Spatial behaviour and habitat use of first-year Bluethroats *Luscinia svecica* stopping over at coastal marshes during the autumn migration period

Juan ARIZAGA¹, Miren ANDUEZA^{1,2} & Ibon TAMAYO³

¹Department of Ornithology, Aranzadi Sciences Society, Zorroagagaina 11, E-20014 Donostia-S. Sebastián, SPAIN, e-mail: jarizaga@aranzadi-zientziak.org

²"Cavanilles" Institute of Biodiversity and Evolutionary Biology, Apdo 22085, E-46071 Valencia, SPAIN
³Epidemiological Surveillance Unit., Basque Government, Avda. Navarra 14, Donostia-S. Sebastián, SPAIN

Arizaga J., Andueza M., Tamayo I. 2013. Spatial behaviour and habitat use of first-year Bluethroats *Luscinia* svecica stopping over at coastal marshes during the autumn migration period. Acta Ornithol. 48: 17–25. DOI 10.3161/000164513X669964

Abstract. Coastal marshes play a relevant role as stopover and fuelling sites for birds during migration period. The importance of tide in such ecosystems is well studied for aquatic species such as waders, but its impact on the stopover behavior of land birds that also depend on these sites is still unknown. Bluethroats *Luscinia svecica* are small-sized passerines that feed on the ground and low vegetation and, therefore, experience continuous changes of habitat availability due to the tide regimens. The aim of this study was to analyse the habitat use and to test the impact of tide on home range size of Bluethroats stopping over at coastal marshes. For that, we used data on radio-tagged birds at a tidal marsh in Northern Iberia. Bluethroats were radiotracked from the 20th of August to the 20th of September. Individuals were surveyed from 3 to 17 days, and birds with lower body mass at the day of capture stayed for longer period. Mean home range size was 2.0 ha (SE = 0.2), and the main habitats occupied were reedbeds (ca. 30% of a home range area) together with tidal flats with both free- and low-halophytic vegetation. Home ranges tended to be larger in birds found to occupy zones close to the sea level, thus with a longer tide-mediated flooding period, suggesting a negative effect of tide on home range size, and/or that Bluethroats staying at lower altitude did not find as much food as at higher altitude, so they were forced to move over larger surfaces.

Key words: Bluethroat, *Luscinia svecica*, autumn migration, fuel management, Northern Iberia, radiotracking, home range, habitat selection, tides

Received — March 2012, accepted — March 2013

INTRODUCTION

During migration birds must often stop over to refuel the energy utilized during flight before facing the next flight bout (Newton 2008). Fuelling at stopover sites is hence a major issue influencing migratory performance (Alerstam & Lindström 1990). A relevant aspect in this context is spatial behaviour during migration, as this is associated with the foraging and fuelling strategy of migrants. Some migrants occupy temporal small home ranges when remaining at stopovers (Lindström et al. 1990, Chernetsov & Mukhin 2006, Arizaga et al. 2011b), whilst others look for food over broad areas (Chernetsov & Manukyan 2000). Understanding which factors shape fuel deposition and foraging, including spatial behaviour at stopover sites has clear ecological and conservation implications. Thus, migrants at suboptimal habitats will experience lower rates of fuel acquisition than in an optimal habitat (Delingat & Dierschke 2000), and/or be forced to occupy larger home ranges, thus reducing the carrying capacity of a particular stopover site.

Theoretically, many animal distribution patterns are classified using the ideal free and despotic distribution concepts (Fretwell 1972). In the first case birds' home ranges should be directly proportional to the amount of a particular resource in a given habitat patch. The despotic distribution assumes that individuals with some characteristics (i.e., subordinates) will avoid to occur in a particular site in order to avoid competition. Typically, small-sized, young, and females are subordinated to larger, older and males (Lindström et al. 1990, Moore et al. 2003).

Coastal marshes play a very important role as stopover and fuelling sites for birds in migration, especially waterbirds (Turpie & Hockey 1993, Atkinson et al. 2007). But coastal marshes also provide proper habitat for several terrestrial species like small passerine birds associated with emergent macrophyte vegetation such as reedbeds (Poulin et al. 2002, Arizaga et al. 2006). Furthermore, some coastal marshes have been reported to be priority for the conservation of small migratory birds such as the endangered Aquatic Warbler, Acrocephalus paludicola (Julliard et al. 2006, Poulin et al. 2010, Provost et al. 2010). Spatial behaviour of migratory passerines at coastal marshes is poorly understood, more particularly in relation to a possible impact of tide regimens on bird movements. Apart from this, coastal marshes are among the most endangered habitats due to the expected sea-level rise as a consequence of the global climate change (e.g., Pickering et al. 2012). Therefore, understanding the relationship of bird movements and habitat use at these particular sites must be a conservation priority.

