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Temporal trends in the timing of autumn migration of short- and long-distance migrating Blackcaps (*Sylvia atricapilla*)

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Several avian species respond in the timing of their annual cycle events to recent climate change and large-scale climate phenomena. We studied autumn migration timing of Blackcaps differentiated by their wing length, i.e., short-, medium- and long-winged individuals. According to the results of previous studies, we assumed short-winged birds as a group, which comprised mostly short-distance migrants spending their winters in the Mediterranean region and long-winged individuals as composed by mostly long-distance migrants wintering in sub-Saharan Africa. We found that all Blackcaps advanced their autumn migration during the 40-year period, but the shift towards earlier dates was nearly two-times greater in short-winged birds (8.8 days) compared to long-winged ones (4.8 days). These results indicate geographical effects in the differential migratory responses of long- and short-distance Blackcaps to environmental changes.

1. Introduction

Recent climate change and the large-scale climate phenomena, like the North Atlantic Oscillation (NAO), have a major impact on the number and distribution of bird populations, as well as their annual cycle, including the timing of spring/autumn migration (Tryjanowski *et al.* 2002, Cotton 2003, Jenni & Kéry 2003, Marra *et al.* 2005, Hüppop & Winkel 2006, Tøttrup *et al.* 2006, Thorup *et al.* 2007). The differences were also shown between long- and short-distance migrants in relation to climate warming (Hüppop & Hüppop 2003, Stervander *et al.* 2005). The former may be constrained in their plastic responses to climate change (Cotton 2003) by rigid endogenous control that could result in reduced flexibility of migration timing (Both & Visser 2001, Pulido & Widmer 2005), although laboratory experiments demonstrate that evolutionary changes in the timing of migration may occur over a short period (Pulido *et al.* 2001, Pulido & Berthold 2010). Long-distance migrants often are unable to react to changing factors on the breeding grounds (early spring, shift of food peak availability) because they winter far to the south, where it is not possible to detect the favourable opportunities occurring at the breeding grounds (Rubolini *et al.* 2007, Jones and Cresswell 2010).

Most of the studies cited above show interspecific difference in response to recent environmental changes. We wanted to elucidate this at the intraspecific level and to check if it could apply to populations of the same species that differed in migration distance. We chose the Blackcap (*Sylvia atricapilla*) – a model species for a wide range of studies on migration strategies and genetics (e.g., Lo Valvo *et al.* 1988, Pulido *et al.* 2001, Pulido & Widmer 2005, Kopiec & Ożarowska 2012). The Blackcap shows very large variation in migration pattern (e.g., short- vs. long-distance migration; migratory vs. sedentary populations; e.g., Yosef & Wineman 2010), as well as differences in biometric traits, which often occur between migratory populations of a single species, which are differentiated by migration distance (Pèrez-Tris & Tellería 2001, Fiedler 2005). Similarly to other migratory species, Blackcap wing length, aspect ratio, wing pointedness and body weight are adaptive to different migratory performance and increase with increasing migration distance (Berthold & Querner 1982, Lo Valvo *et al.* 1988, Fiedler 2005).

Generally, long-distance migrant populations of Blackcaps, which breed in Northern Europe (Fennoscandia, Russia), have longer wings than short-distance migrant conspecifics from central Europe (Fiedler 2005). These two groups differ in migration distance, as the former are mostly long-distance migrants wintering in sub-Saharan Africa, while the latter are mostly short-distance migrants wintering in the Mediterranean region (Mokwa 2004, Bakken *et al.* 2006, Bønløkke *et al.* 2006, Fransson & Hall-Karlsson 2008, Spina & Volponi 2008, Ożarowska 2015). During migration on the Polish Baltic coast, birds of local origin and migrants coming from a broad origin area ranging from Scandinavia and the circum-Baltic region to Russia are recorded. This complex population structure provides an opportunity to study migration phenology of migratory populations of a single species, which are differentiated by distance of migration.

Given the current knowledge and difference observed at an inter-specific level between short- and long-distance migrants (Both & Visser 2001, Pulido & Widmer 2005), we expected long-distance migrating Blackcaps to be less flexible and to show a comparatively limited response/variation in migration phenology over time. We reasoned that it might take them longer to adapt to changing conditions as compared to short-distance individuals.

