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Birds facing climate change: a qualitative model for the adaptive potential of migratory behaviour

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Abstract - Recent climate change is altering the migratory behaviour of many bird species. An advancement in the timing of spring events and a shift in the geographical distribution have been detected for birds around the world. In particular, intra-Palearctic migratory birds have advanced arrivals in spring and shortened migratory distances by shifting northward their wintering grounds. These changes in migratory patterns are considered adaptive responses facilitating the adjustment of the life cycle to the phenological changes found in their breeding areas. However, in some cases, populations exposed to the same selective pressures do not show any appreciable adaptive change in their behaviour. Basing on the comparison of realized and non-realized adaptive changes, I propose here the formulation of a qualitative model that predicts the potential of migratory birds populations to change adaptively their migratory behaviour. The model assumes that the adaptive potential of migratory behaviour is fuelled by both genetic diversity and phenotypic plasticity. Populations of long-distance migrants are exposed to strong environmental canalization that largely eroded their phenotypic plasticity and reduced genetic variability, so that they show a very low amount of adaptive potential regarding migratory behaviour. On the contrary, partial-migrant populations have a highly varied genetic profile and are more plastic at the phenotypic level, and consequently show the highest amount of adaptive potential. Species with mainly social and mainly genetic determination of the migratory behaviour are separately treated in the model. Specific empirical models to foresee the adaptive strategies of wild bird populations that face to climate change can be derived from the general theoretical model. As example, a specific model about the shortening of migratory distances in Western European migratory bird is presented. Finally, a number of future research lines on the topic of adaptive potential of migratory behaviour are discussed, including some examples of concrete study cases. In conclusion, partial-migration emerge as the less known system and future research efforts on this topic are expected to be especially fruitful.

Key words: Evolvability, Behavioural adaptations, Conservation of migratory birds, Future researches lines on migration.

Riassunto - Come gli uccelli affrontano il cambiamento climatico: modello qualitativo sul potenziale adattativo del comportamento migratorio.

Il cambiamento climatico recente sta alterando il comportamento migratorio di molte specie di uccelli. In particolare, un generale anticipo della fenologia primaverile e spostamenti della distribuzione geografica sono stati rilevati per specie di uccelli in tutto il mondo. In particolare, tra gli uccelli migratori intra-paleartici si è registrato un anticipo delle date di arrivo primaverili e un accorciamento delle distanze di migrazione, ottenuti attraverso uno spostamento verso nord dei luoghi di svernamento. Questi cambiamenti negli schemi di migrazione sono considerati come risposte adattative che permettono l'adeguamento del ciclo di vita ai cambiamenti fenologici che accadono nelle aree di riproduzione. Tuttavia, esistono casi di popolazioni esposte alle stesse pressioni selettive ma che non mostrano alcun cambiamento adattivo apprezzabile nel loro comportamento migratorio. Basandosi sul confronto dei cambiamenti adattativi realizzati e non realizzati, propongo qui la formulazione di un modello qualitativo che predice il potenziale delle popolazioni di uccelli migratori di realizzare cambi adattativi del comportamento migratorio. Il modello assume che il potenziale adattativo del comportamento migratorio sia alimentato tanto dalla variabilità genetica quanto dalla plasticità fenotipica. Le popolazioni di uccelli migratori di lunga distanza sono esposte a una forte canalizzazione ambientale, la quale ha ridotto fortemente sia la plasticità fenotipica che la variabilità genetica dei caratteri costitutivi del comportamento migratorio, che come conseguenza ha limitatissime potenzialità adattative in queste popolazioni. Al contrario, le popolazioni di migratori parziali presentano molta variabilità genetica e ampia plasticità a livello fenotipico, e quindi mostrano la più alta quantità di potenziale adattativo del comportamento migratorio. Nel modello, inoltre, sono trattate separatamente le specie di uccelli in cui la determinazione del comportamento migratorio è prevalentemente sociale o prevalentemente genetica. A partire da questo modello teorico generale, si possono derivare modelli empirici più specifici per prevedere e descrivere le strategie adattative delle popolazioni di uccelli selvatici che si confrontano col cambiamento climatico. A titolo di esempio, descrivo quindi il modello specifico del progressivo accorciamento delle distanze di migrazione nelle popolazioni occidentali degli uccelli migratori Europei. Infine, commento una serie di possibili linee di ricerca sul tema del potenziale adattativo del comportamento migratorio, tra cui alcuni esempi di casi di studio concreti. In conclusione, la migrazione parziale migrazione emerge come il sistema meno conosciuto, così che ci si aspetta che futuri sforzi di ricerca in questo campo possano essere particolarmente produttivi.

Parole chiave: Capacità di evolvere, Adattamenti comportamentali, Conservazione degli uccelli migratori, Future linee di ricerca sulla migrazione.

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FROM LONG-DISTANCE TO PARTIAL MIGRATION: ALL BIRDS ARE ON THE MOVE!

Seasonal movements of varied magnitude, generally performed between regions where ecological conditions are alternatively favourable and unfavourable, have evolved and become established in many animal species from any branch of the phylogenetic tree, taking the name of *migration* (Dingle & Drake, 2007; Newton, 2008). However, it is in the class Aves that migration is most conspicuous, in terms of covered distances, complexity of routes and magnitude of the phenomena: 2.1 billion birds are estimated to migrate every year only between Europe and Africa (Hahn *et al.,* 2009). Long-distance migration is likely to have emerged early in the evolution of birds and there is evidence for its presence in some groups, like the Scolopacidae (waders), before the Pleistocene (Matthiensen, 1990; Louchart 2008). Thus, in evolutionary terms, migration is probably as old as the birds themselves (Berthold, 2001).

