

Article

Sex and age-specific differences in wing pointedness and wing length in blackcaps *Sylvia atricapilla* migrating through the southern Baltic coast

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Abstract

The blackcap *Sylvia atricapilla* shows a complex migratory pattern and is a suitable species for the studies of morphological migratory syndrome, including adaptations of wing shape to different migratory performance. Obligate migrants of this species that breed in northern, central, and Eastern Europe differ by migration distance and some cover shorter distance to the wintering grounds in the southern part of Europe/North Africa or the British Isles, although others migrate to sub-Saharan Africa. Based on >40 years of ringing data on blackcaps captured during autumn migration in the Southern Baltic region, we studied age- and sex-related correlations in wing pointedness and wing length of obligate blackcap migrants to understand the differences in migratory behavior of this species. Even though the recoveries of blackcaps were scarce, we reported some evidence that individuals which differ in migration distance differed also in wing length. We found that wing pointedness significantly increased with an increasing wing length of migrating birds, and adults had longer and more pointed wings than juvenile birds. This indicates stronger antipredator adaptation in juvenile blackcaps than selection on flight efficiency, which is particularly important during migration. Moreover, we documented more pronounced differences in wing length between adult and juvenile males and females. Such differences in wing length may enhance a faster speed of adult male blackcaps along the spring migration route and may be adaptive when taking into account climatic effects, which favor earlier arrival from migration to the breeding grounds.

Key words: blackcap, migration, population, wing shape

The avian wings are subject to several interacting and sometimes conflicting evolutionary pressures which include economical flight, effective exploitation of habitat resources, predation avoidance, and in some species—male acrobatic displays during courtship (Marchetti et al. 1995; Swaddle and Lockwood 1998; Voelker 2001; Hall et al. 2004; Hahn et al. 2016; Kennedy et al. 2016; Provinciati et al. 2018). In migratory avian species, the need for

prolonged and economical flight seems to be a major factor that influences wing morphology. Aerodynamic theory predicts that longer, pointed wings are more efficient for long-endurance flight than shorter and rounder wings (Pennycuik 2008). Indeed several studies showed that migrating species traveling over longer migratory pathways have longer (Milá et al. 2008; Newton 2008; Förschler and Bairlein 2011; Nowakowski et al. 2014) and relatively more pointed

wings (Lockwood et al. 1998; Minias et al. 2015) than closely related but more sedentary species as there is selection for high-aspect-ratio wings for fast, sustained flight. The same pattern was documented on subspecies and population levels (Pérez-Tris and Tellería 2001; Fiedler 2005; Bowlin and Wikelski 2008; Förschler and Bairlein 2011; Ponti et al. 2018; Provinciato et al. 2018). Förschler and Bairlein (2011) called this phenomenon “morphological migratory syndrome.”