2. Material and methods

The ringing station "Bukowo-Kopań" (54°20' 17.66"N; 16°14'43.09"E; central Polish Baltic coast) is located in the coastal zone and migrants concentrate in the immediate area. In each of the study years an effort was made to use a constant length of mist-nets in the main habitat types (mature forest, ecotone between forest and open habitat, hedgerows along meadows, open meadows, reedbeds) to control for and limit inter-annual variation in trapping success due to natural habitat changes. The data analysed in this study were collected every autumn over a period of 40 years, between 1967 and 2006 (Appendix 1). The fieldwork followed the standardized protocol of the long-term bird ringing scheme, i.e., the Operation Baltic Program (Busse & Meissner 2015). This included constant effort mist-netting (from dawn to about one hour after dusk) and standard set of biometric measurements including wing length (maximum flattened chord). In a single year the number of nets and their location throughout the whole migration season were stable, but differed slightly between years and was on average 390 m ± 44 m (SD) of mist nests. Also, the time of fieldwork differed slightly between the seasons. In order to standardise the data, a reference period was defined, 14 August–23 October. This period covered 98.5% of the Blackcap migration within the region (Kopiec 1997, Nowakowski 1999). We limited this study to the data of the hatching (first)-year birds only in order to reduce variation in migration phenology due to the differences in migration timing known to occur between the age classes (e.g., Zduniak *et al.* 2013, Wojciechowski *et al.* 2014). As immature male and female Blackcaps are about the same size (Holloway & Edwards 1989, Shirihai *et al.* 2001, Arizaga & Barba 2011), we pooled the data for both the sexes.

The significant relationship between migration date of the Blackcap, wing length, and year of cap-

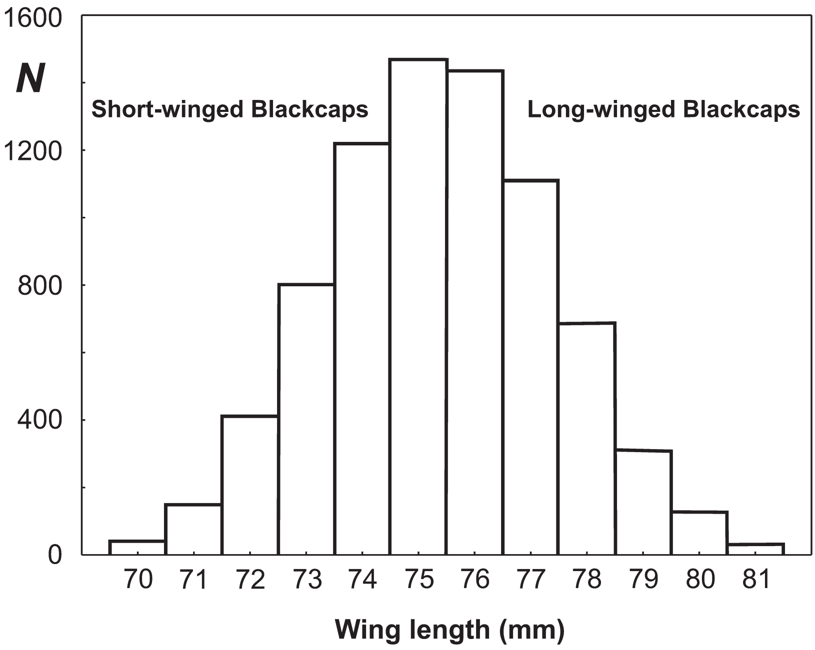

Fig. 1. Blackcaps captured during autumn migration in the central part of the Polish Baltic coast (Bukowo-Kopañ ringing station; 1967–2006), separated according to wing length, i.e., short-winged 70–74 mm, medium-winged 75–76 mm and long-winged individuals 77–81 mm.

ture was studied by Zaniewicz (2014). Therefore we focused on the question of the long-term changes in the timing of autumn migration in Blackcaps as expressed by the different migratory distances. Based on lower and upper quartiles in the wing length distribution of Blackcaps captured on the Polish Baltic coast (Fig. 1), birds were grouped as either short-winged 70–74 mm (*n* = 2,569), medium-winged 75–76 mm (*n* = 2,874) or long-winged individuals 77–81 mm (*n* = 2,244). We applied wing length as a criterion to separate between short-winged and long-winged migratory Blackcaps assuming that the former are likely to comprise mostly short-distance migrants and the latter, the long-distance migrants (cf. Fiedler 2005, Bengtsson *et al.* 2009). As the group of medium-winged individuals is most likely to be composed of both these fractions in unknown proportions, we included them in the analyses, but in the discussion focused on the extremes, i.e., the short- and long-winged Blackcaps. We reasoned that in this manner we would be able to compare groups that are more homogenous and representative of their respective populations, and to exhibit a pronounced difference.