Benefits of migration mainly relate to the possibility of profiting from the continuous availability of resources, without interruption throughout the annual cycle, by tracking the peak of maximum productivity of ecosystems at a planetary scale (Alerstam *et al*., 2003). This type of migrants literally lives in an *endless summer* (def. by Shaffer *et al.,* 2006). For instance, the Arctic tern *Sterna paradisea* breeds north of the Arctic Circle and winters south of the Antarctic Circle. Thus, this bird tracks foraging opportunities throughout the globe and lives in constant light almost during its entire life, except during migration, when it must cross intermediate latitudes (Egevang *et al*., 2009). However, not only the need of tracking food but a complex net of selective pressures have determined the evolution of migration (Dingle & Drake, 2007). Otherwise, it is hard to explain why birds that live most of their life in tropical latitudes migrate for reproduction thousands of kilometres away. In these species, the avoidance of intra- and inter-specific competition is a strong reason to leave the overcrowded tropics and migrate to the much less crowded areas in the north. But, not only tropical birds may face competition. Birds from middle latitudes may need to leave their breeding sites during winter because their breeding quarter is invaded by migrating and wintering conspecifics from northern latitudes (Bell, 2000; Pérez-Tris & Tellería, 2002), making these area unsuitable for wintering because of huge competition even if food availability and winter temperature alone may would not be limiting factors in absence of concurrent wintering birds.

An extraordinary example of a life-history shaped by migration is that of the Eleonora's falcon (*Falco eleonorae*). This species not only performs extraordinary migratory movements but its life cycle is fully dependent on the migration of other birds, because it exploits the huge concentrations of migratory songbirds on the small islands of the Mediterranean Sea during fall migration (Cramp & Simmons, 1998). To do so, it synchronizes its reproduction with the peak of fall migration (late August/September), being among the latest European bird species to breed (Cramp & Simmons, 1998). However, Mediterranean islands do not offer many resources during winter, and thus Eleonora's Falcon need to migrate. During its migration, it crosses Africa tracking the availability of insects during autumn, and finally over-winters in Madagascar, where productivity is at its maximum during the boreal winter (Mellone *et al*., 2012; 2013). The extreme cases of the Eleonora's Falcon and the Arctic Tern should not obscure the fact that migration does not necessary imply crossing the globe. Actually, most birds profit from their large mobility just to move some kilometres, to descend from a mountain, or to move from a rural habitat, where they reproduce, into warmer adjacent urban habitats (Berthold, 2001). On a wider geographic scale, many species show variation in migratoriness depending on breeding latitude, as found in the Paridae, which are mainly sedentary in southern but largely migratory in northern Europe. In the Blackcap (*Sylvia atricapilla*), among-population variation in migratoriness ranges from total residency to long-distance migration (Shirihai *et al.,* 2011). Recent studies demonstrated that even tropical species that were thought to be sedentary show certain degree of migratoriness, so that at least a few individuals within the population migrate, revealing previously unknown patterns of partial-migration (Jahn *et al.,* 2010a). Even resident equatorial species can show migratory restlessness (Helm & Gwinner, 2006), possibly indicating that the endogenous mechanism for migration is still present in their genotype and can revive under certain conditions. Artificial selection experiment demonstrated that any resident populations can resume migratory behaviour in a few generations only (Berthold *et al.,* 1990). The occurrence of migratory and non-migratory taxon among closely-related species (*i.e.* genus *Sylvia*, see Shirihai *et al.,* 2001) is a further demonstration of the liability of the migration traits, so that an exclusive definition of migrant vs. non-migrant species is possibly meaningless. Much more effectively, the migratory status of a population can be treated on a continuous axis, building a trait defined as *migratoriness* in which mean covered migratory distance and proportion of migrants within a population are considered together as related traits (Pulido *et al.*, 1996; Pulido, 2011).

To resume, all the birds are on the move and is of outstanding interest to model the ability of wild bird populations to adapt their migratory status to the concomitant selective pressures to which they are exposed. The main pressures to which birds are nowadays exposed, and that may even threaten their survival over evolutionary times, have mainly anthropogenic causes (IPCC, 2007; 2013) and are generally referred to with the summarizing term of *climate change*.

WINGED MIGRATION IN A CHANGING WORLD

Contemporary climate change is an outstanding evidence (IPCC, 2013), and its consequences directly or indirectly affects a wide range of biological features of living organisms all over the earth (Parmesan & Yohe, 2003; Parmesan, 2006; Letcher, 2009). Migratory species are expected to be among the most affected organisms because they have complex life cycles in which successive phases are spent in different geographical areas, possibly facing different extent of environmental change (Robinson *et al.,* 2009). To stay with the previous example of Eleonora's Falcon: it is easy to understand that the set of selective pressures that shaped such a life-history are finely tuned on the spatial distribution of climatic niches over the globe. This implies that populations of this species are extremely sensitive to any spatial shift of the climate zones in which they live. Indeed, climate change is shifting the distribution of the climatic zones towards the poles (IPCC, 2007), exposing Eleonora's Falcon, as well as all the other migrants, to fundamentally different selective regimes. Populations of these species have no other choice than to move away, adapting to the new conditions, or perish. In this light, novel selective regimes imposed by climate change represent new challenges, when not a serious threat, for the conservation of migratory birds (Berthold *et al.,* 1998; Both *et al.*, 2006; Møller *et al.,* 2008; Saino *et al.,* 2011).

