To be or not to be a migrant: the different movement behaviours of birds and insights into the migratory status of flamingos (Phoenicopteridae)

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Source: Bulletin of the British Ornithologists' Club, 141(4) : 418-427

Published By: British Ornithologists' Club

URL: https://doi.org/10.25226/bboc.v141i4.2021.a5

To be or not to be a migrant: the different movement behaviours of birds and insights into the migratory status of flamingos (Phoenicopteridae)

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Received 26 April 2021; revised 14 July 2021; published 10 December 2021

http://zoobank.org/urn:lsid:zoobank.org:pub:E9696EB5-499D-4C28-AEB0-CDDD9794FEC9

Summary.—Migration encompasses a persistent, directed, often seasonal, redistribution of individuals beyond or between their home ranges, but is often incorrectly used to describe a wide range of other movement behaviours in several animal groups, including birds. Flamingos (Phoenicopteridae) are birds that are frequently, but not universally, classified as migratory. Nevertheless, movements performed by flamingos do not seem to match the scientific and ecological concept of migration *sensu stricto*. We discuss different bird movements and their correct typology. Based on available information concerning flamingo movements, we recommend that they be considered irruptive or nomadic species, and that correct classification is important to avoid wrongly interpreting these birds' ecology in the media and scientific works. Despite that they are not truly migratory, conservation action plans for flamingos still need to take into account their movement behaviour.

All major animal groups, including arthropods, fishes, mammals, birds and reptiles engage in long-distance movements (Hobson *et al*. 2019, Senner *et al*. 2020). Usually, animals move seasonally between discrete regions to avoid unfavourable climatic conditions, to find better feeding grounds, or to breed (Newton 2003, Milner-Gulland *et al*. 2011). Long-distance movements are commonly, but not always accurately, referred to as 'migration' (Dingle & Drake 2007). The term 'migration' evokes four different yet overlapping ideas: (1) a persistent directed movement, (2) redistribution of individuals over much greater spatial and temporal scales than during normal daily activities, (3) seasonal to-and-fro of populations between regions where conditions are alternately favourable and unfavourable, and (4) movement leading to individual redistribution within a population with a large range (Dingle & Drake 2007). These ideas mix individual movements with population-level patterns, often leading to mistakes in the characterisation of movement patterns (Dingle 2006, Dingle & Drake 2007). In recent decades, scientists have developed a more precise definition for 'migration' and a suite of new concepts and terms has been introduced, e.g., 'restricted migration', 'dispersive behaviour', etc. (Chapman *et al*. 2014, Lohmann 2018).

Birds are perhaps the most conspicuous and easily observed group of 'migratory' animals, especially in subtropical and temperate regions (Newton 2003). For example, >80% of bird species from temperate and high latitudes exhibit migratory behaviour (Winger *et al*. 2014). The orders Anseriformes (ducks, geese and swans), Charadriiformes (gulls, terns and shorebirds) and Ciconiiformes (storks and allies) include species often referred to as migratory (Alerstam 1993, Bairlein 2003). Another order frequently considered migratory is the Phoenicopteriformes (e.g. McCulloch *et al*. 2003, IUCN 2018, Somenzari *et al*. 2018, Wijesundara *et al*. 2018), which comprises six extant species of flamingos in three genera: *Phoenicopterus*, *Phoeniconaias* and *Phoenicoparrus* (Winkler *et al*. 2020, Gill *et al*. 2021). Four species occur in the Americas: Caribbean (American) Flamingo *Phoenicopterus ruber*, Chilean Flamingo *P. chilensis*, Andean Flamingo *Phoenicoparrus andinus* and Puna (James's)

ISSN-2513-9894 (Online)

Flamingo *P. jamesi*, whereas Greater Flamingo *Phoenicopterus roseus* and Lesser Flamingo *Phoeniconaias minor* occur in Eurasia and Africa (Winkler *et al*. 2020).

