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Behind the Iron Curtain: Socio-economic and political factors shaped exotic bird introductions into Europe

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ABSTRACT

Little is known about how socio-economic factors quantitatively contribute to shaping introductions of exotic species in space and time. Here, we discover that socio-economic, historical and political factors are largely responsible for shaping exotic bird introductions into Europe. We find that the Cold War and its resulting commercial alliances in Eastern vs. Western Europe led to contrasting patterns in the numbers, composition and origin of birds introduced into each of the two European blocs. The isolation of the Eastern European bloc from the west during the Cold War led to a decline in the number of birds introduced and the number of birds pecies established. Birds introduced during the Cold War originated largely from economically allied countries of each of the two blocs. The Cold War provided a hitherto unexpected benefit to the Eastern European bloc by limiting exotic species introductions, and subsequent population establishment, due to its restrictions on international trade. We suggest that work on the factors shaping invasive species entablishment, spread and impacts should incorporate a socio-economic context. Given the ongoing increase in human movement and trade in Europe and the integration of most former Eastern European countries to the European Union, clear policies should be urgently established to prevent inflow of exotic species into formerly more isolated regions and reduce the risk of future biotic invasions.

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1. Introduction

Invasive species have wide-ranging impacts on native biodiversity (Clavero and Garcia-Berthou, 2005), economy and human well-being (Pimentel et al., 2005; Vilà et al., 2009), leading to attempts to prevent their future introductions (Blackburn et al., 2009). Although there has been much advancement in our understanding of the establishment process of introduced exotic bird species (Cassey et al., 2005), the role of socio-economic and historic factors is rarely examined. During the 18th and 19th centuries, many of the exotic bird introductions around the world were attributed to European settlers who emigrated to other areas overseas, bringing with them species from their home regions (Crosby, 1986). In contrast, the socioeconomic and political factors shaping spatio-temporal trends in species introduction, predominant donor regions of exotic species and invasion pathways in Europe are not well understood (but see Jeschke and Strayer, 2005). These factors, however, provide key information needed in order to increase our predictive ability of species invasions (Hulme et al., 2008).

During the 20th century, Europe experienced significant changes in its political structure. From the late 1940s until 1991, the Cold War (Gaddis, 2006) split most of Europe into two major political and socio-economic blocs (Fig. 1a), isolating the Eastern from the Western European countries for over four decades. Warfare policies and the 'Iron Curtain' almost entirely sealed the eastwest European border affecting most aspects of trade and human travel among the two blocs (Gaddis, 2006). Meanwhile, economic cooperation within each bloc and with different international partners (Fig. 1b) resulted in an increase in commodity and human movement within each bloc (Gaddis, 2006). In Western Europe, the European Economic Community and the European Free Trade Association were established in 1957 and 1960, respectively. Many Western European countries had overseas colonies during the 19th and the 20th centuries (Olson, 1991). Between 1949 and 1991, the Eastern bloc belonged to the Council for Mutual Economic Assistance (COMECON, Fig. 1b), the economic organization of the communist countries (Gaddis, 2006). This unique political background provides an exceptional opportunity to test the effect of political and socio-economic factors on the patterns of exotic species introductions in Eastern versus Western Europe. Birds provide a useful group to test this effect, as relatively good historical records exist on their introductions to various locations (e.g., Long, 1981; Lever, 1987, see also Kark and Sol, 2005) compared with most other

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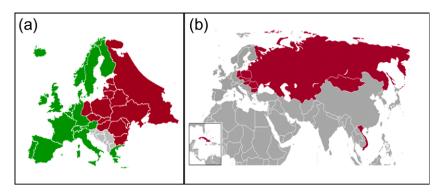


Fig. 1. (a) The Western (in green) and Eastern (in red) European blocs during the Cold War. Current (2009) borders are marked, except for the border between East and West Germany, which is the historical border during the Cold War. (b) The regions belonging during the Cold War to the Council for Mutual Economic Assistance (COMECON) (marked in red). These include the Eastern European countries, Russia, Mongolia, Vietnam and Cuba. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

groups. Birds also show an increase in the number of introduction events during the 20th century (Kark et al., 2009), which could be related to the rise in human immigration into Europe (Jeschke and Strayer, 2005) and to changes in international trade during this period. Many ornamental and waterfowl birds were introduced to large estates and parks for aesthetic reasons and hunting and their presence was often considered a status symbol (Long, 1981), leading subsequently to the deliberate and non-deliberate release of exotic birds in the wild.

