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LIKE A PHOENIX FROM THE ASHES

Grzegorz Zaniewicz and Przemysław Busse

ABSTRACT

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From 1967 until 1990, populations of five *Sylvia* species migrating through the south-western coast of the Baltic Sea were considerably low and significantly decreasing in the Blackcap (*Sylvia atricapilla*), Garden Warbler (*S. borin*) and Barred Warbler (*S. nisoria*). While after that period a rapid increase in the populations of these migratory species was noted. Similar changes that had started about 1991 were shown by all five *Sylvia* species. Such coincidence could indicate some common factors acting upon the studied group of migrants at the same time. Apart from a clear increase in the long-term dynamics of the species observed at Bukowo-Kopań station, the Pearson correlation coefficients of these dynamics calculated for every pair of the analysed *Sylvia* species in 1967-2006 were high and statistically significant.

Based on the distribution of recoveries of the Lesser Whitethroat (*S. curruca*) we assumed that the main fraction of birds passing the south-western coast of the Baltic Sea originated from the Scandinavian Peninsula. Recent climate changes observed in this area were consistent with the time when the increase in the number of caught birds was noted. Consequently, we suspect that the analysed *Sylvia* species passing this part of the coast share vast breeding grounds located mainly on the Fennoscandian Peninsula, where their populations are affected by the same common factors.

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Key words: long-term dynamics, population, migration, climate changes, *Sylvia atricapilla*, *Sylvia borin*, *Sylvia curruca*, *Sylvia communis*, *Sylvia nisoria*

INTRODUCTION

Long-term changes of bird populations give us information, which is usually difficult to connect with numerous plausible factors that can influence population size of a given species. It is also quite complicated to point out the most important factor even if we know most of them. Depending on time and location, different factors and/or their complex influence the size of population. Fluctuations or linear changes in numbers of birds caught every year during autumn migration reflect both changes on breeding and/or wintering grounds and those formed on the migration route. Moreover, according to previous studies on the long-term population dynamics, even within single species different populations might show various patterns of changes (Busse 1973, 1984; Petryna 1976; Woźniak 1997; Zaniewicz and Busse 2008).

Using comparisons of long-term changes and fluctuations in numbers of caught birds in species representing different habitat requirements, wintering places and migration routes, it is plausible to find partial solution of this problem by limiting the number of potential causes. Such an approach restricts potential causes only to these influencing jointly all the analysed *Sylvia* species.

In the present study, we analysed long-term changes in number of caught birds for five *Sylvia* species: the Blackcap (*Sylvia atricapilla*), Garden Warbler (*S. borin*), Whitethroat (*S. communis*), Lesser Whitethroat (*S. curruca*) and Barred Warbler (*S. nisoria*), migrating through three European ringing stations. This paper is partly a continuation of the analysis made by Busse *et al.* in 1995, in which the authors showed a general decreasing trend of the *Sylvia* species for several European stations. From that time a few papers indicated improving conditions on European breeding grounds, probably caused, as the authors suggested, by climate changes (Burton 1995; Žalakevičius 1999, 2001). It was suspected that due to global warming, many bird species breeding in Europe expanded their range in two main directions: to the north, mainly throughout Scandinavia, and northwest, particularly in Great Britain (Burton 1995). Later, it turned out that birds breeding in the eastern part of the Baltic Sea showed a third way of range expansion: to the east and northeast (Žalakevičius 2001).

There are several problems in the studies on the long-term population changes. The first one is that the material used in such analyses usually was collected during short periods of time (surprisingly often it does not prevent authors from drawing a long-term conclusions) and mostly from the restricted areas. On the other hand, some analyses show very general trends based on the material from many countries, where data were collected during different periods (Vorisek *et al.* 2008).

In order to understand the changes and interactions between different populations it is necessary to take a broader look at this problem supported by really long-term data from at least a few distinct places and concerning several species.

The main goal of this study is to define potential causes influencing bird population based on the long-term changes in numbers of migrants. Moreover, we would like to determine the relationship between *Sylvia* species migrating through the territory of central Europe.