Migratory patterns are to some extent flexible (Sutherland, 1998; Newton, 2008). This is true both at the individual and at the population level (Pulido, 2007a,2007b). A single individual is able to adjust its migration to the external conditions it encounters, such as wind (*e.g*. Erni *et al.,* 2005), via phenotypically plastic responses (Saino *et al.,* 2004; and concrete examples in Mellone *et al*., 2012; Stanley *et al*., 2012). Recent evidences even demonstrated that individuals (at least the ones of a long-lived species such as the black kite *Milvus migrans*) can also ameliorate their migratory performance during life (Sergio *et al.,* 2014). However, adaptation does not occur at the individual level but takes place when features characterizing the migratory behaviour of an entire population (or species) change over evolutionary times in response to changes in the selection regime (Merilä & Hendry, 2014). Among the most recent examples of this process there is the northward shifting of the wintering ground of three species of northern European waterbirds (Lehikoinen *et al.,* 2013), or the establishment of several species of trans-Saharan migrants as wintering in Spain (Morganti & Pulido, 2012). A long list of changes in migratory patterns at the population scale have been compiled in the last years and include alterations of the migratory route, shortening or lengthening of the migration distances achieved by moving or expanding winter or breeding ranges and, especially, changes in timing of migration (reviewed in chapter 21 in Newton, 2008). In particular, this last aspect has received most of interest because it is thought to be this particular migratory feature that is most affected by climate change (Knudsen *et al.,* 2011). Both timing of migration and timing of arrival at the breeding grounds have advanced in the last decades (Lehikoinen *et al.,* 2004; Jonzén *et al.,* 2006; Rubolini *et al.,* 2007; Rubolini *et al*., 2010; Végvári *et al*., 2010; Saino *et al*., 2007). These changes are likely to be a response to increasing spring temperatures across Europe (Both & te Marvelde, 2007; Knudsen *et al.,* 2011). However, climate change also affects conditions in the wintering quarters and the areas of passage. The role of these changes in determining the new selective regimes is less clear than the impact of spring warming in the areas of reproduction (Gordo, 2007). The advancement of spring arrival has been sometimes associated with a delay of autumn departures (Lehikoinen *et al.,* 2004; Lehikoinen & Jaatinen, 2012), possibly meaning that at least some species of short-distance migrants are experiencing a lengthening of the reproductive season (Jaffré *et al.,* 2013). Evidences of long-term trends in phenology of autumn migration are less clear than the general advancement reported for spring arrivals (*e.g* Adamik & Pietruszková, 2008). Long- and short-distance migrants in particular repeatedly appeared to respectively advance and delay (or not changing) departure dates from breeding grounds (Jenni & Kéry, 2003; Mezquida *et al.,* 2007). As a result, depending from the study site, the period and the set of species used as model, contrasting findings may emerge, as the observation that duration of reproductive season has not changed for a number of bird species while lengthened for others (Thorup *et al.,* 2007). Another large body of evidence shows that short- and medium-distance migrants are moving their wintering quarters northwards, thus shortening migration distance (La Sorte & Thompson, 2007; Visser *et al*., 2009; Lehikoinen *et al*., 2013). Short-distance migrants are also the group of birds that most strongly have advanced phenology of migration (Rubolini *et al.,* 2007; Végvári *et al*., 2010) and onset of reproductive season (Rubolini *et al*., 2010).

Overall, there is a large body of evidence that migration is a plastic trait and that climate change can shape migration timing and routes as well as the location of wintering areas. In evolutionary times, climate change has probably been one of the most important determinants of migration patterns. Indeed, repeated oscillations in climate regimes during the Pleistocene (about 2.6 Myr - 10,000 years ago) are claimed to have caused continuous adaptive changes of migratory habits in all the lineages of birds living through this period (Bruderer & Salewski, 2008). Thereafter, recolonization from southern refugia during the warming period that followed the last glaciation (last 10,000 years) led to the contemporary latitudinal distribution of populations with increasing degree of migratoriness in northern Hemisphere (Newton, 2008; and specific cases in Peréz-Tris *et al*., 2004; Milá *et al*., 2006).

Thus, the question is no longer if migration can change but whether migratory species will be able to adapt to the contemporary climate change or go extinct. The capacity to develop adequate responses to cope with new selective pressures is often expressed in terms of *adaptive potential*.

A GENERAL MODEL FOR THE ADAPTIVE POTENTIAL OF MIGRATORY BEHAVIOUR

Adaptive potential is defined as the capacity of populations to adapt to environmental changes, measured as the extent to which populations are able to make adaptive phenotypic changes to cope with new selective pressures. This capacity is considered to be also fuelled by phenotypic diversity and plasticity but mainly by genetic diversity (Willi *et al.,* 2006). However, phenotypic plasticity may be sufficient to achieve the phenotypic changes needed to cope with a specific selective pressure (Merilä, 2012). Thus, both genetic variability and phenotypic plasticity fuel the adaptive potential of populations. These two features have phenotypic effects usually impossible to distinguish between them with the types of data generally collected (Merilä, 2012). As a consequence, to date, conclusive examples of (genetic) evolutionary changes in response to climate change are extremely scarce (*e.g*. Balanyá *et al.,* 2006; Pulido & Berthold, 2010; Karell *et al*., 2011; Chermantier & Gienapp, 2014; Merilä & Hendry, 2014). Adaptive potential is sometimes used as synonym of *evolvability* (Houle, 1990; Brown, 2013), a concept that should strictly indicate the capacity for generating heritable phenotypic variation (Kirschner & Gerhart, 1998), irrespective of the possible adaptive value of this variation. Conceptual differences between the terms *evolvability* and *adaptive potential* reflect the problems in distinguishing the occurrence of evolutionary changes or plastic response underlying an observed phenotypic change. This problem has major evolutionary consequences, given that the amount of plasticity of a genotype is limited while (adaptive) evolutionary changes can move further away. Ultimately, this may be crucial for the conservation of species, because populations showing an evolutionary response are likely to persist over evolutionary times, while populations that rely only on their adaptive plasticity may run out of adaptive potential and go extinct, sooner or later.