During high tide, the ground and intertidal vegetation are underwater for a period of time. In this scenario, we establish the following prediction for small terrestrial birds that depend on marsh areas to feed but are not able to forage underwater are expected to (1) relocate to areas without water (to either continue foraging or to rest in a dry place until the tide lowers), so that larger home ranges should result when compared to birds at zones with no tide influence or with much shorter flooding period, or (2) to remain in an area of similar size to that of birds in areas with no tide effect, e.g. whether tidal areas would provide a superabundance of food during the low tide.

The Bluethroat Luscinia svecica is a 14 cm-size bird that breeds across most of the Palaearctic and spends the winter within the circum-Mediterranean region, the Middle East, Southern Asia and the Sahel (Cramp 1988). Typically, it requires < 2 m-high vegetation habitats with open nearby water bodies, from forest-plains ecotones at mountain ranges and tundra to marshlands (Cramp 1988). In West Europe, it mainly occupies wetlands with reed (Phragmites spp.) (Cramp 1988, Arizaga et al. 2006) or saltworks along the coast (Cramp 1988, Geslin et al. 2002), both during the breeding and the non-breeding season. In this type of habitats, Bluethroats forage on invertebrates that are captured on the ground and over low vegetation (Cramp 1988). Stopover duration can vary from some few days to even some weeks

(Arizaga et al. 2010, 2011a). When at coastal marshes, Bluethroats experience continuous changes of habitat availability as a consequence of tide regimens. Information on the habitat use in this type of habitats and on the possible impact of tide regimens is however lacking.

Some Bluethroat populations, especially those breeding along the coast in France, have been considered by several authors (Huntley et al. 2007) to be under a high risk of extinction due to the global climate change. In this scenario, understanding the spatial and habitat use must be priority since this will allow us to know if, certainly, the species has a high dependence on those habitats which have been predicted to be more vulnerable to the global change. In coastal marshes, these would be those situated at lower altitude (e.g., mud flats and low halophytic vegetation) compared to others situated at higher altitude (e.g., reedbeds).

The aim of this work is to analyse the habitat use and to test the impact of tide regimens on home range size of Bluethroats stopping over at coastal marshes. For that, we used data on radiotagged birds at a tidal marsh from Northern Iberia.

MATERIALS AND METHODS

Sampling area

The study was carried out at the Jaizubia stream (43°21'N, 01°49'W; locality of Fuenterrabía), a coastal tidal marsh located in Txingudi marshlands, Northern Iberia. Jaizubia is formed by a mosaic of reed beds *Phragmites australis* and mud flats mixed with halophytic vegetation like *Salicornia* and *Aster*. The zone is used by a high number of migrant bird species, especially passerines during the autumn migration period (Mendiburu et al. 2009), that stop over there in order to refuel before resuming their migration towards wintering areas further south.

Bluethroats are common stopping-over migrants at Jaizubia (Arizaga et al. 2006), especially from August to September (Mendiburu et al. 2009). During that period, they stay at Jaizubia during a period of ca. 15 days and gain mass at a rate of 0.1 g/day (Arizaga, in prep.). Bluethroats do not breed nor overwinter within this area (Aierbe et al. 2001, Mendiburu et al. 2010), so all individuals are true migrants.

Sampling protocol and radiotracking

All Bluethroats were captured with mist nets (16 mm mesh, 2.5 m-high) during the autumn

migration period (August–September) of 2007–2010. The number of nets kept constant during the entire study period (204 linear m; for further details see Mendiburu et al. 2009), and they were always placed in the same site and open during a period of 4 h starting at dawn. Once captured (nets were reviewed hourly), each bird was ringed and its sex and age were determined (Svensson 1996). After that, we measured wing length (± 0.5 mm, method III by Svensson, 1996) and body mass (\pm 0.1 g, digital balance). Once measured, Bluethroats were released. Each bird was retained for no longer than 2 h (usually < 1 h). Only a bird equipped with a transmitter was recaptured; in this case the bird was released from the net just after being caught.

In 2010, 20 Bluethroats captured with mist nets were equipped with PIP41 transmitters (Biotrack, UK), that cover a range of 0.8–3.0 km. For that, the transmitter was fitted to each bird as a backpack with a Rappole harness (Rappole & Tipton 1991). The size of the harness was estimated as indicated by Naef-Daenzer (2007). Used frequencies ranged from 150.020 to 150.913 MHz (Appendix I). All Bluethroats equipped with a transmitter were first-year birds (i.e., born in 2010), ten of which were males and ten females (Table 1). Their body mass ranged from 12.2 to 16.7 g, and the weight of the transmitter and the harness was 0.6 g. Thus, transmitters represented 3.6-4.9% of the birds' body mass (< 5% was the upper limit permissible; Caccamise & Hedin 1985).

We used Sika receivers (30 MHz) with Yagi antennas from Biotrack to detect tagged Bluethroats. Tagged Bluethroats were surveyed upon the capture day until the transmitter last signal (maximum: 17 days; Appendix I). In theory, live of the batteries was ca. 3–4 weeks (source; Biotrack). The survey period per day comprised 4 h starting at dawn and 4 h before dusk. We attempted to obtain a location/bird/hour, although this was not always possible. The location was assessed by biangulation. The number of observations per bird ranged from 5 to 71.