In this study, we examined the effects of political and socio-economic factors on bird introduction and establishment patterns in Europe since 1850, while accounting for variations in the demand for exotic birds. We hypothesized that the formation of two political blocs that existed during the Cold War and the resulting changes in human movement and commercial trade shaped the numbers, geographical origins and composition of the exotic birds introduced into Eastern versus Western Europe. We predicted that the isolation of the eastern European bloc from the west would lead to a decline in the total number of exotic birds introduced (in terms of events and species). We also predicted that species introduced into both the east and the west during the Cold War would originate largely from economically allied countries. Finally, although a full analysis of establishment pattern and its determinants are outside the scope of this paper (see Chiron et al., 2009), we tested to which extent the number of species that established is related with the number of species introduced in Eastern and Western European countries.

2. Methods

2.1. Definitions

We define a species introduction as the release or escape of an exotic species in European countries and its associated islands (e.g. Canaries, Azores, Balearic) where it does not occur naturally. Species native to areas in Europe that were introduced to other European regions were considered exotic to the new region. The number of introduction events was defined as the number of occasions a same species is introduced to the same or to different countries. We considered an introduction as successful if it resulted in the establishment of self-reproducing breeding populations and as unsuccessful if it led to non-breeding or extinct exotic species (DAISIE, 2009).

2.2. Databases on exotic birds and human activities

We examined the introduction of 120 exotic bird species belonging to 29 families (Supplementary Table S1) introduced before the Cold War (1850–1948), during the war (1949–1991) and after it ended (1992–2007). In the framework of the DAISIE European Union consortium (DAISIE, 2009), we collated available information on bird introductions into the regions belonging to the Western and Eastern European blocs during the Cold War (Fig. 1a, including European islands: Azores, Canaries and Madeira) based on several major sources (Long, 1981; Lever, 1987; Hagemeijer and Blair, 1997), complemented by numerous local sources and peer-reviewed by national experts (Kark et al., 2009) (222 sources in total, 1242 known introductions events). For each event, we collected data on the year and location of introduction, motivation for the importation and native geographical range of the species organized by continental areas. Records with incomplete introduction histories were omitted.

Human demand for exotic species depends on the economic and cultural context of the geographical region in focus (Duncan et al., 2006). Within a given continent like Europe, demand will also increase with human population size (Mulliken, 1996) (Supplementary Fig. S1). To control for the effect of human demand on bird introductions, we compiled annual information on human population size at the country-level since 1850 (Mitchell, 2003) to reflect possible variation in people demand for exotic bird species. We included the following trade data per country: the annual total merchandise imports in Euros (value) between 1950 and 2005, and the annual total transportation and travel between 1980 and 2005 (data were not available for earlier periods and for eastern European countries, Eurostat, 2008). We used the annual total merchandise imports and the annual total transportation and travel indices because they may provide a more direct link between importations and consequent introductions of birds in Europe than other indices such as the Gross Domestic Product (GDP). However, annual GDP was strongly correlated with both the total merchandise imports and total annual transportation (Pearson's r = 0.94, pvalue < 0.0001) and with the travel indices between 1980 and 2005 (Pearson's *r* = 0.95, *p*-value < 0.0001).

2.3. Statistical analyses

Compared to the period of the Cold War, World Wars I and II did not lead to the same long-term isolation between Eastern and Western Europe and thus, were combined in the period before the Cold War to improve statistical power. For similar purposes, we also pooled the periods before and after the war for statistical analyses. In both these periods there was more trade and travel opportunities between Eastern and Western European countries compared with the Cold War period (Eurostat, 2008). We tested for differences in the number of introductions (events and species) between the Cold War period and the periods before (beginning in

1850) and after in each bloc. As the three periods differ in their length, we compared the average number of introductions per decade between the Cold War period and the periods before and after. We used a generalized linear model (GLM), specifying a log-link function with Poisson distributions for the number of introductions per decade, and an analysis of variance (ANOVA) after testing for data normality (Kolmogorov-Smirnov test) and homoscedasticity of variances (Levene's test). We assessed differences in bird introductions while controlling for the effect of human population size (as a proxy for variation in demand). We calculated the number of bird species established at the country (or island in cases that a country had both continental and island areas) level. Using Pearson's correlation coefficient, we also tested for a relationship between the number of species introduced and the number of species that established breeding populations in the Eastern and the Western European countries. Numbers of bird species introduced and established were first log-transformed. For other analyses we used χ^2 or Fisher exact tests to test for differences in the native origin and family composition of introduced species during the Cold War compared to the periods before and after. Analyses were performed using R version 2.6.1 (R Development Core Team, 2004).