Bird migration offers a great subject on which to study this problem. Evidences from all over the world describing phenotypic changes in migratory behaviour of birds are nowadays abundant (see examples above). Overall, this bulk of evidences suggests that migration features, like migration routes, timing, and the spatial location of wintering and breeding grounds, may readily change in response to external selective pressures, as the ones imposed by climate change. However, even if exposed to the same selective pressures, some species may show adaptive changes of migratory features, while others may not, as demonstrated in a few studies comparing the reaction of vast sets of populations from the same geographical area (*e.g.* Rubolini *et al.*, 2007; Visser *et al.*, 2009; Végvári *et al.,* 2010; Gordo & Doi, 2012a; 2012b). This is the case, for instance, in short and long-distance migrants that breed in the same area and that are both exposed to selection favouring the advancement of spring arrival but only the first group effectively advance its arrival (*e.g.* Végvári *et al*., 2010). Comparing evidence of realized and non-realized changes permits the formulation of an effective model describing the expected capacity of bird populations to adaptively change their migratory features in response to external selective pressures (Fig. 1). Such a model may help formulating expectations and testing specific hypothesis regarding the adaptive capacity of migratory behaviour of a given population or species. In the model, the term *migratoriness* is used to indicate at the same time the proportion of migrants in a population and the mean migration distance of that population. The two parameters are related and can be expressed in a single continuous axis (Pulido *et al*., 1996; Pulido, 2011). Despite its continuous character, migratoriness can be classified in three main categories to facilitate interpretation: residents, partial-migrants and long-distance migrants. Starting from the resident extreme of the curve, below the migration threshold, genes controlling for migration are not expressed (resident populations) even if present in the gene pool of the population, resulting in phenotypic uniformity of the individuals (Pulido *et al.,* 1996). In this situation, natural selection cannot 'remove' migration genes, and genetic variability (not expressed at the phenotypical level) on migratoriness is maintained (Pulido, 2011): in other words, *migration genes* are likely to be present also in fully resident populations, ultimately pushing well above zero the amount of their adaptive potential on migratory behaviour (Fig. 1). While in a resident population phenotypic homogeneity in migratoriness is achieved because it lays under the threshold of its expression (Pulido *et al.,* 1996), at the other extreme of the curve (*i.e.* long-distance migrants) phenotypic homogeneity is determined because phenotypic variation on migratory patterns limited, because of strong stabilizing selection that only favour individuals arriving on a precise moment of the year (*i.e.* environmental canalization, Pulido & Widmer, 2005).

Thus, even if genetic variability in migratory traits may still be maintained in these populations (Pulido, 2007b), the extent of phenotypic plasticity on the same traits is extremely reduced, negatively affecting their potential for phenotypic adjustment. Hence, their adaptive capacity is limited. Moreover, in long-distance migrants, the expression of migration is generally tuned on external cues that are not altered by climate change (as photoperiod): in this case, any adaptive response is hampered because migration is adequately fit to its tuning parameter even if the climatic parameters affecting the fitness have significantly changed (Coppack & Pulido, 2004). Inability of long-distance migrants passerines to undertake adaptive changes of migratory patterns had been repeatedly suggested (Sutherland, 1998; Pulido & Widmer, 2005) and confirmed, at least, when analysing patterns of arrival dates of one population of Pied flycatcher (*Ficedula hypoleuca*; Both & Visser, 2001). On the other hand, partially migratory populations are supposed to be the ones in which genetic variability on migratory traits is maximal, and represents a *behavioural turntable* for microevolutionary processes on migratory behaviour (definition by Berthold, 1999). These considerations shape the dark curve of Fig. 1 that shows higher adaptive potential for resident compared to long-distance migrant populations, and partially-migratory ones with the highest value among the three groups.

The above arguments hold on the assumption that migratory behaviour is mainly genetically determined. However, although this assumption fits well the findings for night-migrating passerines that show migratory restlessness (*Zugunruhe*), it hardly holds when applied to large long-lived species, in which control of migration is mainly socially and environmentally mediated (*e.g*., Mueller *et al*., 2013). In these species, even if a component of inherited migratory program can be found, this needs to be tuned by social information, as obtained by following experienced birds during the first autumnal migration (Chernestov *et al*., 2004). Thus, different predictions need to be made for birds with a predominant genetic control of migration and for birds in which migration is primarily environmentally and socially controlled. In this text, the coarse but clear distinction in '*passerines'* and '*non-passerines'* will be used to account for this difference. Even if this classification is phylogenetically inaccurate ('*passerines'* refers to the specific order *Passeriformes*, while non-passerines include all other orders of the class *Aves*), it is effective because the two groups roughly represent the two different systems of migration control (genetic *vs* social). Thus, the prediction of the adaptive potential of migratory behaviour among non-passerines species is represent by a different curve (pale line in Fig. 1). Because of the important role of plasticity and environmental stimuli in the determination of migratory patterns among non-passerines, the adaptive potential is expected to be higher than for passerines throughout the entire range of migratoriness. Moreover, for this group of species, differences in genetic variability related to migratoriness would only have a minor effect in determining the amount of adaptive potential. Therefore, populations of non-passerines that differ in migratoriness are expected to show slight differences regarding the adaptive potential of migration. This results in a higher but more flattened curve than for passerines (Fig. 1).