To estimate the accuracy of the method we compared the location of 6 points assessed by biangulation with their real position (obtained with a GPS). We obtained a mean accuracy of 30.0 m (SE: \pm 7.0 m).

Data analyses

Data on tidal regimens were obtained from Pasaia's harbor, situated at 10 km in a straight line from Jaizubia. We identified peak days of spring (i.e., great difference from high to low-tide levels)/neap (i.e. small difference from high to lowtide levels) tide during the months where the study was carried out in Jaizubia. After that, we selected a period of ± 2 days around each peak day of either spring or neap tide in order to obtain 5-day time intervals centered in peak days of spring or neap tide.

Home ranges (home range size) were calculated as 95% kernel area, using ArcGIS 9.2 ESRI and Gearspace software. The distance between the ringing-releasing site and the centroid position of each individual 95% kernel area did not differ between the first day and the rest of survey days (paired t-test: $t_{18} = -1.453$, p = 0.164; Wilcoxon: Z = -0.312, p = 0.755), thus indicating that Bluethroats occupied their home range very soon after releasing. The same result was obtained when removing those birds that were not able to be surveyed the day when they were marked $(t_{14} = -1.469, p = 0.164; Wilcoxon: Z = -0.456,$ p = 0.648). Therefore, we used all survey days to calculate the 95% kernel area of each Bluethroat.

Mean altitude of each individual kernel area was calculated with Digital Terrain Modeling (DTM). We used this variable to estimate tide influence at Bluethroats' home ranges: those found at a higher altitude suffered shorter periods of tide-mediated flooding (i.e., remained shorter periods underwater). ArcGIS was used to create a vegetation map that was used to estimate the proportion of each habitat type within each individual kernel area. This map was done with an orthophoto of Jaizubia obtained in 2009 and available at the official web site of the Basque Government (www.ej-gv.es). Habitats considered for the map were: reedbeds (REED), tidal flats (halophytic vegetation, lime surfaces) (FLAT), free-water areas (WATR), wooded vegetation (mostly tamarisk Tamarix spp., alders Alnus spp., brambles Rubus spp.) (WOOD), grasslands (GRAS), infrastructures (roads, buildings, etc.) (INFR), orchards (ORCH). These were the main habitats detected in the orthophoto.

Home range areas and the proportion of each habitat type within home ranges were normally distributed (K-S test, p > 0.05). However, data on home range area showed a high over-dispersion (SD/mean = 0.48). After log-transformation, such an over-dispersion was diminished up to 0.28. Therefore, we used the log-home ranges area instead of the raw areas for statistical comparisons. A similar problem was detected for the

proportion of each habitat type (SD/mean > 0.46), which were hence arcsin-transformed.

Overall, we obtained a set of home ranges with different size and with different amounts of each habitat type (thus with different levels of tide influence). To test for the relationship between habitat type and home range size, we conducted (1) a Principal Component Analysis (PCA) on altitude and the proportion of each habitat type, used to obtain a variable that summarized habitat-related characteristics as well as to know how the different habitat-related variables were associated among each other; (2) a stepwise linear regression on home range size, with the main PCA components as independent variables. The number of points obtained by biangulation for each bird was also included in this regression as home range size estimation is affected by sampling effort (here, number of points) (Chernetsov & Mukhin 2006). We also included a number of individual-associated variables that could also determine home range size, so to obscure the effects of habitatrelated variables on home range size: days of stay, body mass, body size (as assessed by wing length; Gosler et al. 1998) and sex.

To estimate the impact of tide on home range size we compared home range size during days of spring and neap tide with paired *t*-tests, since we used here birds for which their home range was surveyed both during spring and neap tide periods. For that, we recalculated home ranges using only those days (5-day periods) that coincided with a period of spring or neap tide. Because of this, sample size diminished up to 13 home ranges during neap tide, and 15 during spring tide (home ranges with < 5 survey points were removed from this analysis). In addition to ttest, we calculated the effect size (Arizaga & Barba 2009) as d = (mean_a-mean_b)/SD_{pooled}, and the SD_{pooled} = [[(n_a-1)SD²_a + (n_b-1)SD²_b]/(n_a+n_b)]^{0.5}, where a and b are the two groups compared and n is the sample size. An effect size > 0.5 (difference between means accounts for > 50% of the pooled SD) was considered to reveal a significant difference between samples (Cohen 1969).

SPSS software was used for statistical analyses. All means are given \pm SE.

RESULTS

Overall, Bluethroats were radiotracked from the 20th of August to the 20th of September. Individual survey period ranged from 3 to 17 days (mean: 9.6

 \pm 1.1 days). This period tended to be negatively correlated with body mass at the day of capture (r = -0.568, p = 0.009; residual values of this correlation were normally distributed; K-S test, p = 0.795), so that leaner Bluethroats stayed for longer at Jaizubia.