Flamingos are large, long-legged waterbirds with unique down-curved bills adapted to filter feeding, and pinkish or reddish plumage (Winkler *et al*. 2020). They inhabit wetlands such as shallow inland lakes, lagoons and coastal marine areas (del Hoyo 1992, Anderson 2016, Winkler *et al*. 2020), and move between wetlands to exploit different food resources throughout the year, but mainly in the non-breeding season (e.g. McCulloch *et al*. 2003, Balkiz *et al*. 2007, Zaccara *et al*. 2011). These movements have been frequently characterised as migration (McCulloch *et al*. 2003, Somenzari *et al*. 2018, Wijesundara *et al*. 2018). Nevertheless, movements performed by flamingos do not seem to match the scientific and ecological concept of migration (del Hoyo 1992, Béchet 2016) and various authors have proposed terms to refer to these movements. Here, we review the definitions and concepts related to migratory birds and discuss the movements of flamingos to determine if they fit the definition of migration. We also discuss the importance of this status in conservation policies.

Different concepts of bird movements

Bird movements can be divided into three general categories: station-keeping, ranging, and migration. These categories and their corresponding activities are defined based on the purpose, frequency, pattern, and temporal and spatial scales of the movements involved (Kennedy 1985, Dingle 1996). Station-keeping consists of movements performed within the animal's territory or home range to find food, shelter and mates (Dingle 1996). Home range is defined as the continuous area, usually around a home site, which an animal normally explores to find different resources (Burt 1943), sometimes defending this area against other individuals (Noble 1939, Nice 1941). Station-keeping movements have no fixed pattern in time and space; animals occasionally move from one place to another and are driven by short-term environmental and physiological stimuli like the weather or hunger (Alerstam 1993, Dingle 2006). These movements cease whenever resources are found, or the stimuli cease, e.g., when a vulture perches after locating a carcass or a male initiates courtship after finding a female (Dingle 2006). Sometimes, birds make movements driven by short-term stimuli but outside their home range, finding and colonising new environments. These are ranging movements and cease when the animal finds the resources sought, e.g. when young birds locate new territories (Jander 1975, Kennedy 1985, Dingle 1996). Ranging is therefore defined as a variety of movements that facilitate expanding and exploring a new home range or territory (Dingle & Drake 2007).

Migration *stricto sensu* is a more complex movement that extends beyond the home-range limits and involves physiological, behavioural and population aspects linked to long-distance displacements (Newton 2003, Rappole 2013). Variables such as day length (photoperiod) over the year and life-cycle stage (age class) may promote behavioural and physical changes that result in migratory movements (Newton 2003, Dingle 2006).

Long-distance movements in birds can be described based on four attributes: distance, time, site fidelity, and physiology (Dingle 1996, 2006, Newton 2003). The first of these is related to their scale: long-distance movements take an animal beyond its home range, as noted above (Newton 2003). For some birds, this type of movement is easily recognisable and delimited, as they cover remarkable distances during migration, whereas they usually move shorter distances within their home range, e.g., Buff-breasted Sandpiper *Calidris subruficollis*, which flies 7,600 km between breeding and non-breeding sites, but moves only a few km within either (Aldabe 2016). In some species, however, movements performed within the home range and so-called migratory distances are confused by a large

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continuous home range or by the short distances between each 'migration' site, like for example in Western Gull *Larus occidentalis* (Coulter 1975, Shaffer *et al*. 2017).

The second descriptor of migratory movements is periodicity and seasonality, both related to time. Migration involves a displacement from one site to another at regular time intervals, generally coinciding with the end / start of a climatic season, and that animals do so with a certain periodicity, usually annually (Newton 2003). These movements occur mainly because of environmental changes over the seasons of the year, e.g., temperature and photoperiod changes that can serve as an indication of fluctuations in food availability (Newton 2003, Dingle 2006). Persistence of movement patterns is extremely important for a species' ecology and is intrinsically related to the ecological process both in foraging and breeding areas (Newton 2010, Chapman *et al*. 2011). Several species of terns, e.g. Arctic Tern *Sterna paradisaea*, migrate every year in autumn to escape the Northern Hemisphere winter, instead spending the non-breeding period in the Southern Hemisphere and returning to their breeding sites in spring (Egevang *et al*. 2010). For other species, periodicity and seasonality of these movements are not fixed, with no clear pattern to their movements or a fixed timescale, like in Gouldian Finch *Chloebia gouldiae* and Grey-backed Sparrow-Lark *Eremopterix verticalis* (Dean 1997). In other cases, despite existence of a temporal pattern, the behaviour varies among populations and years, like in Snowy Owl *Bubo scandiacus* (Doyle *et al*. 2017).

