that none one of the four Bitterns left during the cold spells (Table 1 and Figure 1). If residents moved more than 10 km, they apparently did so during September–October or March. Bittern 511, with a high density of GPS points, did not even move within the Netherlands in the period with frozen wetlands in February 2012 (Figure 1).

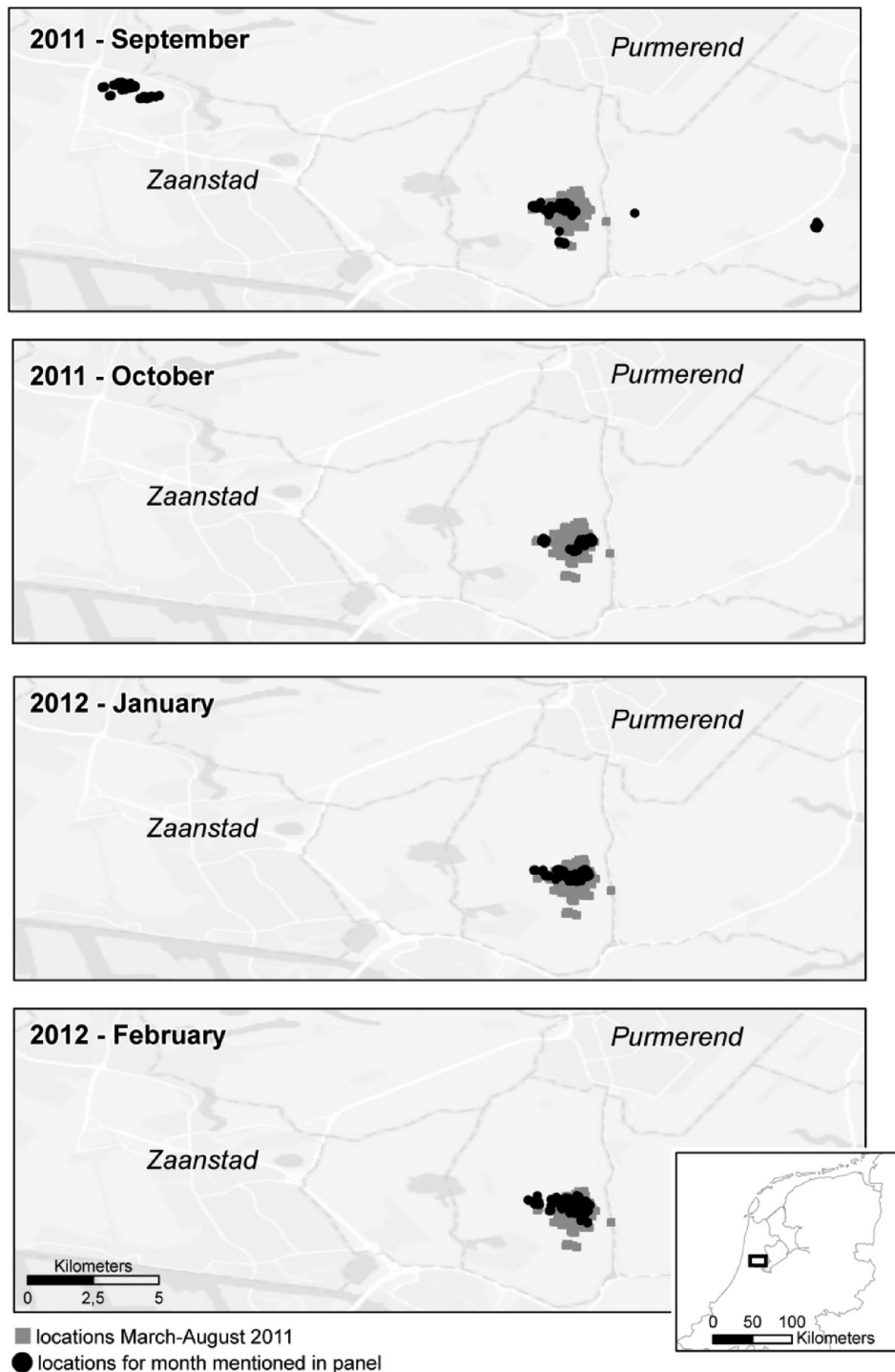


Figure 1. Movements of a resident male Bittern (UVA-BiTS tag 511) during the season 2011–2012. The black GPS locations indicate the non-breeding period (September–February) while the previous reproductive period is presented in grey. In February 2012 an ice period occurred (Table 1).