Home ranges differed in size from 0.68 to 4.43 ha (mean: 2.01 \pm 0.22 ha, n = 20; Fig. 1), and did not differ between sex classes (t₁₈ = 0.229, p = 0.821). Mean altitude of home ranges ranged from 1.8 to 16.4 m above sea level (mean: 6.2 \pm 1.1 m; tides in our area can reach a level of up to ca. 5 m above sea level).

The main habitats that constituted Bluethroats' home ranges were tidal flats and reedbeds (they comprised ca. 60% of the home range area), followed by woodland (ca. 15%) and marginal surfaces of four more habitats (each comprising ca. 5%) (Fig. 2). A PCA on the proportion of each habitat type together with altitude provided three components with an eigenvalue > 1 (Table 1). The PC1 (the component one in Table 1) showed high absolute factor loadings for REED, GRAS, FLAT, WOOD, ORCH, and altitude (Table 1). This PC1 was negatively correlated to FLAT and altitude and positively correlated to REED, GRAS, WOOD and ORCH, so home ranges with positive PC scores tended to have a higher proportion of reedbeds, grasslands, woodland and orchards, as well as less proportion of tidal flats (Fig. 3). The PC2 showed high absolute factor loadings for WATR, GRAS, INFR and altitude (Table 1). In this PC2, WATR showed positive scores whilst INFR, GRAS and altitude had negative scores (Fig. 3), so that home ranges with positive scores

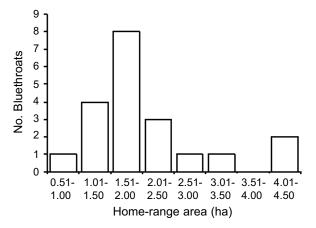


Fig. 1. Frequency distribution of home range size for a sample of 20 Bluethroats radio-tracked during their stopover at Jaizubia.

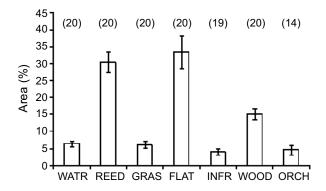


Fig. 2. Proportion of habitat types present at Bluethroat home ranges at Txingudi marshes. Abbreviations as in Table 1. We show in parentheses the number of individual home ranges in which we found each habitat type.

included a higher proportion of free waters, less infrastructures, as well as being situated at a lower altitude. The PC3 showed high absolute factor loadings for WATR, REED and WOOD. High scores of PC3 were correlated to home ranges with a higher proportion of reedbeds and woodland, and less proportion of free water areas.

A stepwise linear regression on home range size with the PC1 to PC3 components, number of survey points, days of stay, body mass, wing length and sex, only included two variables: the PC2 and the number of survey points, both with a positive effect on home range size ($r^2 = 0.162$, p = 0.002; Table 2). Thus, once controlled for the number of survey points, larger home ranges were still found to be positively associated with a higher proportion of free-water areas and lower

Table 1. Factor loadings of a Principal Component Analysis on the relative surfaces of each habitat type and the altitude of Bluethroats home ranges. Abbreviations: WATR — free water area; REED — reedbeds; GRAS — grasslands; FLAT — tidal flats (lime surfaces with halophytic vegetation); INFR — infrastructures; WOOD — woodlands; ORCH — orchards; ALTI — altitude. Significant factor loadings have been shown with (*).

Variable	PC1		PC2		PC3	
WATR	-0.038		+0.458	(*)	-0.584	(*)
REED	+0.297	(*)	+0.248		+0.630	(*)
GRAS	+0.373	(*)	-0.394	(*)	+0.012	
FLAT	-0.518	(*)	+0.028		-0.131	
INFR	-0.129		-0.587	(*)	-0.010	
WOOD	+0.428	(*)	-0.167		-0.409	(*)
ORCH	+0.475	(*)	-0.048		-0.268	
ALTI	-0.279	(*)	-0.445	(*)	-0.072	
Eigenvalue	3.558		2.170		1.305	
% variance	44.5		27.1		16.3	

Table 2. Significant B-parameters from a multiple linear regression used to describe home range size in relation to a several habitat-related variables. Introduced variables were PC2 (obtained from a PCA on the relative surfaces of each habitat type; for details see Table 1), and the number of survey points for each bird (POIN). Non-introduced variables were: days of stay, body mass, wing length, sex and the PC1 and PC3.

Variable	<i>B</i> -parameters (non-standardized)	SE(B)	р
Constant	+0.362	0.036	<0.001
POIN	+0.004	0.001	0.004
PC2	+0.054	0.022	0.022

proportion of grasslands and infrastructures and be situated at lower altitude.

Home ranges did not differ in Bluethroats that were surveyed during spring or neap tide days (paired t-test: $t_9 = 1.450$, p = 0.181; spring tide, 1.21 ± 0.47 ha; neap tide, 0.55 ± 0.18 ha, n = 10; effect size = 0.50). However, when home ranges situated in areas known to have a clearly high (lower marsh) and low (upper marsh) influence of tide were selected (n = 17), we observed a nearly significant difference ($t_{15} = 1.938$, p = 0.072; lower marsh, 2.37 ± 0.30 ha, n = 12; upper marsh, $1.50 \pm$ 0.24 ha, n = 5; effect size = 1.04), thus suggesting an effect of tide on home range area.