These two hypothetical curves may represent an effective qualitative model of the distribution of adaptive potential among wild bird populations that differs in migratoriness and control of migratory behaviour. This simple graphical representation can help in formulate general expectations and hypothesis about the past and future evolution of any traits of migratory behaviour at any geographic scale, and results especially effective in comparative studies in which different expectations should be made for populations differing in migratoriness and migration control. However, empirical studies in ornithology generally need concrete specific hypotheses that can be clearly proved or disproved. Thus, as a first step, one needs to identify a measurable trait of migratory behaviour to focus on (p.e. timing of migration, see Charmantier & Gienapp, 2014) and successively formulate the specific question. The general model presented in Fig. 1 may facilitate both the formulation of expectations of the changes in the considered trait or simply contribute to pose the results in a correct framework, eventually promoting the interpretation of the findings. As example, in the next section I will present a model for a specific study case. As study species I will consider the entire set of European long-distance migrants, ranging from all the phylogenetic tree. As concrete migratory trait I will choose the migration distance and I will rely on the general model of Fig. 1 to formulate specific predictions.

THE SPECIFIC MODEL OF THE ADAPTIVE SHORTENING OF MIGRATION DISTANCE IN EUROPEAN MIGRATORY BIRDS

In the first section I briefly delineated how a strong bulk of studies show that selective pressures imposed by climate change influenced the reproductive phenology of European migratory birds. Overall, an advancement of arrival time at the breeding quarters had been favoured through over Europe in the last decades and it is reasonable to expect that any change in migratory behaviour that allow for such an advancement to be realized is positively selected. For these reasons, several authors have identified the shortening of migration distance as the best possible adaptive response of migratory birds to climate change (Berthold, 2001; Coppack & Both, 2002; Pulido

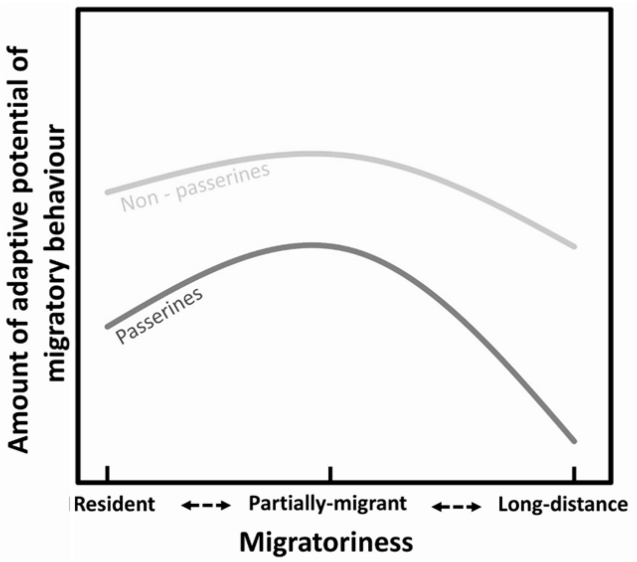

Fig. 1 -Predicted adaptive potential of migratory behaviour of bird populations differing in migratoriness. Depending on the selective regimes, wild populations may adaptively increase or reduce migration distance and the proportion of migratory individuals in the population, as arrows indicate. Partially-migratory populations maintain a high degree of genetic variability and phenotypic plasticity in both traits, thus having the highest adaptive potential. At the extremes of the distribution, environmental canalization is expected to reduce genetic variability and phenotypic plasticity, resulting in a reduced adaptive potential for long-distance and resident populations. However, among long-distance migrants, canalization is considered to be stronger, so that the amount of adaptive potential in this group is further depleted if compared to resident populations. Passerines (dark curve) and non-passerines (light curve) differ in the degree of genetic determination of migratory behaviour, having as a consequence that adaptive potential in the latter is constantly higher and differences between populations at different degree of migratoriness less accentuated in this group (more flattened curve for non-passerines). Overall, adaptive potential of migratory behaviour is considered to be maximum for partially migratory populations of non-passerines and near to zero in long-distance passerines ones. / Distribuzione del potenziale adattativo del comportamento migratorio tra popolazioni di uccelli con diverso comportamento migratorio. In risposta ai regimi selettivi a cui sono esposte, le popolazioni di uccelli possono aumentare o ridurre in modo adattativo la distanza di migrazione e la proporzione di individui migratori nella popolazione, come indicato dalle frecce sull'asse orizzontale. Le popolazioni parzialmente migratricii mantengono un alto grado di variabilità genetica e plasticità fenotipica su entrambe i caratteri, avendo così il maggior grado di potenziale adattativo. Agli estremi della distribuzione, la canalizzazione ambientale riduce sia la variabilità genetica che la plasticità fenotipica, con una conseguente riduzione del potenziale adattativo nelle popolazioni migratrici di lunga distanza e in quelle residenti. Tuttavia, tra i migratori di lunga distanza, la canalizzazione è considerata più forte, così che la quantità di potenziale adattativo in questo gruppo è ulteriormente ridotta rispetto alle popolazioni residenti. Passeriformi (curva scura) e non passeriformi (curva chiara) si differenziano per il grado di determinazione genetica del comportamento migratorio, avendo come conseguenza che il potenziale adattativo nei non passeriformi è costantemente più alta e più uniforme tra popolazioni a diverso comportamento migratorio (si ha quindi una curva più appiattita per i non passeriformi). Nel complesso, il potenziale adattativo del comportamento migratorio è considerato massimo tra le popolazioni parzialmente migratrici di non passeriformi e vicino allo zero in quelle di passeriformi migratori di lunga distanza.