The resident Bitterns are staged mostly within a restricted area situated within or near to the previous breeding site, best documented for Bittern (tag 511) (Figure 1), or up to 75 km from it (tag 35110). This latter Bittern also started its yearly short-range northward movement in early October (in both 2010

and 2011), well before the cold spells (Table 1). The movement pattern and location of wintering sites were rather similar in subsequent years, although Bittern with tag 35110 did not move east to Friesland prior to the winter season of 2013/2014 but remained in the breeding area.

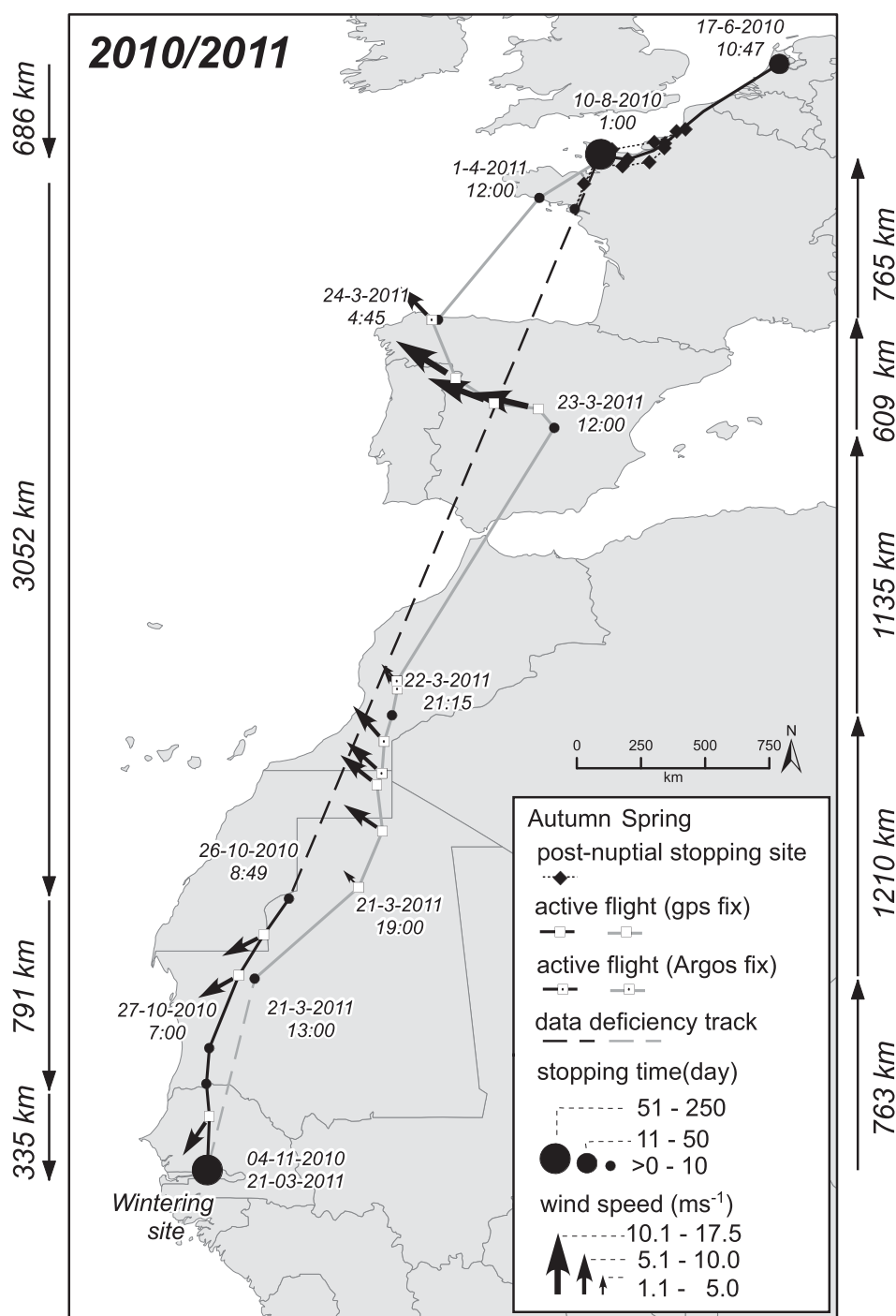


Figure 2. Long-distance migration of a female Bittern (PTT tag 35218) in the non-breeding season 2010/2011. Time stamps are included for some points to give an impression of the progress of migration. Panels include travel distances and routes. The arrows at each GPS fix show the wind direction and the size of the arrow reflects wind speed in ms^{-1} (Kalnay et al. 1996, NCEP data download in 2015). Travelled distances are indicated on the sides of the panels.