We obtained evidence that Bluethroats' home ranges overlapped among each other. In particular, the overlap was 39.4% for six Bluethroats that were surveyed together during more than two consecutive days in late August, and 34.5% for six

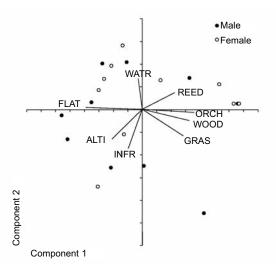


Fig. 3. Biplot obtained from a Principal Component Analysis on relative surfaces of each habitat type (for abbreviations see Table 1). Dots (n = 20) are home ranges of individual Bluethroats.

Bluethroats surveyed in September also during more than two consecutive days.

DISCUSSION

Bluethroats captured at a tidal marsh in Northern Iberia during the autumn migration period occupied home ranges (95% kernel area) of ca. 2 ha. Such relatively small home areas (for a comparison with non-territorial behaviour see Chernetsov 2005, Fransson et al. 2008) agrees with the idea that Bluethroats remain in relatively small areas at their stopover sites, a behavior also reported in other passerine birds (Dierschke & Delingat 2001, Chernetsov & Mukhin 2006, but see Provost et al. 2010). Spatial behavior of migrants at stopover sites is found to be associated with patterns of food distribution (Chernetsov & Bolshakov 2006). Thus, when foraging on prey with unpredictable occurrence distributions, birds move over large home ranges (Chernetsov & Titov 2001, Fransson et al. 2008), whilst when food is more predictable birds occupy/defend a small home range (Bibby & Green 1980, Chernetsov et al. 2004). Moreover, home range area can also be negatively influenced by population size and the degree of competition.

Bluethroat home ranges, however, were larger than in closely related species like Robins *Erithacus rubecula*, which have shown to settle in surfaces of ca. 0.4 ha (Chernetsov & Mukhin 2006). Possibly, such a difference may be due to species-specific habitat characteristics, an aspect that should be considered in future investigations. Whether Bluethroats defend their home areas (i.e., they occupy true territories) or not is a question that also remains to be studied. If they do it, however, high tolerance to intruders is expected, as we observed a high overlap with adjacent conspecifics. Furthermore, the overlap was bigger than the 25% observed at breeding quarters (Peris & Mendes 2010).

We observed that the main habitats occupied by Bluethroats were reedbeds (ca. 30%) and tidal flats which had both free-vegetation areas and zones with low-halophytic herbaceous vegetation highly associated to periodic tide-flooding episodes (30%). Other habitats also existing in the area had no more than a marginal representation within Bluethroats' home ranges. These were both the free-water areas from the marsh and the dry, elevated habitats (wood-, and grasslands) that were found within small islets across the tidal flats. Accordingly, Bluethroats highly depended on a number of habitats that, overall, suffer a considerable effect of tide regimens. Pure reedbeds did not seem to be selected by Bluethroats, as they also included in their home range more open habitats as we have shown above.

We obtained statistical evidence supporting that larger home ranges were situated at lower altitude hence at sites with higher (more prolonged) tide effect. This result suggests that Bluethroats staying at zones with high tide effect might relocate to areas without water during high tide, to either continue foraging or to rest in a dry place until the tide lowers. Alternatively, it could be stated that zones at lower altitude were less productive, so Bluethroats using these sites would be forced to look for food over larger home ranges.

Individuals captured with higher body mass stayed at the site for shorter periods. As body mass in migrants is positively correlated with fuel load (Salewski et al. 2009), it can be concluded that fuel loaded birds tended to stop over for shorter periods. This result is in agreement with the fact that fuel load is one of the main parameters that determines stopover duration (Alerstam & Lindström 1990), and it is in agreement with previous studies on other small passerines (Biebach et al. 1986, but see Salewski & Schaub 2007, Arizaga et al. 2008). Fuel load, however, was not correlated to home range size, thus indicating that, in this case, fuel load did not influence spatial behaviour as reported in other cases (Loria & Moore 1990). Furthermore, home range area was not influenced by body size and sex (which could be also associated with, thus suggesting that the habitat was occupied not under the ideal despotic distribution, but under an ideal free distribution, where home range size would be proportional to the characteristics of a given habitat patch.