MATERIAL AND METHODS

Study area

The data were collected at three main stations (Fig. 1) during autumn migration within the 1967-2006 period:

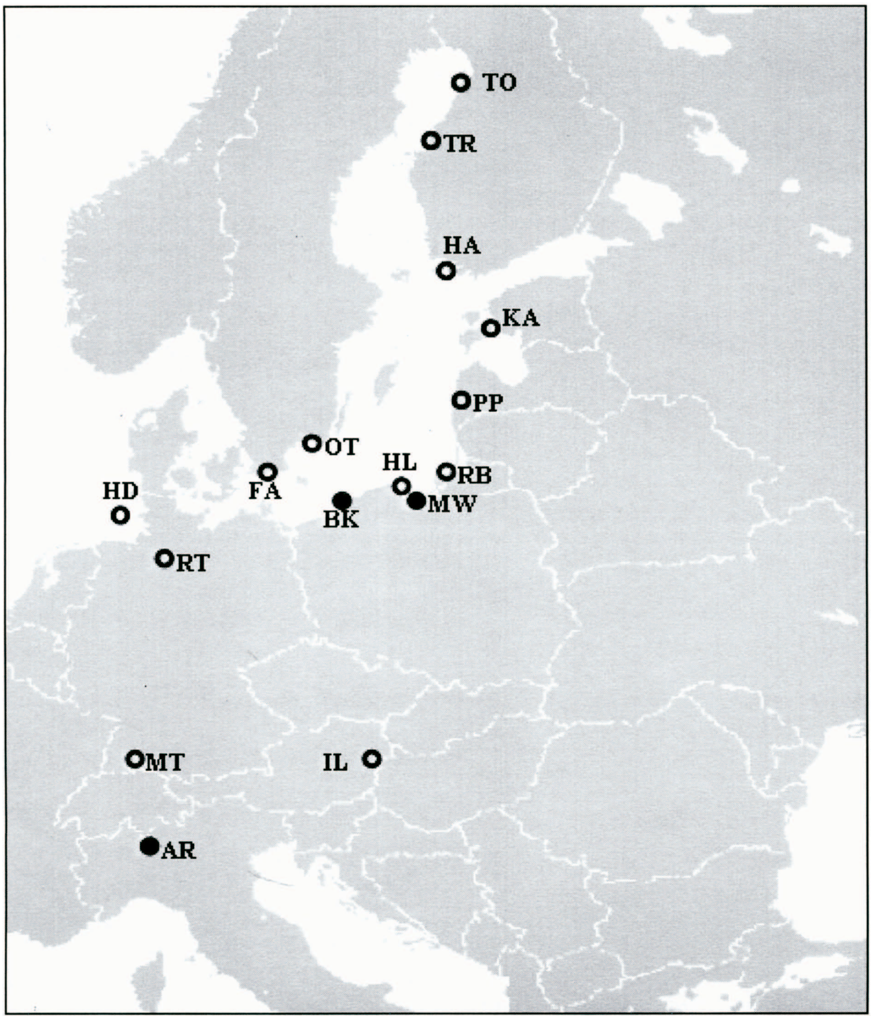

Fig. 1. Location of bird stations from which data were taken into the evaluation.
Full circles – main stations: AR – Arosio, BK – Bukowo-Kopań, MW – Mierzeja Wiślana.
Empty circles – stations where available material includes period until 1990: FA – Falsterbo, HA – Hanko, HD – Helgoland, HL – Hel, IL – Illmitz, KA – Kabli, MT – Mettnau, OT – Ottenby, PP – Pape, RB – Rybatchy, RT – Reit, TO – Tauvo, TR – Tankar.

Bukowo-Kopań, northern Poland (54°21’N, 16°17’E / 54°28’N, 16°25’E). During 1967-1984 the catching site was located on a narrow stripe of land between the sea and Lake Bukowo, and from 1983 to 2006 – 15 km to the northeast in a narrow stripe of forest between the sea and wet meadows.

Mierzeja Wiślana, northern Poland (54°21’N, 19°19’E), situated about 180 km to the east from Bukowo-Kopań. The catching site was located on the Vistula Spit in young pine stands and middle-aged stands mixed with oak, some nets were also placed in reedbeds surrounding the Vistula Lagoon.

Arosio Bird Observatory, Lombardy region in Northern Italy (45°43’N, 9°12’E). This area is situated in the western part of the Pre-Alps at 360 m a.s.l. The station is situated about 1100 km northeast from Bukowo-Kopań. At this station the data were collected from 1977 to 2006 during autumn migration.