Site fidelity, or philopatry, is another fundamental characteristic of true migrants. Migrant birds generally fly from a place where the environment is no longer favourable to another where they can find more food or better conditions to breed and feed offspring. They return to the original place or colony when the season and local conditions change again, making this seasonal to-and-fro movement to the same places, creating a route that is usually well established in the population and is followed rigorously between years (Ketterson & Nolan 1990, Newton 2003, Dingle 2006). Many 'true migrants', like *Calidris subruficollis* (Aldabe 2016) and Magellanic Penguin *Spheniscus magellanicus* (Pütz *et al*. 2007) possess high fidelity to breeding and non-breeding areas, but usually also pause at the same stopover sites during migration. For other species, these places tend to change between years and colonies, with no or very low site fidelity, as is the case in Cliff Swallow *Petrochelidon pyrrhonota* (Brown *et al*. 2017).

Based on the above three attributes, scientists have elaborated a typology to describe the different movements that are important to differentiate the wide variety of patterns in birds (Table 1; adapted from Newton 2010 and Cottee-Jones *et al*. 2015).

The final attribute used in migration definitions are the physiological changes that the individuals go through before, during and after this process (Newton 2010). Often, true migrants gain weight and change behaviour to low calorific expenditure and promote better reserve accumulation weeks before migration starts, increasing flight muscle size and adjusting their hormonal organs to migrate and breed (Price *et al*. 2010, Ketterson *et al*. 2015). Some species, e.g. White-throated Sparrow *Zonotrichia albicollis*, can increase their mass by 50% and reduce the time spent sleeping (Ramenofsky *et al*. 2017), whilst others change the size and volume of digestive organs rapidly but reversibly, e.g., Red Knot *Calidris canutus* (van Gils *et al*. 2005). The energetic reserve and sleep deprivation alter the immune system and increase the tissue repair function of the body in these birds, important during the long flight periods that can sometimes last weeks (Newton 2010, Price *et al*. 2010). Some also change plumage, acquiring breeding feathers that are important in disputes between competing males and courtship rituals on the nesting grounds (Holmgren & Hedenström 1990, Leu & Thompson 2002).

ISSN-2513-9894 (Online)

TABLE 1
Typology classifying the long-distance movements by different groups of birds, with the name, the definition and examples already established in the literature. Adapted from Newton (2010) and Cottee-Jones *et al*. (2015).

Name	Definition	Examples
Migratory *sensu stricto*	Species that perform regular, seasonal movements from the same breeding to non-breeding areas and back (Berthold 2001, Dingle 2006, Newton 2010).	Buff-breasted Sandpiper *Calidris subruficollis* (Aldabe 2016), Arctic Tern *Sterna paradisaea* (Egevang *et al*. 2010)
Dispersive	Species that move but over no fixed direction or distance from their breeding site (Newton 2010)	Western Gull *Larus occidentalis* (Coulter 1975), Diomedeidae (albatrosses) (Newton 2010)
Irruptive	Species that make seasonal movements where the number of individuals, timing, direction, and distance travelled varies greatly between years and colonies (Newton 2010, Bateman *et al*. 2015)	Common Redpoll *Acanthis flammea* (Hochachka *et al*. 1999), Snowy Owl *Bubo scandiacus* (Fuller *et al*. 2003)
Nomadic	Species that move according to no fixed spatial or temporal pattern (Newton 2010, Runge *et al*. 2015a)	Gouldian Finch *Chloebia gouldiae* and Grey-backed Sparrow-Lark *Eremopterix verticalis* (Dean 1997)
Vagrant	An individual that appears in an area far beyond the limits of the species' normal range and migration routes (Newton 2010)	American Robin *Turdus migratorius* in Europe (Svensson *et al*. 2010), Cattle Egret *Bubulcus ibis* in Antarctica (Petersen *et al*. 2015)
Sedentary	Species that move only within their established home range and habitat (Cale 2003, Newton 2010)	Marsh Wren *Cistothorus palustris* (Kroodsma *et al*. 1999), African Stonechat *Saxicola torquatus* (Wikelski *et al*. 2003)