CONCLUSION AND PERSPECTIVES

Bluethroats stopping over at an intertidal marsh were found to occupy home ranges of ca. 2 ha, where the chief habitats were reedbeds together with tidal flats with both free- and low-halophytic vegetation. Home ranges situated at a lower altitudinal level were observed to be larger, suggesting a negative effect of tide on home range size, and/or that Bluethroats being at lower altitude did not find as much food as at higher altitude, so they were forced to move over larger surfaces. Anyhow, lower-marsh would be in these terms suboptimal as compared to the higher places. Some Bluethroat subspecies, such as L. s. *namnetum*, highly depend on coastal marshes (Zucca & Jiguet 2002, Arizaga et al. 2006), and its conservation is thus linked with the conservation of adequate habitats at these sites. Some of these sites could be strongly modified, or even disappear, due to the sea-level rise which is expected to happen as a consequence of the global climate change (Church & White 2011, Pickering et al. 2012). In particular, the lower-marsh areas may be flooded permanently whereas the upper-marsh areas may be transformed into lower-marsh. According to our data, this may reduce the carrying capacity of the coastal marshes for the Bluethroat, since birds at a lower altitudinal level occupy larger home ranges.

ACKNOWLEDGEMENTS

We are grateful to the people who assisted us during the radio-tracking and field work, especially I. López, G. Deán and the members of the Txingudi Ringing Station. This research was funded by the Basque Government and the Gipuzkoa Administration. The Gipuzkoa Administration authorized the ringing activities and the radio-tracking. M. Andueza was funded by a doctoral fellowship from the Spanish Ministry of Education. An anonymous reviewer provided valuable comments that helped us to improve an earlier versions of this work.

REFERENCES

- Aierbe T., Olano M., Vázquez J. 2001. [Atlas of nesting birds in Gipuzkoa]. Munibe 52 (Supl.).
- Alerstam T, Lindström Å. 1990. Optimal bird migration: the relative importance of time, energy and safety. In: Gwiner E. (eds). Bird migration: the physiology and ecophysiology. Springer-Verlag Heidelberg, Berlin, pp. 331–351.
- Arizaga J., Alonso D., Campos F., Unamuno J. M., Monteagudo A., Fernandez G., Carregal X. M., Barba E. 2006. [Do subspecies of bluethroat *Luscinia svecica* show a geographic segregation during the autumn migration period in Spain?]. Ardeola 53: 285–291.
- Arizaga J., Barba E. 2009. Importance of sampling frequency to detect differential timing of migration: a case study with Blackcaps Sylvia atricapilla. Ardea 97: 297–304.
- Arizaga J., Barba E., Alonso D., Vilches A. 2010. Stopover of bluethroats (*Luscinia svecica cyanecula*) in northern Iberia during the autumn migration period. Ardeola 57: 69–85.
- Arizaga J., Barba E., Belda E. J. 2008. Fuel management and stopover duration of Blackcaps *Sylvia atricapilla* stopping over in northern Spain during autumn migration period. Bird Study 55: 124–134.

- Arizaga J., Mendiburu A., Alonso D., Cuadrado J. F., Jauregi J. I., Sánchez J. M. 2011a. A comparison of stopover behaviour of two subspecies of the Bluethroat (*Luscinia svecica*) in Northern Iberia during the autumn migration period. Ardeola 58: 251–265.
- Arizaga J., Schmaljohann H., Bairlein F. 2011b. Stopover behaviour and dominance: a case study of the Northern Wheatear Oenanthe oenanthe. Ardea 99: 157–165.
- Atkinson P. W., Baker A. J., Bennett K. A., Clark N. A., Clark J. A., Cole K. B., Dekinga A., Dey A., Gillings S., Gonzalez P. M., Kalasz K., Minton C. D. T., Newton J., Niles L. J., Piersma T., Robinson R. A., Sitters H. P. 2007. Rates of mass gain and energy deposition in red knot on their final spring staging site is both time- and condition-dependent. J. Appl. Ecol. 44: 885–895.
- Bibby C. J., Green R. E. 1980. Foraging behaviour of migrant pied flycatchers, *Ficedula hypoleuca*, on temporary territories. J. Anim. Ecol. 49: 507–521.
- Biebach H., Friedrich W., Heine G. 1986. Interaction of body mass, fat, foraging and stopover period in trans-Saharan migrating passerine birds. Oecologia 69: 370–379.
- Caccamise D. F., Hedin R. S. 1985. An aerodynamic basis for selecting transmitter loads in birds. Wilson Bull. 97: 306–318.
- Chernetsov N. 2005. Spatial behavior of medium and long-distance migrants at stopovers studied by radio tracking. Ann. N. Y. Acad. Sci. 1046: 242–252.
- Chernetsov N., Bolshakov C. V. 2006. Spatial behaviour of some nocturnal passerine migrants during stopovers. Acta Zool. Sin. 52: 599–601.
- Chernetsov N., Manukyan A. 2000. Foraging strategy of the Sedge Warbler (*Acrocephalus schoenobaenus*) on migration. Vogelwarte 40: 189–197.
- Chernetsov N., Mukhin A. 2006. Spatial behavior of European Robins during migratory stopovers: A telemetry study. Wilson J. Ornithol. 118: 364–373.
- Chernetsov N., Mukhin A., Ktitorov P. 2004. Contrasting spatial behaviour of two long-distance passerine migrants at spring stopovers. Avian Ecol. Behav. 12: 53–61.
- Chernetsov N., Titov N. V. 2001. Movement patterns of European reed warblers *Acrocephalus scirpaceus* and sedge warblers *A. schoenobaenus* before and during autumn migration. Ardea 89: 509–515.
- Church J. A., White N. J. 2011. Sea-level rise from the late 19th to the early 21st century. Surveys in Geophysics 32: 585–602.
- Cohen J. 1969. Statistical power analysis for the behavioral sciences. Academic Press, New York.
- Cramp S. 1988. The birds of the Western Palearctic. Vol. V. Oxford University Press, Oxford.
- Delingat J., Dierschke V. 2000. Habitat utilization by Northern Wheatears (*Oenanthe oenanthe*) stopping over on an offshore island during migration. Vogelwarte 40: 271–278.
- Dierschke V., Delingat J. 2001. Stopover behaviour and departure decision of northern wheatears, *Oenanthe oenanthe*, facing different onward non-stop flight distances. Behav. Ecol. Sociobiol. 50: 535–545.
- Fransson T., Barboutis C., Mellroth R., Akriotis T. 2008. When and where to refuel before crossing the Sahara desert extended stopover and migratory fuelling in first-year garden warblers *Sylvia borin*. J. Avian Biol. 39: 133–138.
- Fretwell S. D. 1972. Populations in a seasonal environment. Princeton University Press, Princeton.
- Geslin T., Lefeuvre J. C., Le Pajolec Y., Questiau S., Eybert M. C. 2002. Salt exploitation and landscape structure in a breeding population of the threatened bluethroat (*Luscinia svecica*) in salt-pans in western France. Biol. Conserv. 107: 283–289.

