In many bird species intraspecific variation in migration strategies is related to sex or size (Hedenström 2008, Newton 2008, Chapman et al. 2011, Duijns et al. 2015). The common pattern that males remain closer to the breeding area than females has been explained in three different, but non-mutually exclusive, ways (Ketterson & Nolan 1976, Newton 2008, Gow et al. 2014, Woodworth et al. 2016): (1) when males are the larger sex they may be better adapted to remain in colder climates, (2) males are dominant and force...
females or juveniles to move further away, and (3) males remain close to the breeding site because they compete for a territory.

Eurasian Bitterns *Botaurus stellaris* (Bittern from here on) are highly sexually dimorphic. Males are almost twice as heavy as females (Cramp & Simmons 1977), with occasional overlap in mass during the non-breeding season (Dmitrenok et al. 2007). Bitterns breed across temperate Atlantic and Mediterranean as well as boreal climates with colder winters from the United Kingdom (UK) in the west to Japan in the east (Cramp & Simmons 1977, Voisin 1991, White et al. 2006). The wintering range is also vast, extending from temperate climates in Western Europe and the Mediterranean to the tropical conditions in the Sahel. The breeding origins of wintering Bitterns are not well known, especially for the many Bitterns reported in January in the Sahel (Zwarts et al. 2009). Sightings during spring migration in Italy (Puglisi & Baldaccini 2000) and during autumn migration in oases in North Africa (Moreau 1967) suggest substantial migratory movements across the Mediterranean and Sahara of European breeding birds.

The northernmost populations of Eurasian Bittern are described to be completely migratory (Voisin 1991), a pattern that is also found in American Bitterns *B. lentiginosus* (Huschle et al. 2013). In contrast, Eurasian Bitterns from areas with warmer winters such as the UK and the Mediterranean regions are suggested to be entirely resident (Voisin 1991, White et al. 2006). As Bitterns are polygamous, the large males defending territories against other males (Cramp & Simmons 1977) may benefit from occupying a high-quality territory early in the season (Polak 2006). This may select for males remaining resident, or only moving short distances in winter. Competition among males and winter hardiness may select for large size. This leads us to predict that especially in breeding areas with temperate climates, there would be sex differences in migration strategies. In such areas we expect obligate or facultative migrants (Newton 2008), as well as residents, with larger males generally staying closer to the breeding area and females having a higher propensity to migrate. However, evidence is lacking and authors have proposed different strategies. For example, Braaksma (1958) suggested that 75% of Dutch Bitterns migrated to (unknown) southern destinations whereas Bijlsma et al. (2001), assumed that most Dutch Bitterns are resident, and suggested that they would perform facultative dispersal movements during cold spells.

To examine the migration patterns of Bitterns breeding in a temperate climate and to test for sex differences, we analysed the available European ringing data and we satellite-tracked ten adult Bitterns (four females and six males) breeding in The Netherlands. Three males and three females were tracked over multiple years which enabled us to also assess the degree of site fidelity during both the breeding and winter seasons.

**METHODS**

**Ringing data**

Data from 276 recoveries from Bitterns marked with metal rings in Europe were provided by EURING (1924–2013). Most birds were ringed as chicks with 104 birds trapped as fully grown (EURING code higher than 1). The sex of these latter individuals was hardly ever recorded (there were 4 females and 7 males). First, we excluded all recoveries within the same or subsequent breeding years (1 May to 1 July) resulting in 250 recoveries linking a breeding site to wintering or migratory stopover site. In contrast to Bitterns ringed as a chick, the hatching area is unclear for fully grown Bitterns ringed between February and November. Their breeding area is uncertain as they may be ringed during migration or at the wintering site. For Bitterns recorded in spring and autumn, the wintering areas were unknown. We assumed all records between 15 November and 15 February were wintering individuals, all records between 15 February and 15 April were spring migrants and that those between 15 July and 1 November were autumn migrants. This enabled us to explore whether movement directions and distances differ for these periods.

Recoveries from the period after the ringing year (e.g. ringed as a chick in May 1957 and recovered dead January 1960), were also used to study migratory movements. As ringing data are strongly influenced by human effort, the data from the countries with few records have been grouped: Central Europe: Switzerland, Austria, Czech Republic, Hungary, Bosnia; Eastern Baltic: Lithuania, Latvia, Estonia, Finland; Eastern Europe: Russia, Ukraine, Belarus.

**Capturing and tagging Bitterns**

Adult males were captured in their territories by luring them with their booming calls in walk-in traps (Huschle et al. 2002). Females were captured on the nests, based on experiences in Poland (M. Polak pers. comm.), with walk-in traps or with a large landing net during the last days of incubation. All our catching attempts for this study were successful as we captured
all birds. In spring 2010 to 2012 five adult males and four females were fitted with a tracking device at Ilperveld (52°26’N, 4°55’E), with the 10th bird, a male, being captured and tagged in spring 2013 near Alkmaar (52°38’N, 4°53’E). Since booming males were trapped, and as the females were trapped on the nest, sex is certain. All females returned to the nest within the same day after being released. We noted that all males had bright blue lores. The six adults were of unknown age but they were at least in their second calendar year.