& Berthold, 2004; Pulido, 2007b). If compared to other possible mechanism of advancing the arrival date at the breeding quarters (*i.e.* fasten the migration or leaving earlier from wintering quarters) the shortening of the migration distance would be favoured because it's the less risky. Indeed, the main problem in shorten migratory distance is that individuals will face to more rigid winters at northern latitudes, but winter conditions are also expected to become progressively milder because of climate change. These arguments can easily be translated into a specific model predicting the diffuse shortening of migration distance in European migratory birds (Fig. 2).

According to the predictions of the threshold model of migration (Pulido *et al.*, 1996), shortening of migration distances should occur gradually, in parallel to the progressive reduction of migratory fraction of the population, and should continue until complete residency or partial migration is achieved and winter and reproductive ranges overlap. Both long and short-distance migrant are equally exposed to climate change induced pressures favouring

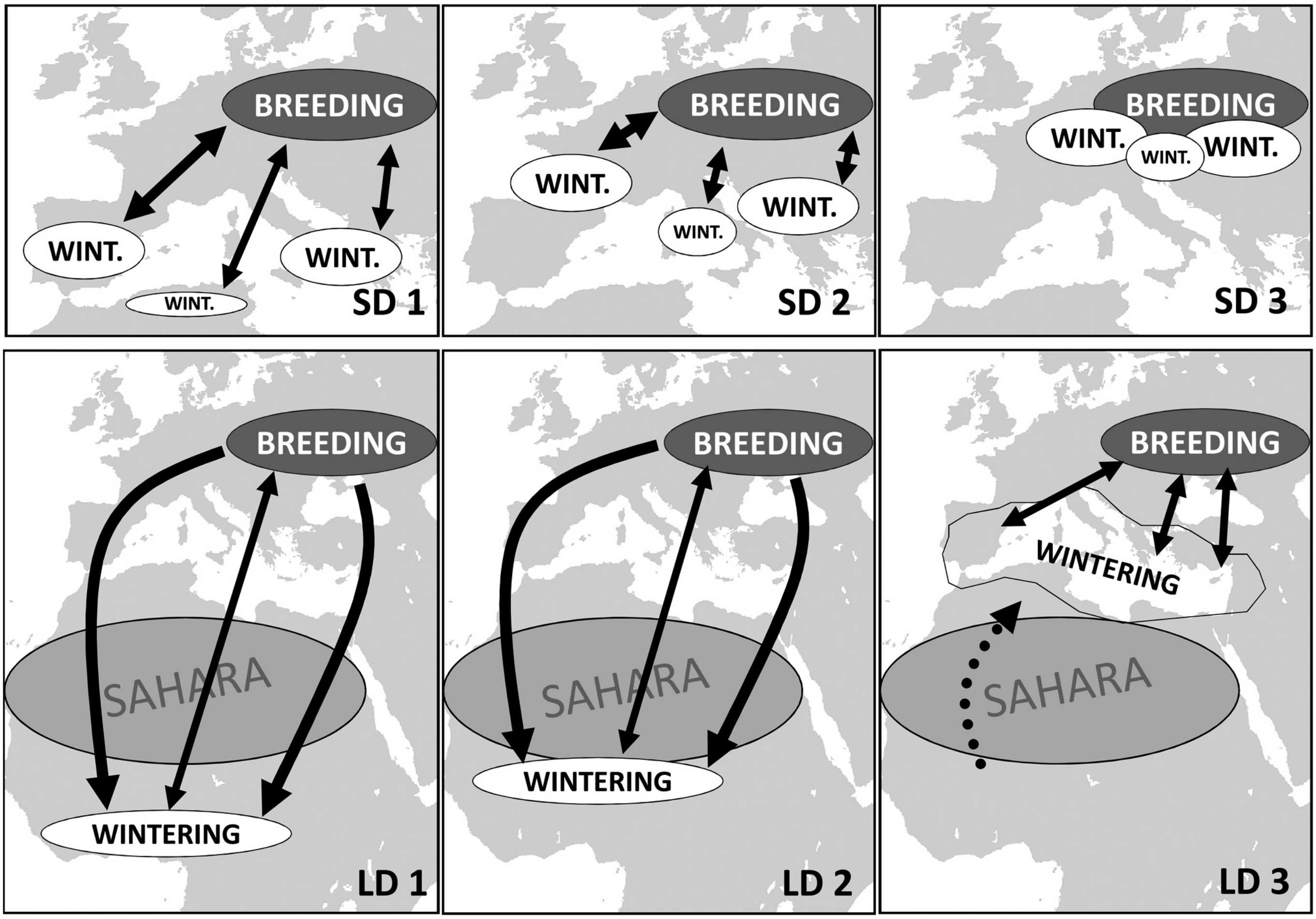

Fig. 2 - Model of the shortening of migration distance in response to climate change for European migratory birds. In the boxes SD1-SD3, the model for middle and short-distance migrants (SD) is shown. In the first step (SD1), the hypothetical populations breed in north-east Europe and winter in Mediterranean. As a response of climate change, the progressive shortening of its migration distance is achieved by northward shifting of the wintering range (SD2). Eventually, wintering and breeding grounds partially or completely overlap, meaning that at least some populations of the species became resident or partial-migrants. Boxes LD1-LD3 show how a progressive shortening of migration distance may be achieved by long-distance migrants (LD). In step 1, the normal situation is given: European breeding quarters are abandoned to cross the Sahara (shaded area) and winter in the Sahel, as most of the trans-Saharan European birds. In step 2, the wintering area has moved northward, reaching the southern edge of Sahara. The next step cannot be gradual anymore, given that Sahara is not a suitable area for wintering, and an abrupt shortening of migration distance is needed to start wintering north of the Sahara (LD3). / Modello di accorciamento della distanza di migrazione in risposta al cambiamento climatico per gli uccelli migratori europei. Nelle caselle SD1-SD3 è presentato il modello per i migratori di medio e corto raggio (SD). Nella prima fase (SD1), le ipotetiche popolazioni nidificano in nord-est Europa e svernano penisola Iberica. In risposta al cambiamento climatico, la riduzione progressiva della loro distanza di migrazione è ottenuta attraverso lo spostamento verso nord dei quartieri di svernamento (SD2). Alla fine del processo, gli areali di svernamento e nidificazione si sovrappongono parzialmente o completamente, implicando che almeno alcune popolazioni coinvolte siano diventate parzialmente migratrici o residenti. Le caselle LD1-LD3 mostrano come un analogo accorciamento progressivo della distanza di migrazione può essere ottenuto dai migratori di lunga distanza (LD). Il punto LD1 presenta la situazione normale: l'areale di riproduzione europeo è abbandonato per attraversare il Sahara (area ombreggiata) e raggiungere l'areale di svernamento nel Sahel, come nel caso della maggior parte degli uccelli trans-sahariani europei. Nel punto LD2, l'areale di svernamento si è spostato verso nord, raggiungendo il margine meridionale del Sahara. Il passo successivo non può essere ulteriormente graduale, dato che il Sahara non è una zona adatta per lo svernamento, ed è necessario un brusco accorciamento della distanza di migrazione e l'istituzione di nuove aree di svernamento a nord del Sahara (LD3).

the advancement of arrivals and eventually the shortening of migratory distances. However, trans-Saharan migrants face a further problem, given that the unsuitability of the Sahara for overwintering hampers the eventual gradual northward shift of the wintering grounds. Thus, slightly distinct predictions need to be made for these two groups of migrants (the two lines of Fig. 2). For short-distance migrants (SD) the progressive shortening should fully develop, as reported in steps SD1 to SD3 in Fig. 2.