Fieldwork

Birds were caught using mist-nets of a stable number throughout the whole period of work. The mist-nets were controlled every hour from dawn to dusk. The caught individuals after ringing and species identification were sexed (only if possible) and aged according to plumage features and sometimes skull ossification (Busse 1990, Svensson 1992). For a detailed description of field methods see Busse and Kania (1970) and Busse (2000).

Analyses of the long-term number dynamics

In order to have as homogenous groups as possible only first-year individuals of the Blackcap, Garden Warbler, Whitethroat, Lesser Whitethroat and Barred Warbler were taken into analysis.

Separately for five *Sylvia* species, we calculated long-term dynamics of individuals caught at Bukowo-Kopań, Mierzeja Wiślana and Arosio stations. In order to obtain a general picture of caught birds’ dynamics we smoothed the numbers using five following years according to the formula:

$$C_{kn} = 0.06a + 0.24b + 0.4c + 0.24d + 0.06e$$

where:
C_{kn} – moving weighted-average number of birds in year C,
a, b, c, d, e – numbers of birds in the five subsequent years.

The Pearson correlation coefficient was applied in the analyses of relationship in the long-term changes in numbers for every pair of analysed *Sylvia* species, separately at Bukowo-Kopań and Mierzeja Wiślana stations.

RESULTS

When analysing the long-term number dynamics of five *Sylvia* species at Bukowo-Kopań station we could clearly define two main periods. The first one lasted from 1967 to 1990 and was characterized by a low number of caught birds. Moreover, three of five analysed species, *i.e.*: the Blackcap, Garden Warbler and Barred Warbler showed significant decreasing trend (Table 1) within that time. Beside the species mentioned above also the Whitethroat and Lesser Whitethroat “touched bottom” more or less between 1985 and 1990. During these few years the lowest catching success was observed for all the analysed species (Fig. 2).

In the following period *i.e.* 1991-2006, the number of caught birds at the aforementioned station rapidly increased in all five *Sylvia* species (Fig. 2). Highly statistically significant long-term increase was shown by the Blackcap, Whitethroat, Lesser Whitethroat, Barred Warbler, and only for the Garden Warbler the increasing trend was a little bit weaker during this period (Table 1). Moreover, the values of the Pearson correlation coefficient calculated for the long-term dynamics for each pair of the analysed species at this station were high and significant (Table 2).

Table 1
Population dynamics trends at three main stations in two periods

		1967-1990 (Arosio 1977-1990)		1991-2006	
		N	*r*	*N*	*r*
S. atricapilla	Bukowo-Kopań	2332	0.45 * ↓	6007	0.85***↑
	Mierzeja Wiślana	1729	0.07	2118	0.04
	Arosio	2488	0.69 **↑	6561	0.54* ↑
S. borin	Bukowo-Kopań	1731	0.50 * ↓	2289	0.44 ↑
	Mierzeja Wiślana	1954	0.69***↓	441	0.38 ↓
	Arosio	1533	0.37 ↑	1474	0.15
S. curruca	Bukowo-Kopań	536	0.2 ↓	1031	0.63 ** ↑
	Mierzeja Wiślana	504	0.67***↓	159	0.09
	Arosio	-	-	-	-
S. communis	Bukowo-Kopań	162	0.1	485	0.69 ** ↑
	Mierzeja Wiślana	163	0.42 * ↑	105	0.35 ↑
	Arosio	-	-	-	-
S. nisoria	Bukowo-Kopań	33	0.49 * ↓	114	0.73 ** ↑

Explanations: *r* – Pearson's correlations of yearly captures, statistical significance: *** - $p < 0.001$, ** - $p < 0.01$, * - $p < 0.05$

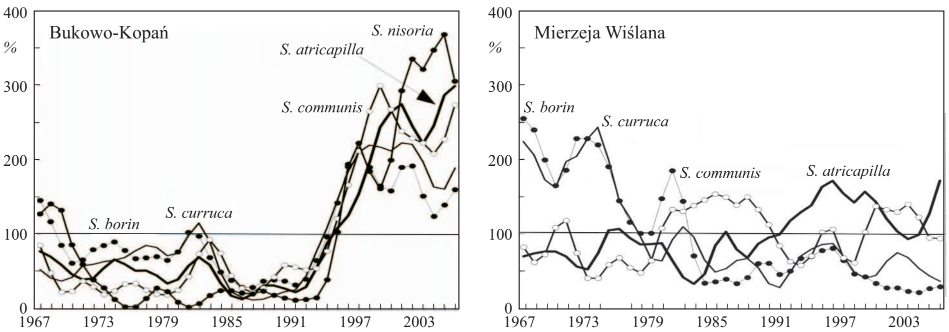

Fig. 2. Changes in five Sylvia species number dynamics over years 1967-2006 (immatures only). Smoothed by moving average.