The blackcap is a species that shows a complex migratory pattern (Hiemer et al. 2018), that is, includes resident populations (Mediterranean and Atlantic Islands races: *S. a. pauluccii*, *heineken*, and *gularis*), partial migrants (southern European populations—north of the Mediterranean and north-western African populations), and obligate migrants which breed in northern, central, and eastern Europe (Shirihai et al. 2001). Hence, this species is an excellent choice for the studies of morphological migratory syndrome, as its populations differ by migration distance and some European populations cover shorter distance and winter in the southern part of Europe/North Africa or the British Isles—short-distance migrants, although other travel as far as sub-Saharan Africa—long-distance migrants. In the southern Baltic region, blackcaps of local origin and transient birds from Scandinavia (Finland, Norway, and Sweden) and from breeding grounds located to the east and north-east from Poland (Lithuania, Latvia, Estonia, and Russia) are recorded (Bønlokke et al. 2006; Bakken et al. 2006; Fransson and Hall-Karlsson 2008). Scandinavian blackcaps and those from north-western Russia are long-distance migrants following the south-east direction and crossing the Sahara to spend winter in East Africa (Bønlokke et al. 2006; Bakken et al. 2006; Fransson and Hall-Karlsson 2008). Birds originating from the Baltic States migrate to south/south-west toward the Apennine Peninsula. Short-distance migrants travel to overwinter there, although long-distance blackcaps only stop over and then continue their migration to the wintering grounds in Central Africa (Bønlokke et al. 2006; Bakken et al. 2006; Fransson and Hall-Karlsson 2008). So far it has not been possible to separate between the populations of the blackcap originating from different regions with molecular methods (Mettler et al. 2013; Pérez-Tris et al. 2004), and as stable isotopes analyses became available quite recently and have some limitations (Bearhop et al. 2005), the criterion of wing morphology has been widely used as a general method to identify populations that differ in migration distance (Lo Valvo et al. 1988; Gustin et al. 1999; Fiedler 2005; Ożarowska 2015; Ożarowska and Zaniewicz 2015; Ożarowska et al. 2016, 2018). Only just recently Delmore et al. (2020) assembled a reference genome for blackcaps and obtained whole-genome resequencing data from individuals originating from different parts of the breeding range of this species. Even though genomic differentiation was low between migratory populations of the blackcap, this comprehensive genomic analysis pointed at candidate genes that might control migratory traits and future work on their expression may allow revealing the differences in those migratory populations as well.

Selective forces acting on avian wing morphology result not only from the conducted migratory movements, but also from predation avoidance, effective feeding, and hunting for prey or displays during courtship and all those may act differently in juvenile and adult birds and/or males and females (Chandler and Mulvihill 1990; Swaddle and Lockwood 1998; Pérez-Tris and Tellería 2001; Voelker 2001; de la Hera et al. 2014; Provinciato et al. 2018). The blackcap is a sexually dimorphic species, and juvenile birds are easily recognizable from adult individuals when captured during the

field studies (Svensson 1992), therefore also sex- and age-related variation in morphological migratory syndrome may be considered in this species. It was shown that juvenile blackcaps had shorter wings than adults in migratory populations (Fiedler 2005), but not in sedentary populations (Pérez-Tris and Tellería 2001; Fiedler 2005), although the variation with age in wing pointedness was found in migratory females only (Pérez-Tris and Tellería 2001). It was hypothesized that it might be due to an increased migratoriness of females in partially migratory blackcap populations (Pérez-Tris and Tellería 2001). However, in the study by Fiedler (2005), sex-related differences were not taken into account, although both sex and age-related variations in wing shape were found in migratory blackcaps wintering in the southern Spain and sedentary population in that area (Pérez-Tris and Tellería 2001). In our study, we explored in more detail age- and sex-related correlations in wing pointedness and wing length of obligate blackcap migrants to understand the differences in migratory behavior of this species. In juvenile blackcaps, we expected shorter and more rounded wings when compared with adults as we hypothesized that, similar to other migratory passerines (e.g., Alatalo et al. 1984; Chandler and Mulvihill 1990; de la Hera et al. 2014), in juveniles the selection pressure for an antipredator adaptation was stronger than selection on flight efficiency for long migration distances. As there is no pronounced latitudinal segregation in the size-monomorphic male and female blackcaps at their wintering grounds (Pérez-Tris and Tellería 2002; Catry et al. 2006), but protandry, that is, earlier arrival to the breeding grounds of males relative to females, was reported in the blackcap (Tøttrup and Thorup 2008), then we expected males of this species to have longer and more pointed wings than females. Such wing shape may enhance their faster spring passage and therefore earlier arrival to the breeding grounds.

Materials and Methods

Field methods

We analyzed data on 8,368 autumn migrating blackcaps captured during 43 years (1967–2009) at Bukowo-Kopań bird ringing station, Poland (54°20′17.66″N; 16°14′43.09″E) on the southern coast of the Baltic Sea. Birds were sexed and aged according to the plumage characteristics following Svensson (1992). Analyzed data set included 3,760 juvenile females, 4,290 juvenile males, 148 adult females, and 170 adult males.