A general linear model (GLM) with identity link function and normal error distribution was used to account simultaneously for the effects of all independent variables. Because in 1986 no short-winged individuals were captured, we excluded it from the analyses and ran a general linear model with migration date (day number in the season) as the response variable, and the categorical factors “group” (i.e., short, medium and long-winged Blackcaps), “year” and the interaction between “group” and year” as explanatory variables. Finally, we used linear regression to estimate the long-term trends in the dates of the captures of short, medium, and long-winged Blackcaps over the study period. The analyses were performed using the STATISTICA 10 software (StatSoft 2011).

3. Results

We analysed the most complex model including all factors, i.e., the group and year, and the interaction between these variables, and found significant effect of all of them on autumn migration phenology of Blackcaps (GLM: Table 1). The effect of the group was consistent, while effects of year and interaction between group and year varied over the study period (Appendix 2). Since 1995, the year had a significant effect on the migration date of Blackcaps. We observed an incremental advance

Table 1. The general linear model testing the effects of the group (i.e., short-, medium- and long-winged individuals), year and interaction between group and year (1986 was excluded as no short-winged individuals were captured) on migration date (day number in the season) of Blackcaps (*Sylvia atricapilla*).

Effect	*F*	df	*p*-value
Intercept	653306.8	1	< 0.0001
Group	21.5	2	< 0.0001
Year	12.7	38	< 0.0001
Year × Group	2.8	76	< 0.0001

of the autumn migration over the study period in all three of the categories assigned as per wing length (Fig. 2, Table 2). According to regression coefficient short-winged and long-winged individuals advanced their autumn migration on average 0.22 and 0.12 day / year, respectively. Thus the shift towards earlier autumn migration was nearly two times larger in short-winged Blackcaps.

4. Discussion

Several avian species advanced their spring migration and breeding, and this advancement is generally attributed to a response of timing of these annual cycle events to climate changes (reviews in Lehikoinen *et al.* 2004, Gordo 2007, Horev *et al.* 2010, Knudsen *et al.* 2011). Long-term (1975–2007) study on the Blackcap arrival and onset of breeding season in the Białowieża primeval forest (north-eastern Poland) also documented an advance of the breeding phenology in the study species (Wesołowski 2010). However, changes in autumn migration timing are more variable and there are either advances or delays observed in the last decades. Sokolov *et al.* (1999) analysing the Rybachy Ringing Station's long-term data on autumn mean migration dates on the Courish Spit (Russian Baltic coast) found no overall difference in the response between long- and short-distance migrating species. In contrast, Cotton (2003) and Tøttrup *et al.* (2006) reported an advance in the departure of the last individual in long-distance migrants, while Jenni & Kéry (2003) found an overall advance of the autumn median departure for 25 long-distance migrants and delayed median departure for 40 short-distance migrants.

One of the factors that may influence the time of departure from breeding grounds and cause this variation is the number of broods in a season. Long-distance, single-brooded species have been shown to advance their migration time, while species with a variable number of broods did not (Jenni & Kéry 2003). In short-distance migrants the relationship to the number of broods is even more complicated: the species with variable num-