At Mierzeja Wiślana station, as compared to Bukowo-Kopań, a relatively stable numbers of caught birds were found in four analysed species: the Blackcap, Garden Warbler, Whitethroat and Lesser Whitethroat (Fig. 2). At this site the observed pattern of number dynamics was strongly correlated only for the Garden Warbler and Whitethroat ($r = 69$, $p < 0.001$; Table 3).

Table 2
Results of Pearson's correlations coefficients for long-term autumn catch dynamics of *Sylvia* species at Bukowo-Kopań station; statistical significance: *** - $p < 0.001$

	S. atricapilla	*S. borin*	*S. curruca*	*S. communis*	*S. nisoria*
S. atricapilla		**0.73** ***	**0.81** ***	**0.86** ***	**0.80** ***
S. borin			**0.81** ***	**0.69** ***	**0.69** ***
S. curruca				**0.86** ***	**0.61** ***
S. communis					**0.62** ***

Table 3
Results of Pearson correlations coefficients for long-term autumn catch dynamics of *Sylvia* species at Mierzeja Wiślana station; statistical significance: *** - $p < 0.001$, *ns* - not significant ($p > 0.05$)

	S. atricapilla	*S. borin*	*S. curruca*	*S. communis*
S. atricapilla		0.18 *ns*	0.26 *ns*	0.16 *ns*
S. borin			**0.69** ***	0.12 *ns*
S. curruca				0.12 *ns*

Similar long-term changes and fluctuations in the number of caught Blackcaps at Bukowo-Kopań were also noted at Arosio station in Italy. At these two stations separated by a distance of about 1100 km, during thirty years (1977-2006), the patterns of changes in the number of caught Blackcaps were strongly correlated ($r = 0.71$, $p < 0.01$; Fig. 3) and an increasing trend in the number of caught Blackcaps was observed.

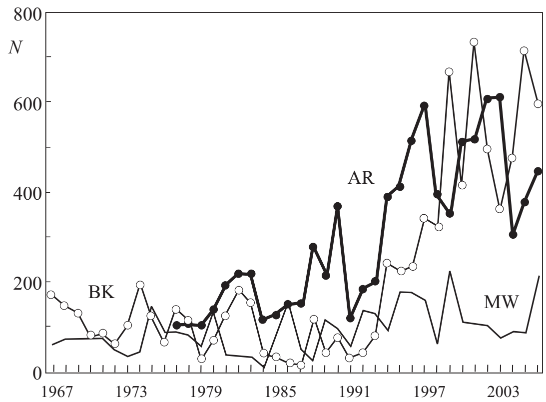

Fig. 3. Long-term changes in the number of caught Blackcaps at three main stations: BK – Bukowo-Kopań, MW – Mierzeja Wiślana, AR – Arosio

A little lower but still significant relationship ($r = 0.39$, $p < 0.05$) was noted for the long-term changes in the number of Blackcaps caught at Arosio and Mierzeja Wiślana stations. Moreover, a similar relationship ($r = 0.41$, $p < 0.05$) was found in Blackcaps passing Bukowo-Kopań and the station located to the east – Mierzeja

Wiślana. The results of this study, particularly the relationship between the long-term number dynamics pattern observed at Bukowo-Kopań (Polish) and Arosio (Italian) stations, could indicate some common factors that influence the population dynamics of the Blackcap passing both these areas during migration.

DISCUSSION

Due to the highly complex relationship between climatic factors and ecological requirements of a given species, it is hard to determine the influence of climate change on bird populations. Usually these difficulties are also the result of indirect chain connections between birds and climate conditions where every link can be extremely crucial. Moreover, the role of potential factors influencing bird populations could be different in different species. There is evidence that the higher humidity of the environment can improve breeding success for some duck species (Mayhew 1955), but for many passerines and large raptors such conditions can be restrictive (Elkins 2004). Among *Sylvia* species analysed in this paper the dissimilarity in their preferences to environmental conditions is evidently smaller but it still exists (Shirihai *et al*. 2001).