Due to complex pattern of different blackcap populations passing along and crossing the southern Baltic coast (Bønlokke et al. 2006; Bakken et al. 2006; Fransson and Hall-Karlsson 2008) we focused on a single station to sample similar group of migrants every year. We applied the standard Operation Baltic and SE European Bird Migration Network methodology, which includes constant mist-netting effort, that is, nets are open throughout the whole migration season and are checked every hour from dawn to ~1 h after dusk, and standard set of biometric measurements (Busse and Meissner 2015). In a single year, the number of mist nets and their location throughout the whole migration season was stable. More than 43 years the distribution of nets relative to habitats was also stable and each year covered mature forest, young forest stands, shrubs, reed beds, and open-habitat. As the time of fieldwork differed slightly between years, a reference period from 14 August to 23 October was defined as a time window for data analysis, and during this period, each year nets were operating every day. This period covered 98.5% of autumn migration of the blackcap in the region (Nowakowski 1999). Biometric measurements included wing

length measured as maximum chord with accuracy of 1 mm using a ruler and the wing formula of the left wing recorded to the nearest 1 mm by measuring the primary distances from the wing-tip to the tip of each 1 of the 7 primaries (P2–P8, numbered in ascending order) on the folded wing using a ruler (Busse and Meissner 2015). Primary feathers of captured birds were carefully checked for any basal sheaths to ensure that feather growth was complete and only full-grown individuals were measured. The measurements were taken by experienced ringers; each year the accuracy and repeatability of the measurements taken by different ringers were checked as described by Busse and Meissner (2015) to ensure the comparability across years.

Data analysis

To estimate the relationship between wing length and its shape in adult and juvenile males and females of migrating blackcaps, we used data on wing chord and wing formulae of first-year individuals in immature plumage and adult birds. To avoid multicollinearity, we applied the simple formula for wing pointedness (e) that did not include wing length. That formula was as follows (Holyński 1965):

$$e = \Sigma p - \Sigma d$$

where:

- Σp – sum of primary distances proximal to wingtip,
- Σd – sum of primary distances distal to wingtip.

We used a generalized linear model (GLM in Statistica) with an identity link function and normal error distribution with wing pointedness as a response variable, sex, age, and sex by age interaction as categorical factors and wing length as an explanatory variable. A criterion based on the Wald statistic (χ^2) was applied to determine which variables had significant influence on wing pointedness. The stepwise method of variable selection was not used as it was criticized because, that is, it produces a bias in parameter estimation and inflates the probability of incorrectly rejecting the null hypothesis of no effect (Whittingham et al., 2006). Therefore, in this article, a model that included all independent variables was presented. The next generalized linear model (GLM) model was applied to test whether wing length was related to age and sex of blackcaps. The Wald χ^2 statistic was used to test for significant differences between those groups. We did not account for a year effect as we assumed that the relationship between wing length and its shape did not change over time. Moreover, in our previous study, we showed that >43 years changes in the numbers of juvenile blackcaps migrating in autumn through the S Baltic were paralleled by changes in wing length of captured individuals and suggested that these trends were due to changing population composition of migrating birds and increase in the number of short-winged (short-distance) blackcaps (Ożarowska et al. 2016). These 2 generalized linear models were checked for the collinearity of the explanatory variables using variance inflation factors. These factors were <10 (ranging from 1.00 to 6.85) suggesting that there was no significant collinearity among the variables (Quinn and Keough 2002). Scaled deviance was used to evaluate the overall fit of each model, with values close to 1 indicating that the model fits the data well (Nelder and Wedderburn 1972), which was the case in our study (1.0006 and 1.0005, respectively).