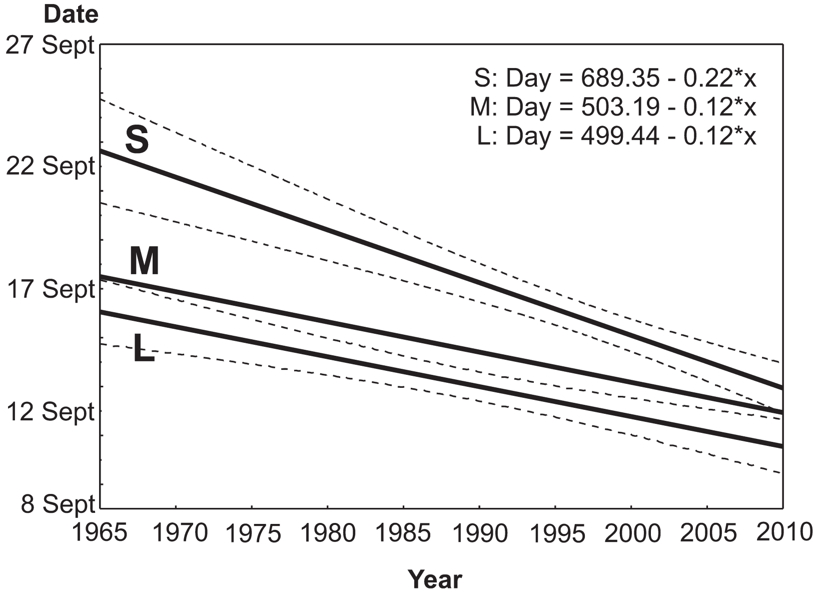

Fig. 2. Temporal trends in autumn migration timing of short-, medium and long-winged Blackcaps captured during autumn migration on the Polish Baltic coast during 1967–2006 (S, M, L – short-, medium- and long-winged Blackcaps, respectively; bold line – regression lines for short-, medium- and long-winged individuals; dashed lines – 95% confidence interval, not-shown for clarity in medium-winged birds.

Table 2. The results of the linear regression analysis used to estimate the long-term trends in the timing of autumn migration of short, medium, and long-winged Blackcaps (*Sylvia atricapilla*) over the study period.

Group	*b* (SE)	*t*	df	*p*-value	Intercept (SE)	*t*	df	*p*-value
Short-winged	–0.22 (0.032)	–6.73	2,567	< 0.0001	689.4 (64.0)	10.78	2,567	< 0.0001
Long-winged	–0.12 (0.024)	–5.11	2,242	< 0.0001	499.4 (47.7)	10.48	2,242	< 0.0001
Medium-winged	–0.12 (0.026)	–4.81	2,872	< 0.0001	503.2 (51.3)	9.81	2,872	< 0.0001

ber of broods delayed autumn migration more than single-brooded and double-brooded species. On the other hand, it was also shown that most migrants probably follow an advanced annual schedule, with little change in the time spent at the breeding grounds (Cotton 2003, Thorup *et al.* 2007). The Blackcap is considered to be mostly a single brooded species (Hoi-Leitner *et al.* 1993, Shirihai *et al.* 2001) and it seems to follow the advanced annual schedule. We found that the populations of the Blackcap differentiated by wing length, and most probably distance of migration, advanced their autumn passage but the rate of this advance was nearly half that in long- compared to short-winged birds. These results prove that similar to long-distance migrants (Both & Visser 2001, Pulido & Widmer 2005), long-winged Blackcaps showed reduced flexibility of migration timing suggesting that it might take them longer to adapt to changing conditions. Short-winged migrants on the other hand may be more flexible in their response, because of the circumstances on the wintering grounds (Mediterranean region in short-distance Blackcaps) will be a better predictor for the optimal arrival time on the breeding grounds (Both & Visser 2001).

Additionally, some species are known to be territorial during winter (Salewski *et al.* 2002) and thus individuals arriving earlier at the wintering grounds might obtain higher-quality territories and achieve higher winter survival. Earlier arrival at the wintering grounds and establishing a territory might be particularly important in populations that show increaseing numbers, which is the case for the Blackcap (Vorisek *et al.* 2008, Wesołowski 2010, Zaniewicz & Busse 2010).

The response of long-winged Blackcaps to changing environmental conditions was significantly weaker than in short-winged individuals, and we consider this to be the result of the fact that the long-distance Blackcaps winter in sub-Saharan Africa and are most probably under selective pressure to minimize the time spent on migration. The best strategy seems to be to initiate the migration south as early as possible in the autumn, maximizing the probability of encountering rich stopover sites in the Sahel at the end of the rainy season before continuing their migration further south (Schaub & Jenni 2001, Jenni & Kéry 2003, Ottosson *et al.* 2005, Gordo 2007, Mezquida *et al.* 2007).

Another plausible explanation for our observations could be that long-winged Blackcaps included in this study are most probably from breeding areas further north than short-winged individuals. Therefore they have to adjust their timing to areas that might have been affected differently by recent climate change compared to birds belonging to more southern breeding areas.

In summary, the Blackcap is known as a species showing high adaptability and flexibility with a great potential for evolutionary change (cf. Pulido & Berthold 2004), and we found significant differences in the migratory responses of long- and short-distance migratory individuals to what we assume are environmental changes.