Although the mixture of populations makes the data collected during migration difficult to interpret, on the other hand, as they represent birds coming from vast areas, they can clearly show a general trend in changes avoiding a very limited local disturbance.

Role of habitat preference during migration

The opposite breeding population trends shown by the Blackcap and Garden Warbler were discovered during 40 years of a monitoring programme in a small deciduous wood in southern Sweden; the result was consistent with habitat changes in this place. Simultaneously with the growth and maturation of deciduous trees the numbers of Garden Warblers decreased and the numbers of Blackcaps increased (Enemar *et al*. 1994). Despite the overlap in habitat choice the Blackcap much more prefers trees than the Garden Warbler and due to earlier arrival in spring can occupy sites favourable for both species (Garcia 1983). The Lesser Whitethroat, usually chooses more open areas with low scrubs as compared to the Garden Warbler. Still for the Whitethroat it is too dense habitat, while for the Barred Warbler it is too poorly structured. To some extent the occurrence of a given species at a catching place during migration can reflect its preference in habitat choice.

An important question in the analyses of migration data collected during the long-term monitoring programmes is how the environmental changes, such as vegetation succession at the study sites, influence the catching effort and consequently the number of trapped migrants representing different species. To tackle this problem, we could look closer at the results from Bukowo-Kopań station. During the passage over the study area, the five analysed *Sylvia* species, of which environmental requirements at their breeding grounds only partially overlap (Shirihai *et al*. 2001), show similar fluctuations and general trends in the number dynamics from year to year. Such simultaneous changes most probably do not reflect natural habitat succession due to its linear character. According to the habitat choices at breeding grounds, we could expect that not all the species achieve the same profits caused with succession. Irrespective of the direction of natural habitat changes, this should not promote or discredit all *Sylvia* species in the same way. However, the clear relations between the long-term dynamics of the analysed species suggest that the habitat choice during migration is far more flexible; this also supports an opinion that after the breeding season the habitat choice can depend more on some other factors, *e.g.* fruit availability (Shirihai *et al.* 2001). Of course during migration the abundance of fruit or other food sources can rather prolong the stopover period than affect the decision where to land after a long flight. It seems that in general, passerines during migration use a broader range of habitats during stopover as compared to breeding season (Chernetsov 2006). Moreover, for nocturnal migrants such as *Sylvia* species, particularly in places where many of them gather after crossing a barrier, *e.g.* an open body of water (in this case the Baltic Sea), every shelter plays an important role, which additionally restricts their potential choice at the coastal Bukowo-Kopań station. On the other hand, highly significant long-term correlation in the number of Blackcaps caught at two stations – Bukowo-Kopań (Poland) and Arosio (Italy) located 1100 km apart (and where habitat is extremely stable because of catching customs) – clearly indicates that the reasons for the observed pattern are not local environmental changes at the study sites.

Relation between species and populations migrating along different routes

The synchronous rapid increase in numbers of caught *Sylvia* warblers at Bukowo-Kopań station from about 1991 suggests that population size of these species depends on some common factors operating in vast areas. There are only two possible locations where these factors can influence the population size of several different species in the same way, *i.e.* breeding grounds and winter quarters. As far as we know there are no wintering grounds where all these *Sylvia* species occur together (Shirihai *et al.* 2001). Consequently, we can assume that these are the conditions on the breeding grounds that influence the populations of migrating *Sylvia* warblers caught on the southern Baltic coast (Bukowo-Kopań station). A different and more complex pattern of the number dynamics is observed at the more eastern station – Mierzeja Wiślana, where an increasing trend, although not so steep as compared to Bukowo-Kopań, is characteristic only for the Blackcap. A relatively stable numbers for 40 years are shown by the Whitethroat, while for both the Garden Warbler and Lesser Whitethroat a strong decrease is found. Despite a relatively short distance (180 km) between the Polish stations, the composition of populations migrating through these sites seems to be different for numerous species (Busse 1973), including the analysed warblers. In general the origin of *Sylvia* species caught at Bukowo-Kopań could be partly determined based on the pattern represented by the Lesser Whitethroat. All European populations of this species expanded their range north and northwest from southeast via the Balkan Peninsula; it means that during the autumn migration this species moves south and southeast around the Mediterranean (Shirihai *et al.* 2001). The analyses of ring recoveries' distribution (Busse 1987, 2001; Yosef 1997; Bakken *et* *al.* 2006) and orientation experiments (Ożarowska *et al.* 2004) also support the assumption of the origin of these migrants. The northern end of the route joining the Balkan Peninsula and Bukowo-Kopań points clearly at the Scandinavian Peninsula as the area which most of birds could come from. Taking into account a documented range expansion of such species as the Blackbird (*Turdus merula*) (Spencer 1975) we can not exclude a part of southern Finland as a breeding territory for birds passing the south-western coast of the Baltic Sea (in this case Bukowo-Kopań). The complex pattern of the long-term changes in the numbers of *Sylvia* warblers passing Mierzeja Wiślana station suggests that migrants caught at this site most probably originate from breeding grounds in different regions. Most probably these populations of *Sylvia* warblers and also some other species originate from more continental areas, which causes this complexity (Busse 1973, Zaniewicz in prep.).