Flamingo movements

The six flamingo species have been frequently, but not unanimously (see below), considered migratory (Espino-Barros & Baldassarre 1989, McCulloch *et al*. 2003, Johnson & Cézilly 2007, Sanz-Aguilar *et al*. 2012, Béchet 2016, Wijesundara *et al*. 2018). Indeed, these birds appear to possess variable types of movements that do not match the above-mentioned attributes required to be considered strictly migratory (*cf*. Table 1). For example, distances covered by flamingos are very variable and can vary both individually and at population level. As they can fly >700 km in a single night (Johnson & Cézilly 2007), the so-called migratory distance is very similar to daily home-range distances (Béchet 2016).

The time attribute is also questionable. Flamingos show opportunistic behaviour, moving among nearby areas in response to food availability, without clear periodicity (Brown & King 2005, Ayache *et al*. 2006). Some individuals never really disperse from their colonies, whereas others relocate at different periods of the year from one place to another, and may never return to their natal breeding sites (del Hoyo 1992, Sanz-Aguilar *et al*. 2012, Béchet 2016). Although such variation is common among flamingos, it is especially pronounced in Caribbean, Greater and Lesser Flamingos, most of whose populations occur at tropical latitudes with more stable temperatures and rainfall (Espino-Barros & Baldassarre 1989, Balkiz *et al*. 2007, Zaccara *et al*. 2011, Sanz-Aguilar *et al*. 2012, Behrouzi-Rad 2013, Parasharya *et al*. 2014, Pretorius *et al*. 2020). Lesser Flamingos display irregular movement patterns in Africa, with individuals flying between alkaline lakes in response to environmental variables like rain and food (McCulloch *et al*. 2003), each one of which has its own population but with genetic flow between them due to this 'nomadic' type of movement (Zaccara *et al*. 2011). This phenomenon occurs because of the highly unpredictable environmental characters of these places (Newton 2006) and is important

ISSN-2513-9894 (Online)

for the genetic structure of Lesser Flamingo populations on the continent, with direct impacts on their conservation (Zaccara *et al*. 2011). However, Pretorius *et al*. (2020) recently evidenced that Lesser Flamingos in central-southern Africa may be 'partial migrants', not true nomads, as some movements followed a regular, repeated pattern between just two locations.

Movements by temperate-breeding Chilean, Andean and Puna Flamingos appear more frequent and seasonal, but are flexible and vary between colonies (Caziani *et al*. 2007). For these species, movements are usually elevational, from high-altitude to lower altitude habitats, rather than longitudinal / latitudinal (Caziani *et al*. 2007, Derlindati 2008, Romano *et al*. 2011, Derlindati *et al*. 2014). Andean and Puna Flamingos, and some Chilean Flamingos, breed at high-elevation wetlands in north-central Argentina and Chile, but move to the lowlands of Chile, Peru, Uruguay and southern Brazil in the non-breeding season (Mascitti & Bonaventura 2002, Somenzari *et al*. 2018). Nevertheless, some individuals that remain at their breeding sites year-round do not return to these areas for several years, e.g., the resident population of Chilean Flamingos at Lagoa do Peixe, southern Brazil (Delfino & Aldana-Ardila 2020).

At least three movement patterns have been more frequently observed in flamingos (e.g. del Hoyo 1992, Sanz-Aguilar *et al*. 2012, Béchet 2016): (1) some individuals within a colony do perform typical migrations, respecting the same non-breeding and colony areas; (2) others, mainly young males, occasionally abandon the original colony and join other groups along the route; and (3) some choose to remain in the non-breeding or breeding areas for prolonged periods, sometimes not migrating at all. Behaviour is thus influenced by environmental conditions, age and sex, but social dynamics between colonies seem to affect individual choices as well (Sanz-Aguilar *et al*. 2012, Béchet 2016). Body condition can also directly affect dispersal capacity, with birds in poorer condition staying longer in areas whilst well-conditioned birds tend to fly more within and between colonies (Barbraud *et al*. 2003).