- Gosler A. G., Greenwood J. J. D., Baker J. K., Davidson N. C. 1998. The field determination of body size and condition in passerines: a report to the British Ringing Committee. Bird Study 45: 92–103.
- Huntley B., Green R. E., Collingham Y. C., Willis S. G. 2007. A climatic atlas of European breeding birds. Lynx, Barcelona.
- Julliard R., Bargain B., Dubos A., Jiguet F. 2006. Identifying autumn migration routes for the globally threatened Aquatic Warbler Acrocephalus paludicola. Ibis 148: 735–743.
- Lindström Å., Hasselquist D., Bensch S., Grahn M. 1990. Asymmetric contests over resources for survival and migration — A field experiment with Bluethroats. Anim. Behav. 40: 453–461.
- Loria D. E., Moore F. R. 1990. Energy demands of migration on red-eyed vireos, *Vireo olivaceus*. Behav. Ecol. 1: 24–35.
- Mendiburu A., Aranguren I., Elosegi Z., Jauregi J. I., Sánchez J. M., Cuadrado J. F., Alonso D., Arizaga J. 2009. [Results of the first ringing campaign during the autumn migration period at the Jaizubia basin (Txingudi marshlands, Guipúzcoa)]. Revista de Anillamiento 23: 26–34.
- Mendiburu A., Sánchez J. M., Jauregi J. I., Arizaga J. 2010. [The community structure and dynamics of wintering passerine birds and allies at the reed bed of Jaizubia (Txingudi marshlands, Gipuzkoa)]. Munibe 58: 173–185.
- Moore F. R., Mabey S., Woodrey M. 2003. Priority access to food in migratory birds: age, sex and motivational asymmetries.
 In: Berthold P., Gwinner E., Sonnenschein E. (eds). Avian migration. Springer-Verlag Heidelberg, Berlin, pp. 281–291.
- Naef-Daenzer B. 2007. An allometric function to fit leg-loop harnesses to terrestrial birds. J. Avian Biol. 38: 404–407.
- Newton I. 2008. The migration ecology of birds. Academic Press, London.
- Peris S. J., Mendes S. 2010. Estimating breeding Bluethroat (*Luscinia svecica azuricollis*) population by territory mapping. In: Bermejo A. (ed.). Bird Numbers 2010 "Monitoring, indicators and targets". Book of abstracts of the 18th Conference of the European Bird Census Council. SEO/BirdLife, Madrid, pp. 115-116.
- Pickering M., Wells N., Horsburgh K., Green J. 2012. The impact of future sea-level rise on the European shelf tides. Cont. Shelf Res. 35: 1–15.
- Poulin B., Duborper E., Lefebvre G. 2010. Spring stopover of the globally threatened Aquatic Warbler *Acrocephalus paludicola* in Mediterranean France. Ardeola 57: 167–173.
- Poulin B., Lefebvre G., Mauchamp A. 2002. Habitat requirements of passerines and reedbed management in southern France. Biol. Conserv. 107: 315–325.
- Provost P, Kerbirou K., Jiguet F. 2010. Foraging range and habitat use by Aquatic Warblers *Acrocephalus paludicola* during a fall migration stopover. Acta Ornithol. 45: 173–180.
- Rappole J. H., Tipton A. R. 1991. New harness design for attachment of radio transmitters to small passerines. J. Field Ornithol. 62: 335–337.
- Salewski V., Kéry M., Herremans M., Liechti F., Jenni L. 2009. Estimating fat and protein fuel from fat and muscle scores in passerines. Ibis 151: 640–653.
- Salewski V., Schaub M. 2007. Stopover duration of Palearctic passerine migrants in the western Sahara; independent of fat stores? Ibis 149: 223–236.
- Svensson L. 1996. [Guide for the identification of European passerines]. SEO/BirdLife, Madrid.
- Turpie J. K., Hockey P. A. R. 1993. Comparative diurnal and nocturnal foraging behaviour and energy intake of premigratory Grey Plovers *Pluvialis squatarola* and Whimbrels *Numenius phaeopus* in South Africa. Ibis 135: 156–165.
- Zucca M., Jiguet F. 2002. [The Bluethroat (*Luscina svecica*) in France: breeding, migration and wintering]. Ornithos 9–6: 242–252.