Potential impact of changes on breeding grounds

One of the main factors limiting the breeding success and consequently the population growth of bird species is the food abundance on breeding grounds. The availability of food can also enhance formation of a new wintering ground, as for the Blackcap wintering in Great Britain, and therefore influence population size (Stafford 1956, Leach 1981, Berthold and Terrill 1988, Berthold *et al.* 1992, Busse 1992, Toms 2002, Chamberlain *et al.* 2005). The Blackcap and also other *Sylvia* species analysed in this paper are known from annual changes in their food composition. During migration the Blackcap menu includes mostly, and sometimes exclusively, fruits, but earlier – during breeding season – insects are the main source of energy (Zelenova 2001). For many passerines, including *Sylvia* warblers and several species from other taxonomic groups, the most important food source during the period of feeding nestlings are insects – in the breeding season even typically frugivorous species often enrich their chicks' diet by this rich in fat and proteins food (Cramp *et al.* 1998, Anderson 2006).

To see how crucial insects are for small passerines it is necessary to trace the history of birds' evolution. In the early Tertiary, just after a quick development of flying insects, small singing birds evolved due to a new source of food (Reichholf 1996). If insects, as a special kind of fuel enabling flight, had so strong influence on birds in that time, we can expect that nowadays their accessibility also plays an important role for some populations. For instance the Grey Partridge (*Perdix perdix*) chick survival rate is closely related to the insect abundance (Green 1984).

Some fractions of birds migrating through the southern coast of the Baltic Sea breed on the Scandinavian Peninsula. As reported by Alexandersson and Eggertsson Karlström (2001) after Räisänen and Alexandersson (2003), the decade 1991-2000 was 0.8°C warmer than the preceding, 1961-1990 period in Sweden. This fact supports the results of the present study as since about 1991 a rapid increase in the number of caught *Sylvia* species was observed at Bukowo-Kopań station. Moreover, the largest difference (almost 2°C) was noted in winter. Warmer winter temperatures could be important in increasing the insects' populations due to their lower winter mortality (Harrington *et al.* 2001, Bale and Hayward 2010). Due to high reproduction rates and short generation times, insects are more likely to respond quicker to climate changes than plants and vertebrates including birds (Menéndez 2007). Usually the abundance, speed of population growth and range expansion of many insect species (source of fat and proteins for many bird species) is strongly linked with warm temperature (Savage *et al.* 2004, Frazier *et al.* 2006, Rouault *et al.* 2006, Menéndez 2007). Development periods become shorter and development rates rise with increases in temperature (Varley *et al.* 1974, Ayres 1993, Wermelinger and Seifert 1998, Farnesi *et al.* 2009, Reznik *et al.* 2009). Moreover, many insect species may accelerate their population growth by additional generations per unit of time due to warmer temperatures (Altermatt 2010).