Flamingos' movements are clearly versatile and cannot be described as migratory *sensu stricto*. Some authors tried to provide new names for this type of displacement, terming them 'irruptive migrants', 'partial migratory', 'restricted migratory', or 'nomadic species', without explicitly defining the meaning of these concepts and sometimes using specific population variables (i.e. genetic patterns of population variation) to justify their nomenclature for the species or group (Hayes *et al*. 1994, Caziani & Derlindati 2000, Childress *et al*. 2004, Caziani *et al*. 2007, Rendón *et al*. 2011, Zaccara *et al*. 2011, Sanz-Aguilar *et al*. 2012, Deville *et al*. 2014, Pretorius *et al*. 2020). In these cases, use of different nomenclature or typology, with no consensus in the current literature or with outdated definitions, have complicated a broader and more comprehensive classification of the group with potential impacts for conservation. According to the typology presented here (*cf*. Table 1), flamingos seem to best fit the definition of nomadic and irruptive movements: they move between places but with much variation in temporal, spatial and population-level behaviour, and no fixed pattern. Teitelbaum & Mueller (2019) even considered irruptive movements to be a form of nomadism, wherein long-distance movements are unpredictable in time and direction but punctuated by periods of residency, i.e. irruptive nomadism. Considering flamingos as irruptive, nomadic, or irruptive-nomadic (*sensu* Teitelbaum & Mueller 2019) species helps to correctly define their movements, thereby avoiding confusion in both scientific literature and popular media, and differentiates their movements from true migrants, such as *Calidris subruficollis* and *Spheniscus magellanicus*, which fit the specific definition of migratory movement (*cf*. Table 1).

ISSN-2513-9894 (Online)

The importance of classification and further discussion

Considering a species to be migratory is more than just a biological classification. Currently, the concept includes an important political and practical side. Migratory species are protected by laws in many countries and continents (Runge *et al*. 2015b). There is also an international effort to protect these species and their habitats, as the effectiveness of conservation policies is low if countries that a species uses both for breeding and feeding do not work together (Dunn *et al*. 2019, Xu *et al*. 2019). The main global mechanism for the conservation of migrant species, the Convention on the Conservation of Migratory Species of Wild Animals (CMS), an international treaty signed by 108 different countries, prohibits the capture and apprehension of endangered species, including many migratory birds, and seeks to conserve their habitats. The treaty also regulates that the parties must seek agreements for conservation of migratory species, including less threatened taxa, and work at a continental level (CMS 1979).

Four species of flamingo are currently included in the CMS: James's and Andean Flamingos are protected by the convention itself, both being covered by a high-priority conservation act in South America to protect their colonies and habitats (CMS 1979, 2008). Lesser Flamingo has a single-species action plan for conservation that unites many African countries (Childress *et al*. 2008) whilst Greater Flamingo is protected under the African–Eurasian Waterbird Agreement (AEWA) (EU 2006). The other species, Chilean and American Flamingos, are not directly covered by any international agreement or treaty, despite their presence across country borders and in habitats subject to great human impact (Caziani *et al*. 2007, Derlindati 2008, Derlindati *et al*. 2014, Rose 2020). However, all flamingos are listed in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES 1963, 2021).

Although we argue that flamingos are not truly migratory, we support the various efforts to protect these species and their habitats in many countries. Their classification as irruptive or nomadic seeks merely to correctly identify and define their movements, and should not be taken as an argument to question their inclusion in agreements covering the conservation of migratory species. This classification is only in the biological and theoretical field, and should not affect efforts to monitor and protect flamingos. In fact, we support expanding protection programmes to other species that do not perform migration *sensu stricto*. Correctly defining different behaviours helps fulfil the movement shortfall in conservation policies and scientific studies, not only for flamingos but for other species with a similar movement pattern (Cottee-Jones *et al*. 2015). Flamingos, despite being geographically very widespread and popular, are impacted by many anthropogenic threats, such as pollution of lakes, human use of water, habitat destruction, tourism, and fishing near breeding sites, among others (Ugarte-Nuñes & Mosaurieta-Echegaray 2000, Moreno-Opo *et al*. 2012, Kumar & Rana 2021). Therefore, an international effort is needed to conserve these species and more studies are needed to better identify the many different and complex movements and displacement strategies of these birds, as well as to expand conservation efforts to include species that might not be considered strictly migratory but do frequent several sites across various international borders.