[Wielkość areałów i wybiórczość siedliskowa podróżniczków na nadmorskim miejscu przystankowym podczas jesiennej migracji]

Nadmorskie obszary zalewowe pełnią bardzo ważną rolę jako miejsca przystankowe, na których ptaki uzupełniają zasoby niezbędne do dalszej wędrówki. Znaczenie pływów morskich w takich ekosystemach jest dobrze poznane dla ptaków żerujących na odsłanianych podczas odpływu plażach (np. ptaki siewkowe), zaś ich wpływ na inne ptaki, jest ciągle mało poznany. Zalewanie terenu podczas przypływów może powodować, że ptaki muszą mieć odpowiednio większe areały, żeby znaleźć wystarczająco dużo pożywienia. Choć możliwe jest także, że tereny odsłaniane podczas odpływów mogą charakteryzować się większą obfitością lub dostępnością pożywienia.

Podróżniczki poszukują pokarmu na ziemi lub w niskiej roślinności, więc na miejscu przystankowym narażonym na pływy, ptaki te doświadczają stałych zmian środowiska. Celem pracy było określenie wybiórczości środowiskowej oraz zbadanie roli pływów w kształtowaniu wielkości areału tych ptaków na miejscu przystankowym w północnej Hiszpanii. Do tego celu użyto danych zebranych dla 20 ptaków wyposażonych w nadajniki telemetryczne (apendyks 1).

Ptaki były chwytane, mierzone, ważone i wyposażane w nadajniki, a następnie namierzane od połowy sierpnia do połowy września 2010 r. Ptaki na terenie miejsca przystankowego przebywały 3–17 dni, a długość przebywania związana była z masą ptaka, a więc zasobami do dalszej wędrówki (ptaki schwytane jako lżejsze pozostawały dłużej). Stwierdzono, że wielkość areałów wynosiła od 0,68 do 4,43 ha (Fig 1). Głównymi siedliskami w obrębie badanych areałów podróżniczka były trzcinowiska oraz murawy nadbrzeżne z niską roślinnością słonoroślową lub pozbawione roślinności (Fig. 2). Dane siedliskowe zostały zgrupowane przy pomocy analizy głównych składowych (Tab. 1, Fig. 3). Stwierdzono, że wielkość areału wzrastała ze wzrostem m.in. otwartej toni wodnej, niższym udziałem terenów trawiastych oraz liczbą lokalizacji uzyskanych dla danego osobnika. Większe areały znajdowały się także na niższej bezwzględnej wysokości (Tab. 2). Wyniki wskazują, że areały podróżniczków są większe, gdy są one położone bliżej morza, a więc na terenach dłużej zalewanych podczas przypływów.

Frequency	Marked	Last signal	Survey days	Points detected	Wing length [mm]	Body mass [g]	Sex
150.780	20/08	28/08	9	43	63.5	14.0	Female
150.581	21/08	01/09	12	47	65.0	13.4	Female
150.527	23/08	08/09	17	51	68.0	12.2	Female
150.808	04/09	13/09	10	8	65.0	14.0	Female
150.160	06/09	18/09	13	33	65.5	12.5	Female
150.746	06/09	20/09	15	36	65.0	13.3	Female
150.913	06/09	20/09	15	28	66.0	12.9	Female
150.095	08/09	13/09	6	11	67.0	13.1	Female
150.603	08/09	10/09	3	5	72.0	14.8	Female
150.700	08/09	13/09	6	15	66.0	13.2	Female
150.020	20/08	22/08	3	11	68.0	13.2	Male
150.415	21/08	06/09	17	71	70.0	13.6	Male
150.342	23/08	08/09	17	57	68.0	12.2	Male
150.078	24/08	05/09	13	30	70.0	14.5	Male
150.665	04/09	10/09	7	8	71.0	14.6	Male
150.240	08/09	11/09	4	7	68.0	14.1	Male
150.172	10/09	13/09	4	8	69.0	15.1	Male
150.849	10/09	19/09	10	24	71.0	15.0	Male
150.637	15/09	20/09	6	15	69.5	14.3	Male
150.760	16/09	20/09	5	16	68.5	16.7	Male

Appendix I. Individual Bluethroats captured and equipped with transmitters at Jaizubia during the autumn migration period of 2010.