To explore the relationship between wing shape and wing length in blackcaps, we used only the recoveries of individuals (cf. Appendix A), which we assumed were short- or long-distance migrants based on their ringing/recovery data (date and location) and published data (Shirihai et al. 2001; Bakken et al. 2006;

Fransson and Hall-Karlsson 2008; Yosef and Wineman 2010; Valkama et al. 2014) and for which wing length and wing formula were measured. These were only 9 individuals over the 43 years of the study which were ringed or recovered at Bukowo-Kopań and reported or ringed during the wintering period in Europe (Italy, Ireland, and Portugal; short-distance migrants), or during spring/autumn migration in the Middle East (Israel, Syria), or in Scandinavia (Finland, Norway, Sweden), that is, the regions where long-distance blackcaps migrate or originate from (Shirihai et al. 2001; Bakken et al. 2006; Fransson and Hall-Karlsson 2008; Yosef and Wineman 2010; Valkama et al. 2014). Based on these recoveries, we studied the relation between wing length and wing pointedness of individuals that differed in migration distance. We did not account for age differences as this sample was very limited, yet it comprised mostly juvenile blackcaps. To illustrate this relationship, we also used the linear regression calculated from the entire data set of adult and juvenile blackcaps captured at Bukowo-Kopań.

The analyses were performed using the STATISTICA version 12 software (StatSoft 2014).

Results

Wing pointedness significantly increased with increasing wing length of migrating blackcaps, irrespective of their age or sex (GLM, Wald $\chi^2 = 1,233.05$, $P < 0.001$, Table 1). Within each sex, adults had more pointed wings than juveniles (GLM, Wald $\chi^2 = 6.09$, $P = 0.014$; Table 1 and Figure 1), although there was no significant difference in this parameter between males and females in each age class (GLM, Wald $\chi^2 = 0.02$, $P = 0.898$; Table 1 and Figure 1). Non-significant interaction between age and sex (GLM, $\chi^2 = 1.37$, $P = 0.242$; Table 1) indicates a similar tendency in the differences among age and sex classes (Figure 1).

Sex had a significant influence on wing length, and males had longer wings than females (GLM, Wald $\chi^2 = 4.63$, $P = 0.031$; Table 2 and Figure 2), and adult blackcaps had longer wings than juveniles (GLM, Wald $\chi^2 = 42.88$, $P < 0.001$; Table 2 and Figure 2). Non-significant interaction between age and sex (GLM, $\chi^2 = 1.31$, $P = 0.252$; Table 2) indicates a similar tendency in the differences among age and sex classes (Figure 2).

To illustrate the significant relationship between wing length and wing pointedness in migrating blackcaps, we also used the linear regression calculated from the entire data set of adult and juvenile blackcaps captured at Bukowo-Kopań (juveniles $e = -23.59 + 0.66$ * wing length; t -test, $t_{8048} = 34.45$, $P < 0.001$; adults: $e = -19.25 + 0.61$ * wing length; t -test, $t_{316} = 6.51$, $P < 0.001$; Figure 3). Based on biometric characteristics of blackcaps recovered during the winter season in Europe (Italy, Ireland, and Portugal) or spring/autumn migration in the Middle East (Israel and Syria) or in Scandinavia

Table 1. Effects of wing length, age, and sex on wing pointedness of migrating blackcaps according to the generalized linear model

Explanatory variable	Coefficient	SE	Wald χ^2	P-value
Constant	-23.241	1.423	266.69	<0.001
Wing	0.658	0.019	1,233.05	<0.001
Age (juvenile)	-0.245	0.099	6.09	0.014
Sex (male)	0.013	0.099	0.02	0.898
Age* Sex	-0.116	0.099	1.37	0.242

Estimated coefficients are set to zero for baseline categories of categorical variables (sex: male and age: juvenile).