Onset of migration, timing, and landscape

Two female Bitterns migrated over long distances to winter in warmer climates than the winter climate in their breeding range (Figures 2 and 3). These migrants took off in the period July–October, well before any snow or ice events. Female 35218 left the

Netherlands in July and returned in April, while female 514 left in October–early November and returned in March. The Bitterns did not continue migration after arrival at these wintering sites (Figure 2 and 3). Both females started their flights at the end of the day and migrated at night, covering distances between 200 and 600 km before landing. In October

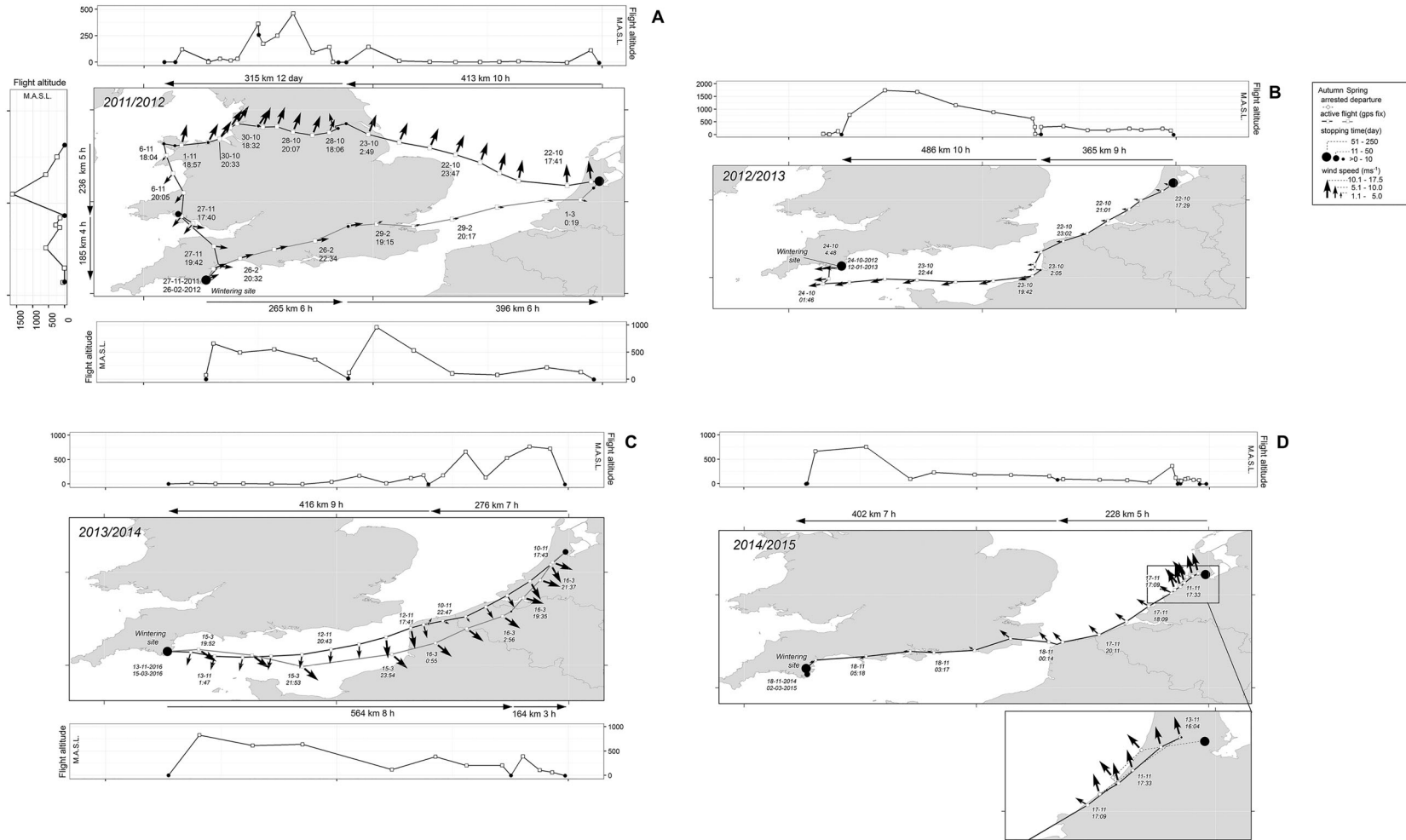


Figure 3. (A–D) Migration of a female Bittern (Uva-BiTS tag 514) from the Netherlands to Great Britain in the seasons 2011/12–2014/15. Panels include distances and routes, encountered wind direction and speed (Kalnay et al. 1996, NCEP data download in 2015), at each GPS fix as well as flight altitudes in m asl (bottom and side panels). Travelled distances are indicated on the sides of the panels.