However, for long-distance migrants (LD) such a progressive reduction is hampered by the Saharan desert: after a progressive northward shifting of the wintering area within Africa as shown in steps LD1-LD2 of Fig. 2, populations of these species should undertake a sudden shortcut of the migration and start to winter in the Mediterranean Basin (step LD3 in Fig. 2). Such populations of long-distance migrants that successfully start to winter in the Mediterranean basin (LD3, Fig. 2), and for which selective pressures for advancing of arrivals persists, should continue to shorten their migratory distance following the model for the short-distance migrants (steps SD1-SD3). Finally, the model of Fig. 1 suggests at least two refinement of the above hypothesis. First, given the different amount of adaptive potential on migratory behaviour, short-distance migrants would realize the predicted shortening of migratory distance more often and possibly in a faster way than long-distance ones. Second, independently of their degree of migratoriness, passerines species (and those where migration is under strict genetic control in general) are expected to rarely perform the adaptive shortcut, proportionally to the amount of their adaptive potential, considered near to zero among long-distance migrant passerines.

Some of the above expectations have been already confirmed by empirical studies. Evidences from both Europe and North America show that the adaptive shortening of migration distance has been occurring in the last decades in short-distance migrants, which find suitable wintering areas along all their migratory route (Valiela & Bowen, 2003; La Sorte & Thompson, 2007; Maclean *et al.,* 2008; Visser *et al*., 2009; Lehikoinen *et al.,* 2013). Thus, steps SD1 and SD2 of Fig. 2 are widely confirmed. However, the complete description of a specific population that after progressive shortening of migratory distance finally became entirely resident (step SD3) is still lacking. This is possibly due to the extreme technical difficulties that are implied to obtain such a complete description, both in terms of individual-marking effort and time span needed of surveying over vast spatial scales. Papers focusing on this topic generally use the mean winter location of an entire species over a vast area as measured parameter (*e.g*., Lehikoinen *et al.,* 2013), without the possibility to discern among different breeding populations of the observed birds. Thus, populations already became resident probably exist but are going undetected.

Long-distance migrants are mainly studied during their migration or breeding season, due to the simple fact that the number of researchers in their wintering areas is much lower than in their breeding quarters. Thus, despite the huge number of studies that dedicated to explore changes in migration phenology of trans-Saharan migrants, almost none has been dedicated to the study of possible shifting in the wintering quarters of this group of species. The only notable exception is one study that considered the whole dataset of African recoveries of Barn swallows (*Hirundo rustica*) ringed in Europe during a century to assess that sub-Saharan wintering quarter of this species significantly shifted northward in this period (Ambrosini *et al*., 2011). Thus, this study represent the best evidence so far that steps LD1 and LD2 of Fig. 2 actually occurred. About the occurrence of step LD3, it is well known that trans-Saharan migrants sporadically overwintered in Mediterranean basin (Berthold, 2001; Sutherland, 1998). However, it is only from Spain that clear evidences exist that both number of species and of individuals belonging to trans-Saharan species overwintering in the country had been increasing much more than anecdotally at least starting from around 1980 (Morganti & Pulido, 2012). The set of overwintering species included around 40 species, mainly non-passerines, the Booted eagle (*Aquila pennata*) being the most common species found as winterer (Morganti & Pulido, 2012). These results from Spain were confirmed by the data collected during systematic winter censuses in Spain in more recent years, when many trans-Saharan species where found in meaningful numbers during surveys (SEO/Birdlife, 2012). Thus, evidence from the Iberian peninsula seems to confirm the LD3 step of the model presented in Fig. 2. To complete the model description, evidence should be provided that for populations of European long-distance migrants that finally establish wintering population in Western Mediterranean, if selection towards residency persists, migration distances continue their shortening until the condition of partial-migrants or residents is achieved (*i.e*. breeding and wintering quarters overlap, steps SD1 to SD3 in Fig. 2).