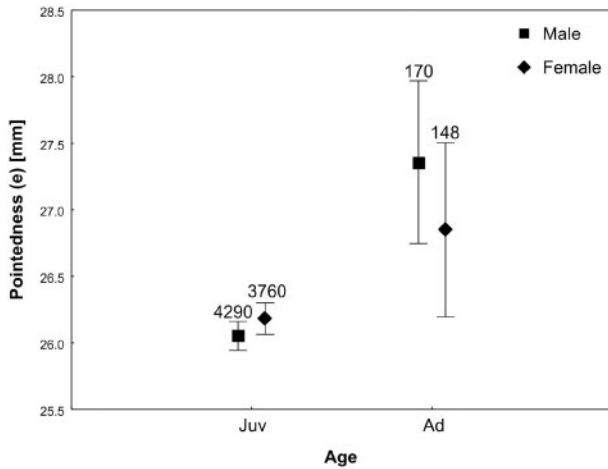


Figure 1. Differences in wing pointedness between juvenile (Juv) and adult (Ad) males and females of autumn migrating blackcaps captured at Bukowo-Kopań station on the S Baltic coast as shown by the GLM. The sample size is given for each group.

Table 2. Effects of age and sex on wing length of migrating blackcaps according to the generalized linear model

Explanatory variable	Coefficient	SE	Wald χ^2	P-value
Constant	75.778	0.006	1,721,223.61	<0.001
Sex (male)	0.124	0.058	4.63	0.031
Age (juvenile)	-0.378	0.058	42.88	<0.001
Age* Sex	-0.066	0.058	1.31	0.252

Estimated coefficients are set to zero for baseline categories of categorical variables (sex: male and age: juvenile).

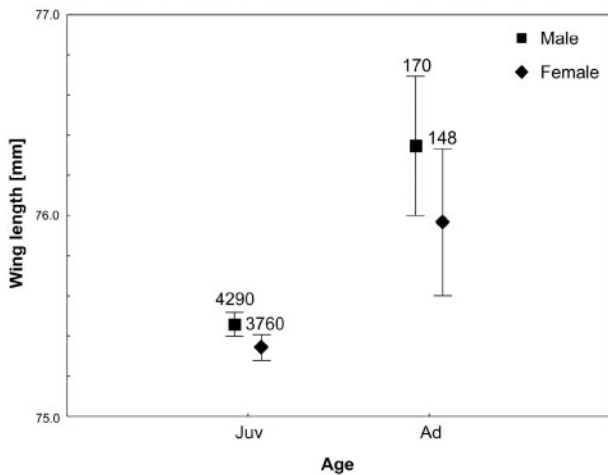


Figure 2. Differences in wing length between juvenile (Juv) and adult (Ad) males and females of autumn migrating blackcaps captured at Bukowo-Kopań station on the S Baltic coast as shown by the GLM. The sample size is given for each group.

(Finland, Norway and Sweden) wing length tends to increase with increasing migration distance (Figure 3). Such trend in wing pointedness is weak. This may be due to the fact that the sample size is very low and these are mostly juvenile blackcaps, in which the relation

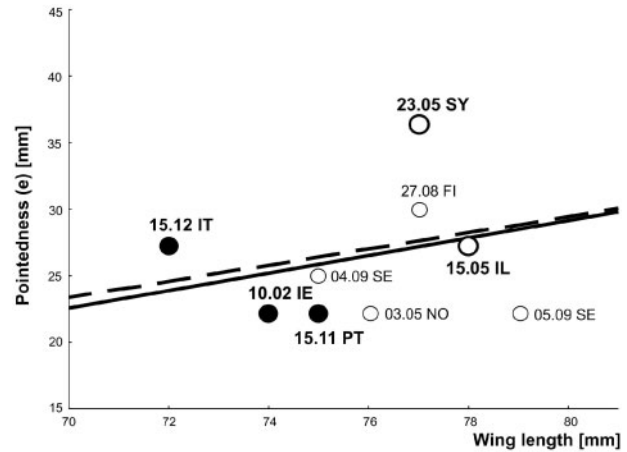


Figure 3. Biometric characteristics of blackcaps ringed and later recovered or ringed elsewhere and recovered at Bukowo-Kopań station on the S Baltic: black dots—individuals recovered at wintering sites in Europe; white bold dots—individuals recovered during spring migration in the Middle East; white dots—biometrics of individuals ringed/recovered during spring/autumn migration in Scandinavia; the linear regression calculated from the entire data set: solid line—juveniles; dashed line—adults; the 2-letter country codes: FI, Finland; IE, Ireland; IL, Israel; IT, Italy; NO, Norway; PT, Portugal; SE, Sweden; SY, Syria.

between wing length, wing pointedness, and long migration distances may be not so well pronounced as in adults.