Table 2. Migration characteristics of a female Bittern (UvA-BITs tag 514) on short distance migration from the Netherlands to the UK in autumn (2011–2014) and back in spring (2012, 2014). Data from spring 2013 and flight speed from 2012 are lacking. For sample sizes see Figure 3. Straightness index is the deviation from a hypothetical direct flight line (great circle distance) between breeding and wintering area.

parameter	Autumn 2011	2012	2013	2014	Spring 2012	2014
Total flight distance covered (km)	1148	852	691	811	663	729
Actual flight time (h)	30	16.6	16.2	25.3	12.1	12.1
Total migration time (days)	36	9.2	2.4	7	4.1	1.2
Longest stopping time (days)	20.8	0.7	1.7	3.9	2.8	0.7
Number of stops	7	1	1	3	2	1
Stopping time total (days)	34.9	8.5	1.7	6.1	3.6	0.7
Mean flight distance between stops (km)	143	425	345	203	221	364
Mean flight speed (ms^{-1}) (sd)	11.6 (3.5)	No data	11.4 (2.4)	13.2 (5.1)	15.2 (4.6)	18.2 (3.8)
Mean altitude (m above sea level) (sd)	187 (322)	454 (530)	206 (277)	182 (202)	356 (283)	353 (262)
Straightness index	1.79	1.33	1.08	1.26	1.03	1.14

2010, Bittern 35218 stopped twice during daylight in the Sahara (Figure 2), and in spring 2011 she continued flying during daytime as she covered 519 km between 13:00 and 19:00 UTC. The Bitterns flew over all landscape types, including mountain plateaus, seas, deserts, forests, and urban or industrial areas; there was even a flight over the city of London at an altitude of 957 m above sea level on the evening of 29 February 2012 and one two evenings later over Amsterdam near Schiphol, at an altitude of 106 m above sea level (Figure 3(a)).

Migration speeds and stopping sites

The female migrating from the Netherlands to Devon (tag 514) provided most information on flight speed and stopping sites, with substantial differences between years (Table 2). Her fastest flight to the breeding area took 1.1 day, with mean flight speeds around 11–18 ms^{-1} (Table 2). During three such trips, she only used one stopping site between the wintering area and breeding site. She stopped at small or larger wetland patches in dunes (France) and agricultural areas.

In spring 2011 a female Bittern (tag 35218) crossed the Sahara with no identifiable stops and an average travel speed of 18.6 ms^{-1} . She covered 1203 km from the first fix on 21 March 2011 in southern Mauritania to the first stop in southern Morocco. During the next nonstop flight, to Spain, she flew 1239 km. In total, this Bittern migrated about 4900 km in 126 days during southward migration and the same distance in 11 days during northward migration. This difference was mainly caused by a long pause between July and October at several stopping sites in Normandy, France (Figure 2). Calculated flight speeds ranged from 12.8 to 21.7 ms^{-1} . This Bittern stopped during the day within the Sahara near rock formations, or near or in a solitary tree. All GPS points (mostly four per day) at

these stops were within 24 m and several at the exact same spot between subsequent measurements.

Track direction, altitude, and wind direction

Both migrants showed deviations from the shortest route between their wintering and breeding site, most clearly visible for Bittern 514 – as it differs substantially between different migration tracks (Table 2). The movements seem to be influenced by wind direction and speed. For example, Bittern 35218 experienced wind from the east and had a westward bias over the Sahara in both October and March (Figure 2). While passing over central Spain in March, and facing strong winds (10–17 ms^{-1}) from the east, she drifted far westwards (Figure 2). The multiple migration routes of the female migrating from the Netherlands to Devon showed variation in flight speed, direction, and altitude. Instantaneous flight speeds ranged from 3.6 to 26.4 ms^{-1} . Against the wind she flew just above sea level (Figure 3(a)) increasing to over 1500 m above sea level with tail winds (Figure 3(b)).