At capture, the four males weighed 1420–1710 g (average 1514 g) and the six females 740–864 g (average 801 g). With a wing length from 312 to 314 mm in females versus 352 to 360 mm in males, the females were also 11% smaller. The transmitters were attached to the back using lightweight Teflon backpack harnesses, adjusted with elastic in order to enable increase in mass and maximise flight manoeuvrability (van der Winden et al. 2010). Seven birds (four males and three females) were equipped with a 22-g solar panel Platform Transmitter Terminal (ARGOS-PTT)/GPS (Microwave Telemetry, USA). Including the harness, this comprised 1.7–3.1% of the body mass. The transmitters provided standard ARGOS fixes with an 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 sufficiently charged, the 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. Two males and one female received an 18-g UvA-BiTS GPS tracking device (University of Amsterdam; Bouten et al. 2013). These loggers included a radio transceiver for bidirectional communication with a ground-based antenna network, enabling users to download data and upload new measurement schemes remotely. The GPS measurement interval was set to 15–30 min once a Bittern arrived within the antennae network which was set up in the breeding area. Before expected departure for migration, at the end of September or early October, the interval was set to either 30 min or 1 h to account for the shorter daylight period and battery charging.

Male Bittern showing distinctive clear blue lores, deployed with a UVA transmitter (photo M. Collier, April 2011, Ilperveld, The Netherlands).
times. From four out of ten tagged individuals we did not get any information on migratory movements as one male and one female were found dead within the same breeding season, and in two cases transmitters stopped working before September for unknown technical reasons. All individuals were additionally marked with a metal ring and colour rings, the latter to enable resightings.

Due to cloud cover, short daylight periods and the tendency of the birds to stay in dense reed vegetation, tracking measurements of birds wintering in The Netherlands were scarce or absent in the period October–March. However, the combination of a few fixes during the winter without movements in autumn or spring and additional field sightings of birds with a coded colour ring gave enough information on the (lack of) migratory movements.

Bitterns seldomly fly and if so, only short distances, so the onset of migration was easily identified when a Bittern started flying in a clear direction for more than 10 km. For bitterns identified as migratory, a wintering area was defined as the location where a Bittern was present for at least a month after initial migratory movement and before they return to the breeding area in spring.

**RESULTS**

Ring recovery data show that birds breeding in northern regions, like Scandinavia, Poland or Russia, have large migration distances to wintering areas in temperate or temperate winter climates near the Atlantic or Mediterranean (Figure 1). Most of their
movements are in south-westerly directions. Average shorter distances are found for Bitterns breeding in Germany, The Netherlands and Great Britain. Bitterns recovered on spring or autumn migration do not provide complete information on the final destination. For example, ring recoveries south of the Sahara are completely lacking. However, the few southward long-distance movements in spring and autumn could be indicative of Bitterns en route to Africa. The incomplete spring recovery data still support the notion that northerly breeding populations show longer migrations. However, the incomplete autumn recovery data do not indicate different travel distances for northerly breeding individuals compared with south-westerly ones.

The six Bitterns fitted with trackers showed great variation in migratory distances (Table 1). All males stayed in The Netherlands within 75 km of the breeding site (Table 1). These males used the same wintering area over the years apart from one male which wintered for two years in the province of Friesland, in the north of The Netherlands, and then remained during the third winter in its breeding area (Table 1; tag 35110). The females were either resident or migratory. One female crossed the Sahara. In 2010/2011 she wintered in The Gambia in West-Africa, 4900 km from the breeding site. In the 2011/2012 winter she did not migrate further than Morocco (2200 km). In the last three winters that we could follow her, she wintered in Normandy, France (600 km), in an area used as a staging site in previous years. A second female moved for three successive winters to the same location in Devon, UK (700 km). The third female stayed within her breeding area (Ilperveld) for three winters. While we observed much more variation in migration distance among females than males (Figure 2), as well as within the migratory females among years, we lacked the statistical power to demonstrate a relationship between maximum migration distance and body mass ($r^2 = 0.26$, $t_5 = 0.28$, $P = 0.39$).

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DISCUSSION

The data from six Bitterns fitted with transmitters at a breeding site in The Netherlands showed substantial variation in wintering destinations. While all males were resident, the lighter females showed a range of migratory behaviours, including residency, migrating short distances, and the crossing of the Sahara to winter at 4900 km from the breeding site. The movements of the latter female represents the first direct evidence of the breeding origin of the thousands of Bitterns wintering in the Sahel (Zwarts et al. 2009). It aligns with Moreau’s (1967) suggestion, based on autumn sightings, that oases are used as stopovers by northern breeders during their migration to the Sahel. Most Bitterns showed high fidelity to the breeding and wintering areas although one male and one female progressively wintered closer to the breeding area in three successive years. This might be a result of random flexibility in the choice of wintering areas, although the shortening of the migration distance by more than 4000 km across two years suggest a relation with age, perhaps reflecting the ecological fine-tuning of migratory behaviour (Guilford et al. 2011, Sergio et al. 2014).