Much evidence indicates that relation between birds and insects is extremely complex and can be very selective; as an excellent example the Brambling (*Fringilla montifringilla*) can be given. In this species, unlike in other seed-eaters, high breeding success in the northern Europe is strongly linked to the outbreaks of a single insect species – the Autumnal Moth, *Epirrita autumnata* (Enemar *et al.* 1984, Lindström 1987, Enemar *et al.* 2004., Lindström *et al.* 2005). Moreover, like many other insect species, also these moths show higher development rate in warmer temperatures, which was discovered by comparing natural populations with those inside greenhouses. Higher temperatures inside greenhouses speed up caterpillar growth and decrease their development period (Ayres 1993). Despite this widespread reaction in fast growing non-diapausing species, or those which are not dependent on low temperature to induce diapause, we also have to bear in mind that some insects (such as mountain and boreal species) need low temperatures to induce diapause and they suffer range contractions (Bale *et al.* 2002) and slow down their development during warming (Honěk 1996). Consequently bird species which adapted themselves to use the cryophilic insects as a main food source can also suffer by limitation their quantity. Taking this into account we cannot generalize that all insectivorous passerine species should outbreak due to insect populations' growth caused by warmer temperatures. The relationship between these two animal groups is still poorly known and it requires further investigations.

Temporal and spatial population changes

When analysing bird population changes and trends one should look at the broader scale both temporal and spatial. This enables the researcher to define the source/origin and the course of the observed changes. The Blackcap, as the one of the most abundant and well known species in Europe, can deliver numerous information from a wide area. The geographical distribution of the long-term changes in the Blackcap migratory population for the two distinguished periods shows a regular pattern (Fig. 4). During the first analysed period, 1967-1990, an increasing trend in the number of caught migrants was observed mainly at Scandinavian and German stations; at the same time further eastward the decreasing trends were noted at most stations, including Bukowo-Kopań (Poland), Hel (Poland), Pape (Latvia), Kabli (Estonia), Hanko (Finland) (Busse *et al.* 1995). In that period we can define relatively distinct border between areas showing different population trends, which is between central and eastern parts of Europe more or less along 15°E longitude. In the second period, 1991-2006, a strong increase in breeding populations was still recorded in Germany (Flade *et al.* 2008). The rapid increase in the number of caught warblers was also observed at Bukowo-Kopań station and in West Hungary, where beside the Blackcap also the Garden Warbler numbers increased (Gyurácz and Bánhidi 2008). It seems as if the border mentioned above moved further east. A similar estward shift in the whole species range border was described for the Blackbird (Spencer 1975). Nevertheless, to estimate such a shift in the border of the Blackcap population, further detailed studies are essential.

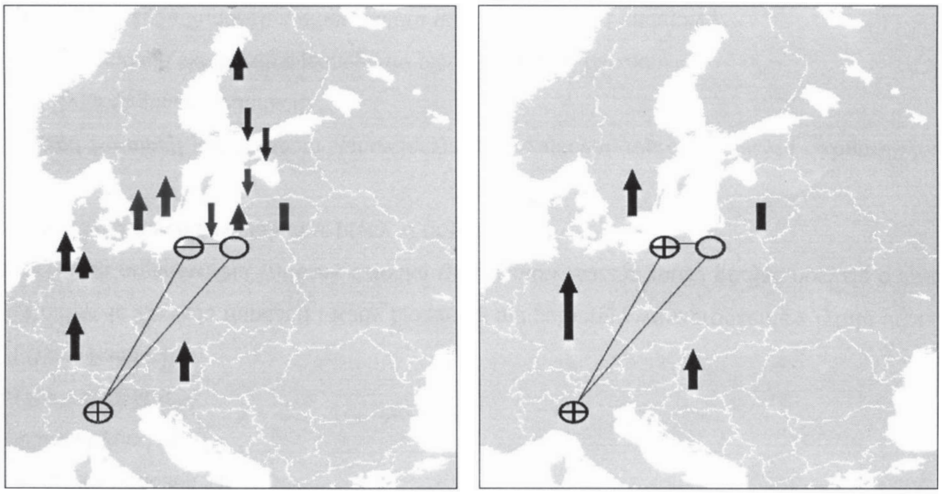

Fig. 4. Comparison of long-term population trends in different parts of Europe for the Blackcap between two periods of time: left 1967-1990, right 1991-2006.

We suspect that the discovered "outbreak" of migrating *Sylvia* species passing the south-western coast of the Baltic Sea represents the changes taking place in the large breeding areas. The consistency in the noted long-term pattern at different places can reflect the approximate migration route for some populations, particularly in the areas passed by little diverse birds' groups.

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