In November 2014, when the wind was blowing from the southeast, she flew via an almost direct track to the wintering site (Figure 3(d)). However, in autumn 2011, with strong winds blowing from southwest, she used a route at low altitude over the northern North Sea (Figure 3(a)). This route ended up in Anglesey, northern Wales and she made some longer and shorter stops, only starting to move south to Devon when the wind started blowing from the northeast. In autumn 2013 she initially followed the French coast as the wind was northwest. Halfway through this journey, the wind had moved to north-northeast, resulting in a higher flight altitude and bending her route northwest (Figure 3(c)). In autumn 2014 she faced strong headwinds (13–14 ms^{-1}) at take-off and this resulted in a U-turn and delayed departure

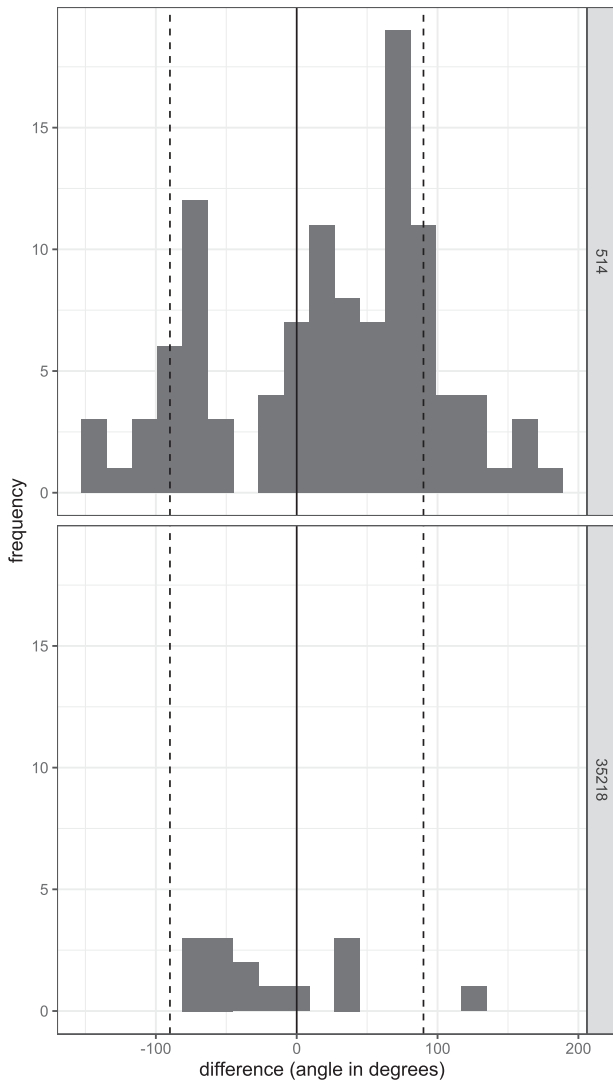


Figure 4. Frequency of the difference (angle in degrees) between track heading and encountered wind direction (0° is exact head wind, 180° is exact tail wind) by two Bitterns during migration. See also Figures 2 and 3.

(Figure 2(d)). She left Ilperveld on 11 November but returned the same night to a location close to the breeding area (Figure 3(d)). Another departure attempt on 13 November was again suspended in the coastal dunes of the Netherlands, from where she finally left on 17 November for the flight to Devon.

For both migratory Bitterns, track segments with headwinds were significantly less common than track segments with tailwinds (Figure 4; $\chi^2 = 37.902$, $df = 1$, $P << 0.0001$, $n = 222$). For Bittern 514 tailwind assistance significantly and positively influenced flight speed (m/s) ($P << 0.0001$, $F = 29.86$, $df = 3$ and 84), while season and seasonal interaction did not have a statistically significant impact on flight speed ($P = 0.3693$ and $P = 0.0733$) ($r^2 = 0.52$, $P << 0.0001$, $n = 108$).