This study also augmented our understanding of the movement patterns of Bitterns ringed in Europe. It confirms that Bitterns can be resident or short- and long-distance migrants (Voisin 1991). The better thermoregulatory properties of the larger males and their need to settle in territories early (Polak 2006) would explain why males are more resident or remain close to the breeding sites in areas where this is possible. More northern Bitterns would be more likely to migrate greater distances because of a lack of food if wetlands are frozen over in winter. Such northerly birds moving to or from the Sahel or Mediterranean wintering sites may explain the autumn and spring records in the Mediterranean. Further south, residency should increase as the frequency and severity of cold spells is lower. That the complete absence of long-distance ring recoveries from the UK and the Mediterranean indicates an absence of long-distance migrating Bitterns, is confirmed by radio-tagged breeding males in the UK staying put in winter (Gilbert et al. 2002, 2005). As the patterns may well differ for the smaller-sized British females as well, further studies are needed to determine if Bittern females from the UK, with a rather similar climate to The Netherlands, show migrations comparable to Dutch females.

Apart from mortality during the occasional cold northern winters, we expect dry Sahel periods to reduce winter survival (Zwarts et al. 2009). If so, Bittern populations with predominantly long-distance migrants would show a population decline in response to the Sahel drought of the 1970s, comparable to what has been observed for other Sahel migrants such as Purple Heron Ardea purpurea (Den Helder 1981). In populations with mixed migration strategies, populations are expected to decline after severe winters in the north and dry years in the Sahel. The Dutch and British population indeed showed declines from the early 1970s to the late 1990s, with a recovery thereafter (van Turnhout et al. 2010, Gilbert et al. 2010). During the period of decline, some severe winters in The Netherlands (e.g. in 1985 and 1986) coincided with dry winters in the Sahel. As a result, the proportion of migrants should follow differences in winter mortality from cold spells or Sahel droughts. If the sexual difference in migration distances is real, this would also affect sex-ratios, with a pressure on long-distance migratory females during dry periods in the Sahel and on resident males during cold winters in temperate areas.

Eurasian Bittern are polygamous (Cramp & Simmons 1977). If in a wet Sahel period, males are affected more by the impact of cold northern winters than females, surviving males might attract more returning females in the remaining territories. This would result in sex ratio differences between years, which could have reproductive consequences (Catry et al. 2005). Since the Bittern population trends are mainly based on a census of booming males (van Turnhout et al. 2010), we might thus overestimate the impact of cold northern winters on subsequent recruitment. Conservation efforts currently focus mostly on the restoration of breeding habitat (e.g. Brown et al. 2012, Wotton et al. 2011). As the present study makes clear, Mediterranean and African wintering habitats are important even for West-European breeding Bitterns and require more conservation attention.

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SAMENVATTING

Nederlandse broedgebieden met zenders uitgerust en over een periode van 2–5 jaar gevolgd. Alle drie de mannetjes en één vrouw overwinterden in of nabij hun broedgebied, maar twee vrouwjes trokken over grote afstanden weg. Eén vrouwje trok zelfs naar Gambia, een afstand van 4900 km. Dat is het eerste bewijs voor trans-Sahara trek van de soort, waarvan wel bekend is dat er duizenden exemplaren in de Sahel overwinteren. Een ander vrouwje overwinterde gedurende vijf opeenvolgende jaren in Devon (ZW Engeland), een afstand van 700 km van haar broedgebied. De Roerdompen waren plaatsvrouw aan hun broedgebied en meestal ook aan hun overwinteringsgebied. Onze resultaten suggereren dat in gebieden met afwisselend zachte en koude winters, de mannetjes (groot) overwegend standvogel zijn, terwijl de vrouwjes (kleiner) gedeeltelijk trekvogel zijn met individueel flexibele strategieën. Mochten mannetjes vaker sterven door koud winterweer dan onder gunstiger omstandigheden, dan kunnen de overlevende mannetjes in de overgebleven optimale gebieden meer vrouwen aantrekken. De trend van roerdompoppulaties is voornamelijk gebaseerd op tellingen van roepende mannetjes. We zouden daarom in gematigde streken het negatieve effect van strenge wintersterfte op de populatie wel eens kunnen overschatten. De overlevende mannetjes kunnen immers meerdere vrouwjes in hun territorium aantrekken. Bescherming van de Roerdomp zal zich veel meer dan nu moeten oriënteren op de Mediterrane en Afrikaanse overwinteringsgebieden.

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