3. Results

3.1. Pattern and origins of birds introduced

As predicted, there were more introduction events of a wider variety of species in Western Europe compared with Eastern Europe (Fig. 2). We also found clear differences among the two regions in the origin of the species introduced during the Cold War (Table 1). While most introduction events and species introduced into Western Europe during the Cold War were of non-European origin, the majority of events and of species introduced into Eastern Europe during the Cold War originated from other parts of Europe where they are native (Table 2). During the Cold War, there were more attempts to introduce species originating from North America and Africa into Western, but not into Eastern Europe (Table 1).

3.2. Motivations for introduction

The motivations behind the introductions during the Cold War were different than those during the periods before and after in both Eastern (Fisher's exact test, p = 0.02, Fig. 3) and Western Europe (χ^2 = 12.22, df = 4, *p* = 0.01, Fig. 3). In Western Europe there was an increase in the proportion of species released for what was then believed to be 'improvement' of the local avifauna during the Cold War compared to the periods before and after the war (Fig. 3, χ^2 = 3.88, df = 1, p = 0.05). In Eastern Europe, during the Cold War, there was a significant increase in the proportion of introductions of species imported for hunting purposes (55% of all events) compared to before and after (Fisher's exact test, p = 0.01). Only after the end of the Cold War did the motivations in eastern Europe change to resemble those seen in the west (Fig. 3) ($\gamma^2 = 6.07$, df = 4, p = 0.19). The majority of alien species established in Europe are still localised to the country to which they were introduced (83% of species) and only 12% have naturally spread from the original country of introduction to neighbouring countries (14 out of 121 species).

3.3. Distribution of introductions among families

Variations in the motivations for introduction were not reflected in the representation of families introduced during the Cold War compared to the periods before and after (Supplementary Table S1 and Supplementary Fig. S2). Although not statistically significant (p > 0.05), several trends in the proportion of families represented were observed. The Phasianidae (pheasants and partridges) and Anatidae (ducks and geese) families were almost equally represented before the Cold War in the east and in the west (47% and 51% of species, respectively). However, during the Cold War their proportion of the total species introduced into Western Europe declined compared to other families, while an opposite trend was seen in Eastern Europe (Supplementary Fig. S2). In Western Europe, the number of introduced bird species of the Psittacidae (parrots), Estrildidae (weaver-finches) and Ploceidae (weavers) families, originally imported for zoos and the pet market (Mulliken et al., 1996), increased since the Cold War period

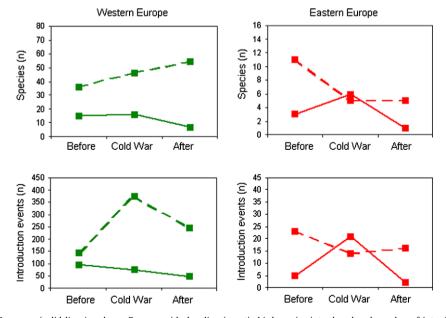


Fig. 2. The total number of European (solid lines) and non-European (dashes lines) exotic bird species introduced and number of introduction events into Eastern and Western Europe before, during and after the Cold War. Note the scale difference between Eastern and Western Europe in the graphs.

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Table 1

The number of exotic bird species introduced into the Eastern and Western European blocs and the number of introduction events in the periods before, during and after the Cold War shown by continent/s of native origin. Plus and minus signs indicate a statistically significant increase or decrease in values, respectively, during the Cold War using the χ^2 statistic or Fisher's exact test.

Number of	Bloc	Period	North-America	South-America	Africa	Europe	Asia	Australia	Total (n)
Species (n)	West	Before/after Cold War <i>P</i> -value	10/11 11 0.92	7/10 12 0.73	14/26 23 0.92	15/7 16 0.58	27/34 31 0.53	1/3 3 0.95	74/91 96
	East	Before/after Cold War <i>P</i> -value	3/2 3 1	4/1 2 0.44	0/1 2 0.58	3/1 6 0.31	8/4 9 0.90	1/1 2 1	19/10 24
Introduction events (n)	West	Before/after Cold War <i>P</i> -value	54/37 124(+) <0.001	16/67 79 0.56	32/105 165(+) <0.01	97/47 75(–) <0.001	166/318 371(-) 0.02	5/16 13 0.44	370/590 827
	East	Before/after Cold War <i>P</i> -value	7/2 6 0.12	3/1 2 0.69	0/1 4 0.39	5/2 21 0.14	10/12 35 0.85	0/1 2 1	25/19 70

Table 2

Results of the analysis of variance for the number of bird species introductions and number of introduction events calculated per decade during the Cold War compared with the period before/after. Plus and minus signs indicate a statistically significant increase or decrease in the number of introductions during the Cold War. NS indicates statistically non-significant results (*p* > 0.05).