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Syysmuuton ajoittuminen lähi- ja kaukomuuttavilla mustapääkertuilla

Monet lintulajit säätävät vuosikiertonsa tapahtumien ajoittumista vasteena ilmastonmuutokseen ja

suursäätilan heilahteluihin. Tutkimme mustapääkertun (*Sylvia atricapilla*) syysmuuton ajoittumista suhteessa siiven pituuteen, luokiteltuna lyhyt-, keskipitkä- ja pitkäsiipisiin yksilöihin. Aiempiin tutkimuksiin nojaten oletimme, että suurin osa lyhytsiipisistä yksilöistä ovat lähimuuttajia, jotka talvehtivat Välimeren maissa, kun taas pitkäsiipiset linnut ovat Saharan eteläpuolisessa Afrikassa talvehtivia kaukomuuttajia.

Tuloksemme osoittavat, että kaikki mustapääkertut aikaistivat syysmuuttoaan 40-vuotisen tutkimusjakson aikana, mutta aikaistuminen oli lähes kaksi kertaa voimakkaampaa lyhytsiipisillä linnuilla (8,8 päivää) verrattuna pitkäsiipisiin lintuihin (4,8 päivää). Nämä tulokset viittaavat maantieteellisiin tekijöiden vaikutukseen lähi- ja kaukomuuttavien mustapääkerttujen vasteessa ympäristön muutoksiin.

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Appendix 1. Characteristics of autumn migration of the Blackcap (*Sylvia atricapilla*) in central Polish Baltic coast (reference period: 14 August–23 October): number of captured birds (*N*), mean passage date, standard deviation (SD), first and last capture in the reference period, median passage date and lower/upper quartiles.

Year	*N*	Mean	SD	First	Last	Median	25%	75%
1967	144	21 Sept	15.29	18 Aug	23 Oct	19 Sept	10 Sept	29 Sept
1968	147	18 Sept	15.66	16 Aug	23 Oct	21 Sept	4 Sept	28 Sept
1969	126	11 Sept	17.96	17 Aug	23 Oct	10 Sept	26 Aug	25 Sept
1970	81	21 Sept	9.16	7 Sept	10 Oct	17 Sept	12 Sept	21 Sept
1971	81	11 Sept	15.90	19 Aug	12 Oct	10 Sept	27 Aug	24 Sept
1972	61	17 Sept	13.13	20 Aug	20 Oct	17 Sept	8 Sept	21 Sept
1973	98	17 Sept	18.29	14 Aug	12 Oct	20 Sept	2 Sept	4 Oct
1974	185	18 Sept	11.58	22 Aug	21 Oct	17 Sept	11 Sept	26 Sept
1975	117	10 Sept	14.74	15 Aug	17 Oct	12 Sept	27 Aug	21 Sept
1976	60	22 Sept	17.71	17 Aug	17 Oct	21 Sept	12 Sept	10 Oct
1977	125	17 Sept	18.15	16 Aug	23 Oct	18 Sept	2 Sept	2 Oct
1978	103	24 Sept	19.37	14 Aug	23 Oct	29 Sept	7 Sept	9 Oct
1979	30	8 Sept	15.74	16 Aug	16 Oct	8 Sept	25 Aug	17 Sept
1980	56	23 Sept	20.02	14 Aug	23 Oct	22 Sept	6 Sept	14 Oct
1981	83	21 Sept	15.26	16 Aug	15 Oct	24 Sept	12 Sept	1 Oct
1982	113	14 Sept	20.36	14 Aug	23 Oct	11 Sept	29 Aug	2 Oct
1983	151	10 Sept	12.19	16 Aug	18 Oct	11 Sept	31 Aug	18 Sept
1984	39	18 Sept	17.33	17 Aug	20 Oct	24 Sept	4 Sept	30 Sept
1985	26	7 Sept	14.39	14 Aug	10 Oct	8 Sept	31 Aug	13 Sept
1986	17	5 Sept	19.40	16 Aug	21 Oct	29 Aug	25 Aug	15 Sept
1987	15	20 Sept	23.64	20 Aug	19 Oct	25 Sept	1 Sept	14 Oct
1988	116	23 Sept	17.23	18 Aug	23 Oct	29 Sept	8 Sept	9 Oct
1989	42	15 Sept	17.38	14 Aug	20 Oct	18 Sept	31 Aug	26 Sept
1990	58	18 Sept	16.52	14 Aug	23 Oct	19 Sept	6 Sept	25 Sept
1991	31	25 Sept	13.64	22 Aug	22 Oct	23 Sept	19 Sept	4 Oct
1992	39	5 Sept	12.62	19 Aug	12 Oct	5 Sept	29 Aug	8 Sept
1993	57	14 Sept	21.63	14 Aug	22 Oct	19 Sept	24 Aug	30 Sept
1994	235	16 Sept	12.80	18 Aug	17 Oct	18 Sept	6 Sept	24 Sept
1995	178	20 Sept	14.37	19 Aug	23 Oct	20 Sept	10 Sept	30 Sept
1996	220	14 Sept	16.99	15 Aug	19 Oct	15 Sept	29 Aug	26 Sept
1997	338	9 Sept	14.25	15 Aug	19 Oct	8 Sept	28 Aug	17 Sept
1998	310	13 Sept	13.56	14 Aug	22 Oct	15 Sept	4 Sept	21 Sept
1999	587	11 Sept	12.19	14 Aug	16 Oct	12 Sept	4 Sept	19 Sept
2000	393	13 Sept	16.40	14 Aug	23 Oct	13 Sept	31 Aug	26 Sept
2001	695	16 Sept	14.21	15 Aug	19 Oct	17 Sept	5 Sept	26 Sept
2002	487	7 Sept	13.40	14 Aug	23 Oct	6 Sept	28 Aug	16 Sept
2003	342	10 Sept	14.92	14 Aug	20 Oct	11 Sept	30 Aug	21 Sept
2004	459	13 Sept	14.99	14 Aug	21 Oct	14 Sept	1 Sept	24 Sept
2005	697	14 Sept	15.76	14 Aug	22 Oct	13 Sept	3 Sept	26 Sept
2006	545	18 Sept	17.00	14 Aug	23 Oct	19 Sept	6 Sept	1 Oct