FUTURE PERSPECTIVES AND CONCLUSIONS

The qualitative models presented here delineate a framework connecting questions about the control of migration, the evolutionary trajectories of migratory behaviour and the conservation of migratory species. It is evident that most of these questions remain unsolved and claim for further investigation, but the models aim at providing a general framework for interpreting the outcome of past and future empirical studies on changes in migration distances in response to changing climate. As a first point, the general model for the adaptive potential of migratory behaviour need support across the phylogenetic tree. In fact, overall knowledge about partial migrant populations is still very poor. The integration of cutting-edge technologies with great field efforts seems the only reliable way to approach the study of partial migration, especially on small-sized birds. In this sense, a series of recent paper is delineating a promising research field around passerines partial-migration (Jahn *et al*., 2010a, 2010b; Fudickar & Partecke, 2012; Fudickar *et al.,* 2013; Morganti *et al*., 2014). Satellite tracking technologies would be extremely efficient in study partial migration in larger species if a consistent proportion of a breeding population would be tracked at the same time. Unfortunately, the costs of tracking devices are still too high to structure such a study and to date research has been mainly focused on disclosing migratory routes of long-distance migrants (p.e. Mellone *et al*., 2013). Among non-passerines, life style and migratory strategies of pelagic birds are too distinct from the ones of terrestrial birds, possibly deserving a third curve in the model of Fig. 1. The general model of Fig. 1 may also need to be adapted to include migratory systems of tropical latitudes. Indeed, almost the whole bird migration theory is based on evidences gathered from migratory species from temperate latitudes and migratory systems of tropical areas have started to be disclosed only recently. At tropical latitudes, variation of the adaptive potential among populations differing in migratoriness may be quite reduced, given that external cues eventually may drive migratory decisions more than genetic ones also among passerines (p.e. Boyle, 2008; Jahn *et al*., 2010a). However, this is still largely unexplored (Sekergiolu, 2010).

A part from the main knowledge gaps concerning tropical migratory systems and pelagic birds, a number of basic questions on plasticity of migratory behaviour may found answer even using much more easily approachable study systems: in Tab. 1 I give four of these examples, especially focused for birds from the Mediterranean region.

Despite the large body of studies and the extraordinary interest that migration historically aroused among researchers, a number of basic questions on the how, where, and why of bird migrations are still unanswered. Theoretical models like the ones presented here may help to connect available knowledge in a common framework and identify the main gaps to which dedicate future research efforts. In the specific case of the model for the adaptive potential of migratory behaviour, this should be improved and eventually extended to model the adaptive potential of any migration-related traits, including the non-behavioural ones (*i.e*. morphology or life-history traits). Studies on partial-migrant populations will be especially advisable in the future to approach the main unresolved questions on migration control and adaptive potential. Finally, any considerable progress in our ability to foresee the adaptive strategies of wild bird populations facing climate change will crucially increase the effectiveness of conservation strategies, ultimately enhancing their survival probability across evolutionary time scales.

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Tab. 1 - Examples of four possible study cases to approach the problem of adaptive potential of migratory traits in birds of the Mediterranean region. Table lists the species, the type of study and the main reasons that makes the species a suitable study model. Many other cases would be added to this list. / Esempi di quattro possibili casi di studio per affrontare il problema della potenziale adattativo del comportamento migratorio in uccelli della regione mediterranea. La tabella elenca le specie, il tipo di studio da condurre e le principali ragioni che rendono la specie di un modello di studio adeguato. Molti altri casi analoghi potrebbero essere aggiunti a questo elenco.

Species	**Study type**	**Main reasons of interest**
Blackcap (*Sylvia atricapilla*)	Focus on partial-migrant populations from all over Mediterranean, identifying residents and migrants and year-to-year variations.	(1) Extremely abundant species having populations of all degree of migratoriness that overlap in Mediterranean during winter. (2) Well-known species with a huge amount of previous studies on many aspects of ecology, biology and genetics.
Black-Redstart (*Phoenicurus ochruros*)	Study association between migratory behaviour, flight morphology and elevation of the breeding sites.	(1) Abundant species all over Mediterranean region, easy to capture for ringing. (2) Occupies breeding sites with a huge altitudinal range (from 0 to >2000 m.a.s.l.).
Little Bittern (*Ixobrychus minutus*)	Establishing origin of recent-established wintering populations in Mediterranean (by isotopes or satellite-tracking).	(1) Long-distance migrant that recently established wintering populations in Mediterranean (Morganti & Pulido 2012) (2) Among the few non-passerines species that present a relative easiness of study, given that wintering populations are concentrated in marshlands were should be easy to capture during winter.
Lesser Kestrel (*Falco naumanni*)	Identifying resident individuals within the population and measure fitness advantage of these against migrant ones.	(1) Non-passerine long-distance migrant with a number of registered wintering cases and with at least few near-to-sedentary populations in Iberia (SEO/Birdlife 2012) (2) Well-known species with a huge amount of previous studies on many aspects of ecology, biology and genetics.

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