Numbers of	Native Origin	Region of introduction	
		Western Europe	Eastern Europe
Species (per decade)	European Non-European	NS, $F_{1,13} = 0.13$, $p = 0.72$ NS, $F_{1,13} = 1.17$, $p = 0.30$	NS, $F_{1,13} = 1.27$, $p = 0.26$ (-) $F_{1,13} = 5.21$, $p = 0.02$
Introduction events (per decade)	European Non-European	$ (-) F_{1,13} = 6.44, p = 0.01 $	$ (+) \ F_{1,13} = 4.79, \ p = 0.03 \\ (-) \ F_{1,13} = 4.17, \ p = 0.04 $

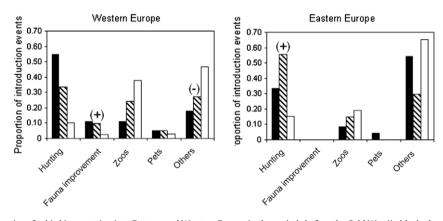


Fig. 3. Distribution of the motivations for bird importation into Eastern and Western Europe in the periods before the Cold War (in black, the number of introduction events is 232 and 24 for Western and Eastern Europe, respectively), during the war (dashed, 432 and 27 introduction events for Western and Eastern Europe, respectively) and after the war (white, 329 and 26 introduction events for Western and Eastern Europe, respectively). Plus and minus signs mark a statistically significant increase or decrease, respectively, during the Cold War. Others = includes individuals imported for biological control, birds that naturally dispersed from other alien regions and those imported for unknown purposes.

(Supplementary Fig. S2) compared to other bird families (χ^2 = 8.95, df = 2, *p* = 0.01).

tries ($r_s = 0.88$, p < 0.001) and in Western European countries ($r_s = 0.91$, p < 0.001).

3.4. Patterns of establishment

In all, 70 exotic bird species successfully established breeding populations in Western Europe; 52 (74%) originated from outside Europe and 18 from European regions. In Eastern European countries, only 12 bird species established populations. Six of these bird species (50%) originated from outside Europe. The number of exotic bird species that succeeded in establishing self-reproducing populations per country was positively correlated with the number of exotic bird species introduced, both in Eastern European coun-

4. Discussion

During the 20th century, Europe experienced dramatic changes in its political and socio-economic structure (McGlade, 2001). Here, we show that socio-economic and political changes shaped the spatial and temporal patterns of bird introductions at the scale of the European continent. Exotic bird introductions differed between the Eastern and Western blocs in the numbers, composition and geographical origin of the birds introduced during the Cold War, compared with the periods before and after. Information on the

political history and economy of Europe during this period supports our results.

During the Cold War. North America had trade agreements with Western Europe, but not with Eastern Europe (Gaddis, 2006). North America rapidly became the leading exporter of goods to Western Europe (Eurostat, 2008), which led to an increase in the number of North American birds introduced into Western Europe during the Cold War (Table 1). Imports and movements of commodities from North America into Western Europe were facilitated by Western European efforts to open markets with the passage of the Treaty of Rome and the establishment of the European Economic Community in 1957. In addition, waves of Western European expatriates returned to their homelands in Europe, along with an influx of colonial immigrants that arrived from Africa into Western Europe in the 1950s until the 1970s as a result of decolonization agreements (Olson, 1991). Migrants from Africa comprised the largest proportion of non-European immigrants to Western European countries from the 1950s until the present day (Eurostat, 2008). Immigration from Africa likely resulted in the increase in the number of African birds imported into Western Europe during the Cold War (Mulliken et al., 1996). For example, of 30 exotic bird species native to Africa that have been introduced into Western Europe since 1850, fifteen were introduced for the first time during the Cold War period (1949-1991). These 15 species all naturally occur in African countries that were formerly colonized by Western European nations (Belgium, France, Italy, Spain, Portugal, the UK) until the end of the 1980s. This increase in the number of non-European birds introduced into Western Europe mirrors the general increase in the global merchandise (Supplementary Fig. S3) and bird trade in Western Europe during and after the Cold War (Mulliken et al., 1996) as well as the increase in total transportation and travel to Western Europe from other continents that occurred at least since the 1980s (Supplementary Fig. S4). Although we observed a substantial increase in the number of birds introduced since the 1950s, the rate of introductions slowed in the early 1970s after the signing of the Convention on International Trade in Endangered Species (CITES) in 1973 (Mulliken et al., 1996, Supplementary Fig. S3). Since the 1950s, Africa has become the largest exporter of wild-caught birds such as passerines, as well as an important source of parrots, providing over two thirds (68%) of all CITES-listed bird species recorded in trade in 1988 (Mulliken et al., 1996). Available trade data for these periods indicate that the European Community was the largest importer of African and Asian species in the world during the 1980s (Mulliken et al., 1996). The deliberate or non-deliberate release of these imported wild-caught birds likely led to the increasing proportion of introductions during the second half of the 20th century into Western Europe.