Acknowledgements

We thank our referees Felicity Arengo and Ignacio Barberis for carefully reading the manuscript and for their helpful comments. Our studies were supported by the Coordenação de Pessoal de Nível Superior (CAPES), Brazil.

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References:

Aldabe, J. 2016. Light-level geolocation reveals migration patterns of the Buff-breasted Sandpiper. *Wader Study* 123: 29–43.

Alerstam, T. 1993. *Bird migration*. Cambridge Univ. Press.

Anderson, M. J. (ed.) 2016. *Flamingos: behavior, biology, and relationship with humans*. Nova Science, London.

Ayache, F., Gammar, A. M. & Chaouach, M. 2006. Environmental dynamics and conservation of the flamingo in the vicinity of Greater Tunis, Tunisia: the case study of Sebkha Essijoumi. *Earth Surf. Processes & Landforms* 31: 1674–1684.

Bairlein, F. 2003. The study of bird migrations – some future perspectives. *Bird Study* 50: 243–253.

Balkız, Ö., Özesmi, U., Pradel, R., Germain, C., Sıkı, M., Amat, J. A., Rendón Martos, M., Baccetti, N. & Béchet, A. 2007. Range of the Greater Flamingo, *Phoenicopterus roseus*, metapopulation in the Mediterranean: new insights from Turkey. *J. Orn*. 148: 347–355.

Barbraud, C., Johnson, A. R. & Bertault, G. 2003. Phenotypic correlates of post-fledging dispersal in a population of greater flamingos: the importance of body condition. *J. Anim. Ecol*. 72: 246–257.

Bateman, B. L., Pidgeon, A. M., Radeloff, V., Allstadt, A., Akçakaya, H. R., Thogmartin, W. E, Vavrus, S. J. & Heglund, P. J. 2015. The importance of range edges for an irruptive species during extreme weather events. *Landscape Ecol*. 30: 1095–1110.

Béchet, A. 2016. Flight, navigation, dispersal, and migratory behavior. Pp. 97–106 *in* Anderson, M. J. (ed.) *Flamingos: behavior, biology, and relationship with humans*. Nova Science, London.

Behrouzi-Rad, B. 1992. On the movements of the Greater Flamingo, *Phoenicopterus ruber*, in Iran. *Zool. Middle East* 6: 21–28.

Berthold, P. 2001. *Bird migration: a general survey*. Oxford Univ. Press.

Borello, W. D., Mundy, P. J. & Liversedge, T. N. 1998. Movements of greater and lesser flamingo in southern Africa. Pp. 201–218 *in* Leshem, E., Lachman, E. & Berthold, P. (eds.) *Migrating birds know no boundaries*. Torgos Publications, Tel Aviv.

Brown, C. & King, C. (eds.) 2005. *Flamingo husbandry guidelines: a joint effort of the AZA and EAZA in cooperation with WWT*. Dallas Zoo, Dallas, TX.

Brown, C. R., Roche, E. A. & Brown, M. B. 2017. Why come back home? Breeding-site fidelity varies with group size and parasite load in a colonial bird. *Anim. Behav*. 132: 167–180.

Burt, W. H. 1943. Territoriality and home range concepts as applied to mammals. *J. Mammal*. 24: 346–352.

Cale, P. G. 2003. The influence of social behaviour, dispersal and landscape fragmentation on population structure in a sedentary bird. *Biol. Conserv*. 109: 237–248.

Caziani, S. M. & Derlindati, E. 2000. Abundance and habitat of high Andes flamingos in northwestern Argentina. *Waterbirds* 23: 121–133.

Caziani, S. M., Olivio, O. R., Ramírez, E. R., Romano, M., Derlindati, E. J., Tálamo, A., Ricalde, D., Quiroga, C., Contreras, J. P., Valqui, M. & Sosa, H. 2007. Seasonal distribution, abundance and nesting of Puna, Andean, and Chilean Flamingos. *Condor* 109: 276–287.

Chapman, B. B., Brönmark, C., Nilsson, J.-Å. & Hansson, L.-A. 2011. The ecology and evolution of partial migration. *Oikos* 120: 1764–1775.