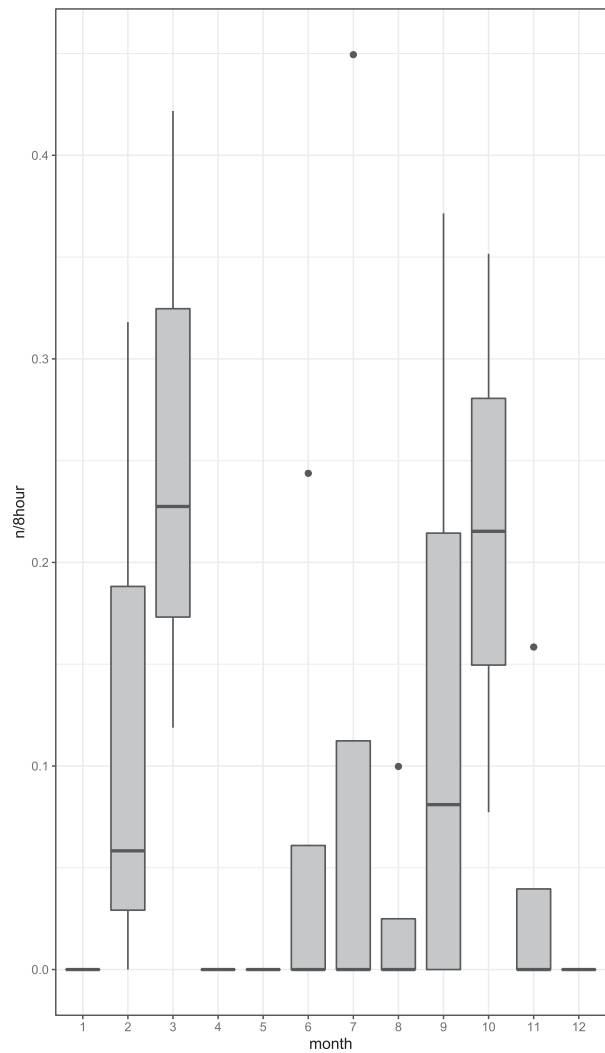


Figure 5. Average monthly number of nocturnally passing Bitterns ($n = 33$ calling Bitterns) at Maarn, the Netherlands, June 2015–December 2018 (3152 h nocturnal recordings with an average of 66 h per month (range 21–124 h); monthly values are expressed as number of Bitterns per 8 h, source: www.trektellen.nl).

Discussion

The present observations reject the idea that Bitterns are facultative migrants. In this study, we failed to observe migratory responses to multiple severe cold winter spells. In fact, the onset of migratory movements was always in July–early November, well before severe weather later in the winter. Some of the residents moved to a nearby wintering site in autumn, indicating some flexibility in the choice of wintering sites in the same climatic zone for residents between years.

These observations are consistent with the results of studies on tagged Bitterns in the UK, where males only

moved substantially in October, returning weeks or months later to the breeding site (White *et al.* 2006). Movements of Bitterns at night, based on sounds (Gillings *et al.* 2018) recorded at Maarn, a location central to the Netherlands (52°03'N 5°22'E), are fully consistent with the idea of well-defined migration periods in spring and autumn (Figure 5). Thus, the increase of Bittern sightings in December–January reported by Toms (2002) is most likely the result of a higher sighting probability of Bitterns that were already present. This might be caused by the higher visibility in the snowy landscape, in combination with ice covered waters and snowfields forcing them to get out of cover to find suitable open waters or snow-free patches. As a result of increased visibility, Bittern counts in severe winter periods give a better indication of the local wintering population size.

Just as in Bitterns breeding in Russia and wintering in China (Gu *et al.* 2019), Dutch Bitterns were site-faithful to breeding and wintering sites (van der Winden *et al.* 2019). However, one Bittern tracked for several years showed substantial variability in routes between years. The variation in routes suggests the strong influence of air as a moving medium. In strong crosswinds, Bitterns allowed themselves to drift (e.g. Figures 2(a) and 3(a) with birds detouring). The Devon-wintering bird is a nice example, as she uses the same wintering and breeding area, with the autumn route 250 km more to the north in the year with winds from the south. With tail winds, Bitterns flew high and fast in a more or less direct line between breeding and wintering sites. With western winds prevailing, spring flights were faster than autumn flights for the Bittern wintering in Devon, UK.

For their diurnal stops, the Bitterns did not necessarily use wetlands. It seems they just tried to find a stopping place where they could hide during the day. We do not know if they (need to) feed for fuelling during such stops. The female crossing the Sahara stopped during the day during southward migration. The mainly nocturnally migrating Purple Herons always continued their southward flights during daytime over the Sahara (van der Winden *et al.* 2010). Given that Bitterns are smaller and less agile flyers than Purple Herons, we propose that this reflects different responses to the perceived threat from raptor predation (Ydenberg *et al.* 2007).

We were able to enlighten some aspects on the migration behaviour of Bitterns. Not finding any facultative response to cold weather and the well-defined onset of migration in autumn and spring, our findings suggest that Bitterns breeding in the Netherlands are either resident or obligate migrants.

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