Discussion

Morphology of avian flight apparatus is the result of a complex set of trade-offs shaped by various selective pressures. In migratory species, natural selection favors the evolution of longer and more pointed wings (Nowakowski et al. 2014; Minias et al. 2015; Provinciati et al. 2018) as these birds perform prolonged endurance flights and such wing shape increases the efficiency of sustained flight (Bowlin and Wikelski 2008). According to the results of our study, wing pointedness significantly increased with increasing wing length in blackcaps migrating in the S Baltic region. This pattern was consistent in all age/sex groups. Unfortunately, the number of the recoveries of blackcaps ringed/recovered during migration at Bukowo-Kopań ringing station >43-year period was very limited, but a low recovery rate is typical of a small passerine migrant, for example, in the Robin: 0.09–0.28%, Remisiewicz 2002; Korner-Nievergelt et al. 2014; in the Barn Swallow: 0.08–0.38%, Burman et al. 2018, and even lower in the Reed Warbler: Procházka et al., 2017). It seems plausible that short- and long-winged blackcaps are likely to comprise mostly short- and long-distance migrants, respectively (Fiedler 2005; Bengtsson et al. 2009; Ożarowska and Zaniewicz 2015; Ożarowska et al. 2018). Indeed, the recoveries of blackcaps analyzed in this study may indicate that wing length tends to increase with increasing migration distance as the individuals characterized by long wings migrating through the Middle East were most probably long-distance migrants wintering in East Africa (Yosef and Wineman 2010), although birds with shorter wings recovered wintering in Europe were short-distance migrants.

The results of our study documented the difference in wing pointedness and wing length in juvenile and adult blackcaps migrating in the S Baltic region. Within each sex, adults had longer and more pointed wings than juvenile birds. Different optimal wing

shape for juveniles and adults is likely to be adaptive, and we suppose that these 2 age categories may have different wing shape optima (Hall et al. 2004). In inexperienced juvenile individuals selection for improved maneuverability and take-off performance as an antipredator adaptation is stronger than selection on flight efficiency for long migration distances (Alatalo et al. 1984; Kullberg et al. 1996; Pérez-Tris and Tellería 2001; Fiedler 2005). These age-related differences in wing morphology may partly explain age differences in spring migration phenology, as adults arrive earlier than juveniles on the breeding grounds (Potti 1998) and may achieve higher breeding success (de la Hera et al. 2014). Later migration timing of juveniles relative to adults may be an adaptive strategy to avoid the high costs of fast migration and competition for breeding territories with experienced adults (McKinnon et al. 2014). Selection on wing pointedness may also result from climatic effects, which favor earlier arrival from migration (Saino et al. 2017), and indeed that may be the case in adult blackcaps. Moreover, we documented a profound difference in wing length between adult male blackcaps and juvenile males and females. Adult males are the class particularly prone for earlier spring passage resulting in earlier arrival to the breeding grounds (Kokko 1999; Kokko et al. 2006; Briedis et al. 2019) and settling in higher-quality territories. Their earlier arrival to the breeding sites may be due to sex-specific differences in departure timing and migration duration (Ouweland and Both 2017; Briedis et al. 2019). During spring, migration male blackcaps remained significantly shorter than females in an oasis that is a refueling site in Eilat (Israel) (Yosef and Wineman 2010). These authors suggest that males may minimize time spent at stop-over sites and maintain a slightly faster speed along their route toward the breeding grounds. Earlier arrival may be enhanced by the wing shape better adapted to faster migration (Hedenström and Pettersson 1986), then we might expect males of this species to have longer and more pointed wings than females. Indeed this was the case in adult male blackcaps. When taking into account that there is no geographical segregation between male and female blackcaps at their wintering grounds (Pérez-Tris and Tellería 2002; Catry et al. 2006), still males arrive significantly earlier than females at the stop-over site on their spring migration route (Izhaki and Maitav 1998) and remain there significantly shorter than females (Yosef and Wineman 2010), we may conclude that age-related differences in wing morphology shown in our study enhance a faster speed of adult male blackcaps along the spring migration route and therefore their earlier arrival to the breeding grounds.