Chapman, B. B., Hulthén, K., Wellenreuther, M., Hansson, L.-A., Nilsson, J.-Å. & Brönmark, C. 2014. Patterns of animal migration. Pp. 11–35 *in* Hansson, L.-A. & Åkesson, S. (eds.) *Animal movement across scale*. Oxford Univ. Press.

Childress, B., Harper, D., Hughes, B., van den Bossche, W., Berthold, P. & Querner, U. 2004. Satellite tracking Lesser Flamingo movements in the Rift Valley, East Africa: pilot study report. *Ostrich* 75: 57–65.

Childress, B., Nagy, S. & Hughes, B. (eds.) 2008. *International single species action plan for the conservation of the Lesser Flamingo Phoeniconaias minor*. CMS Tech. Ser. 18 & AEWA Tech. Ser. 34. https://www.cms.int/sites/default/files/publication/ts18_ssap_lesser_flamingo_3_0_0.pdf (accessed 21 December 2020).

Convention on the Conservation of Migratory Species of Wild Animals (CMS). 1979. *Convention text*. https://www.cms.int/sites/default/files/instrument/CMS-text.en_.PDF (accessed 21 December 2020).

Convention on the Conservation of Migratory Species of Wild Animals (CMS). 2008. *Memorandum of understanding on the conservation of high Andean flamingos and their habitats*. https://www.cms.int/flamingos/sites/default/files/basic_page_documents/mou_text_e.pdf (accessed 21 December 2020).

Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). 1963. *Text of the convention*. https://cites.org/sites/default/files/eng/disc/CITES-Convention-EN.pdf (accessed 5 July 2021).

Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). 2021. *Appendices I, II and III*. https://cites.org/sites/default/files/eng/app/2021/E-Appendices-2021-06-22.pdf (accessed 5 July 2021).

Cottee-Jones, H. E. W., Matthews, T. J. & Whittaker, R. J. 2015. The movement shortfall in bird conservation: accounting for nomadic, dispersive and irruptive species. *Anim. Conserv*. 19: 227–234.

Coulter, M. C. 1975. Post-breeding movements and mortality in the Western Gull, *Larus occidentalis*. *Condor* 77: 243–249.

ISSN-2513-9894 (Online)

Dean, W. R. J. 1997. The distribution and biology of nomadic birds in the Karoo, South Africa. *J. Biogeogr*. 24: 769–779.

Delfino, H. C. & Aldana-Ardila, O. M. 2020. Comments on the population status of Chilean flamingos at Lagoa do Peixe National Park, southern Brazil. *Flamingo* e3: 21–26.

Derlindati, E. J. 2008. Conservation of high Andes flamingo species (*Phoenicoparrus andinus* and *P. jamesi*): habitat use and activity patterns in two contrasting wetland systems of Argentina. Rep. to Rufford Foundation. http://ruffordorg.s3.amazonaws.com/media/project_reports/22.09.06%20Detailed%20Final%20Report.pdf (accessed 21 December 2020).

Derlindati, E. J., Romano, M. C., Cruz, N. N., Barisón, C., Arengo, F. & Barberis, I. M. 2014. Seasonal activity patterns and abundance of Andean Flamingo (*Phoenicoparrus andinus*) at two contrasting wetlands in Argentina. *Orn. Neotrop*. 25: 317–331.

Deville, A.-S., Labaude, S., Robin, J.-P., Béchet, A., Gauthier-Clerc, M., Porter, W., Fitzpatrick, M., Mathewson, P. & Grémillet, D. 2014. Impacts of extreme climatic events on the energetics of long-lived vertebrates: the case of the greater flamingo facing cold spells in the Camargue. *J. Exp. Biol*. 217: 3700–3707.

Dingle, H. 1996. *Migration: the biology of life on the move*. Oxford Univ. Press, New York.

Dingle, H. 2006. Animal migration: is there a common migratory syndrome? *J. Orn*. 147: 212–220.

Dingle, H. & Drake, V. A. 2007. What is migration? *BioScience* 57: 113–121.

Doyle, F. I., Therrien, J.-F., Reid, D. G., Gauthier, G. & Krebs, C. J. 2017. Seasonal movements of female Snowy Owls breeding in the western North American Arctic. *J. Raptor Res*. 51: 428–438.