Appendix 2. Results of the general linear model testing the effects of the group (i.e., short-, medium- and long-winged individuals), year and interaction between group and year (1986 was excluded as no short-winged individuals were captured) on migration date (day number in the season) of Blackcaps (*Sylvia atricapilla*). Estimated regression coefficients are set to zero for baseline categories, i.e., the group of medium-winged individuals and year 2006. The results of interaction between group and year are omitted to simplify the table.

Parameter	Estimate	SE	*t*	*p*-value
Intercept	259.203	0.321	808.274	< 0.0001
Short-winged	3.129	0.522	5.999	< 0.0001
Long-winged	–2.363	0.409	–5.777	< 0.0001
Med-winged	0	0	–	–
1967	7.119	1.403	5.075	< 0.0001
1968	2.034	1.262	1.611	0.1072
1969	–4.684	1.359	–3.447	0.0006
1970	4.150	1.852	2.241	0.0251
1971	–3.360	1.832	–1.834	0.0667
1972	0.332	2.776	0.120	0.9048
1973	3.188	1.695	1.881	0.0601
1974	2.592	1.226	2.114	0.0345
1975	–7.222	1.749	–4.128	< 0.0001
1976	7.454	2.159	3.452	0.0006
1977	2.340	1.488	1.573	0.1158
1978	7.683	1.482	5.183	< 0.0001
1979	–7.694	3.983	–1.932	0.0534
1980	10.355	2.757	3.755	0.0002
1981	5.254	1.667	3.152	0.0016
1982	–0.174	1.519	–0.114	0.9090
1983	–2.999	2.267	–1.323	0.1859
1984	2.262	2.378	0.952	0.3414
1985	–9.425	3.116	–3.024	0.0025
1987	6.251	4.533	1.380	0.1680
1988	6.664	1.406	4.740	< 0.0001
1989	–0.736	2.336	–0.315	0.7526
1990	3.282	2.154	1.524	0.1277
1991	9.230	2.951	3.128	0.0018
1992	–4.669	3.298	–1.416	0.1568
1993	–1.407	2.132	–0.660	0.5091
1994	–0.261	1.035	–0.252	0.8012
1995	3.287	1.249	2.631	0.0085
1996	–2.829	1.072	–2.638	0.0084
1997	–6.656	0.891	–7.473	< 0.0001
1998	–3.132	0.940	–3.332	0.0009
1999	–4.192	0.727	–5.769	< 0.0001
2000	–3.422	0.813	–4.211	< 0.0001
2001	–0.739	0.645	–1.146	0.2518
2002	–8.723	0.747	–11.671	< 0.0001
2003	–6.139	0.877	–6.998	< 0.0001
2004	–2.963	0.782	–3.791	0.0002
2005	–2.216	0.689	–3.214	0.0013
2006	0	0	–	–