In Eastern Europe, the east-west embargo during the Cold War largely limited movement of people and goods. North American trade with the Former Soviet Union, which totalled \$236 million in 1946, dropped to \$10 million in 1950 and to less than \$2 million with countries in the entire COMECON by 1956 (McGlade, 2001). The volume of merchandise exported from Western to Eastern European countries during the Cold War never exceeded 5% of the total volume traded from Western Europe to other regions of the world (McGlade, 2001). As a result of the embargo, Eastern Europe received fewer introductions of exotic species from overseas. However, the rise in human movement and trade within the Eastern bloc during the Cold War (Gaddis, 2006) enabled the trade in exotic bird species native to Europe within the Eastern European bloc and their introduction to areas that were not originally part of their native range in Eastern Europe.

Range expansion of already established bird populations from where they were first introduced to other European regions and countries has not been examined in detail for Europe yet (Kark et al., 2009). Because introductions of most exotic bird species introductions in Europe were human-induced and not from natural dispersal, we hypothesize that natural dispersal of established exotic birds is less likely to have shaped spatial and temporal patterns of bird introductions during the last 150 years. However, natural dispersal may play a larger role in future species introductions as established populations grow larger. We are aware of potential biases when using historical data that result in an increase of sampling effort and data reporting rates over time (Costello and Solow, 2003) and, in this case, potentially less records in Eastern Europe compared with Western Europe during the Cold War period (Kark et al., 2009). Such biases are difficult to overcome in most largescale biological invasion studies (Sol et al., 2008). Nevertheless, we would have expected such biases during the Cold War to be reflected in a reduction in the known number of both non-European and European species introduced into Eastern Europe, which is not the case here.

The decline in game bird introductions during the Cold War (and until the present day) in Western Europe (Fig. 3) reflects the global trend (Blackburn et al., 2009), which was modified by the Cold War in Eastern Europe. The relative increase in the proportion of birds introduced for hunting in Eastern Europe during the Cold War may reflect the availability and abundance of game species, mainly of the Phasianidae (pheasants and partridges) and Anatidae (ducks and geese) families (Blackburn et al., 2009), many of which are European in origin. Pheasants introduced into Eastern Europe originated mainly from Asia and could have been transported during the Cold War from allied communist countries such as Vietnam. In Western Europe, the number of introduced bird species of the Psittacidae (parrots), Estrildidae (weaver-finches) and Ploceidae (weavers) families increased during the Cold War period (Supplementary Fig. S2), reflecting the increasing worldwide demand for these traded species since the 1950s (Mulliken et al., 1996; Blackburn et al., 2009).

Recent studies have stressed the importance of the number of bird species introduced as the major cause and predictor of the number of species that successfully established breeding populations (Blackburn et al., 2008; Chiron et al., 2009). In addition to shaping patterns of species introductions, our results suggest socio-economic and political factors also determine the distribution and origin of species that successfully established breeding populations in Europe. As a consequence of Eastern Europe's isolation from Western Europe during the Cold War period, a greater number of species established populations in Western European countries than in Eastern Europe. Compared to Western Europe, Eastern Europe shows a higher proportion of species originating from European regions.

5. Conclusions

We find that the Cold War provided a hitherto unknown benefit to the countries of the Eastern European bloc by restricting human movement and trade from many other parts of the world and hence the introduction of exotic species. Given the trends of increasing human movement and trade in Europe (Appendix A), and especially the ongoing integration of most former Eastern European countries to the European Union, it is urgent that both single nations and the European Union as a whole establish clear policies to prevent a new inflow of exotic species into the formerly more isolated countries and thus reduce the risk of future invasions. Because introduction, as the first stage of an invasion process, largely determines the subsequent stages (Cassey et al., 2005; Chiron et al., 2009), we suggest that work on the factors affecting establishment, spread and impacts of invasive species

should incorporate a socio-economic and political context into the interpretation of the results.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2009.10.021.

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