Summing up, the results of our study showed that wing pointedness significantly increased with increasing wing length in blackcaps migrating in the S Baltic region. Moreover, adults had longer and more pointed wings than juvenile birds. This indicates that antipredator adaptation is stronger than selection on flight efficiency in juvenile blackcaps. More pronounced differences in wing length between adult and juvenile males and females may enable adult males to maintain a faster speed along the spring migration route and to reach faster their breeding grounds. And that might be particularly important when taking into account climatic effects, which favor earlier arrival from migration. We also reported some more evidence supporting the criterion of wing morphology as applicable to identify the blackcap's populations that differ in migration distance and migratory behavior.

Conflict of Interest

The authors declare that they have no conflict of interest.

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Appendix A

Ringing/recovery data and biometrics of blackcaps *S. atricapilla* captured/recovered during migration at Bukowo-Kopań or other sites and reported during spring/autumn migration or wintering period

Ring No.	Ringing data			Recovery data					BIOMETRICS		
	Sex	Age	Date ringed	Place of ringing	Coordinates	Date recovered	Place of recovery	Coordinates	WL*	e**	
HA99668	F	IMM	21 September 1970	Bukowo-Kopań ringing station, PL	54°21'00.0"	23 May 1971	Damas, SY	33°30'00.0"	36°18'00.0"	77	36
2375494	M	Full grown, age unknown	5 September 1972	Enskar, Balinge, SE	58°41'00.0"	15 September 1972	Bukowo-Kopań ringing station, PL	54°21'00.0"	16°17'00.0"	79	22
J369990	F	IMM	27 August 1978	Eckero, FI	60°12'00.0"	04 September 1978	Bukowo-Kopań ringing station, PL	54°21'00.0"	16°17'00.0"	77	30
KA96530	F	IMM	25 September 1980	Bukowo-Kopań ringing station, PL	54°21'00.0"	15 November 1980	Herdade de Pinheiro, PT	38°27'00.0"	-8°42'00.0"	75	22
KY73169	M	IMM	26 April 2004	Bukowo-Kopań ringing station, PL	54°27'00.0"	03 May 2004	Store Faerder, Tjome, NO	59°04'00.0"	10°32'00.0"	76	22
KZ20705	M	AD	23 September 2004	Bukowo-Kopań ringing station, PL	54°27'00.0"	15 May 2005	Bird Sanctuary, IBRCE, Eilat, IL	29°33'00.0"	34°57'00.0"	78	27
KZ27885	F	IMM	3 May 2005	Bukowo-Kopań ringing station, PL	54°27'00.0"	04 September 2005	Sandby Strand, Borrbj, SE	55°25'00.0"	14°13'00.0"	75	25
KN63201	M	IMM	22 August 2007	Bukowo-Kopań ringing station, PL	54°28'00.0"	15 December 2014	C. Timponazzo, Noto, IT	36°46'34.3"	15°04'34.0"	72	27
K1N6877	M	IMM	28 September 2014	Bukowo-Kopań ringing station, PL	54°20'13.0"	10 February 2015	Ballygambon, IE	52°26'00.0"	-7°42'00.0"	74	22

*WL – wing length, **e – wing pointedness