Dunn, D. C., Harrison, A.-L., Curtice, C., DeLand, S., Donnelly, B., Fujioka, E., Heywood, E., Kot, C. Y., Poulin, S., Whitten, M., Åkesson, S., Alberini, A., Appeltans, W., Arcos, J. M., Bailey, H., Ballance, L. T., Block, B., Blondin, H., Boustany, A. M., Brenner, J., Catry, P. Cejudo, D., Cleary, J., Corkeron, P., Costa, D. P., Coyne, M., Crespo, G. O., Davies, T. E., Dias, M. P., Douvere, F., Ferretti, F., Formia, A., Freestone, D., Friedlaender, A. S., Frisch-Nwakanma, H., Froján, C. B., Gjerde, K. M., Glowka, L., Godley, B. J., Gonzalez-Solis, J., Granadeiro, J. P., Gunn, V., Hashimoto, Y., Hawkes, L. M., Hays, G. C., Hazin, C., Jimenez, J., Johnson, D. E., Luschi, P., Maxwell, S. M., McClellan, C., Modest, M., di Sciara, G. N., Palacio, A. H., Palacios, D. M., Pauly, A., Rayner, M., Rees, A. F., Salazar, E. R., Secor, D., Sequeira, A. M. M., Spalding, M., Spina, F., Van Parijs, S., Wallace, B., Varo-Cruz, N., Virtue, M., Weimerskirch, H., Wilson, L., Woodward, B. & Halpin, P. N. 2019. The importance of migratory connectivity for global ocean policy. *Proc. Roy. Soc. B*. 286: 20191472.

Egevang, C., Stenhouse, I. J., Phillips, R. A., Petersen, A., Fox, J. W. & Silk, J. R. D. 2010. Tracking of Arctic Terns *Sterna paradisaea* reveals longest animal migration. *Proc. Natl. Acad. Sci. USA* 107: 2078–2081.

Espino-Barros, R. & Baldassarre, A. G. 1989. Numbers, migration chronology and activity patterns of nonbreeding Caribbean Flamingos in Yucatan, Mexico. *Condor* 91: 592–597.

European Union (EU). 2006. On the conservation of African-Eurasian migratory waterbirds. *Off. J. Eur. Union* https://www.unep-aewa.org/sites/default/files/basic_page_documents/agreement_text_english_final.pdf (accessed 21 December 2020).

Fuller, M., Holt, D. & Schueck, L. 2003. Snowy owl movements: variation on a migration theme. Pp. 359–366 *in* Berthold, P., Gwinner, E. & Sonnenschein, E. (eds.) *Avian migration*. Springer Verlag, Berlin & New York.

Gill, F., Donsker, D. & Rasmussen, P. (eds.) 2021. IOC world bird list (v10.2). doi:10.14344/IOC.ML.10.2 (accessed 19 February 2021).

van Gils, J. A., Battley, P. F., Piersma, T. & Drent, R. 2005. Reinterpretation of gizzard sizes of red knots world-wide emphasises overriding importance of prey quality at migratory stopover sites. *Proc. Roy. Soc. B.* 272: 2609–2618.

Hayes, F. A., Scharf, P. A. & Ridgely, R. S. 1994. Austral bird migrants in Paraguay. *Condor* 96: 83–97.

Hayne, D. W. 1949. Calculation of size of home range. *J. Mammal*. 30: 1–18.

Hobson, K. A., Norris, D. R., Kardynal, K. J. & Yohannes, E. 2018. Animal migration: a context for using new techniques and approaches. Pp. 1–23 *in* Hobson, K. A. & Wassenaar, L. I. (eds.) *Tracking animal migration with stable isotopes*. Second edn. Academic Press, London.

Hochachka, W. M., Wells, J. V., Rosenberg, K. V., Tessaglia-Hymes, D. L. & Dhondt, A. A. 1999. Irruptive migration of Common Redpolls. *Condor* 101: 195–204.

Holmgren, N. & Hedenström, A. 1995. The scheduling of molt in migratory birds. *Evol. Ecol*. 9: 354–368.

del Hoyo, J. 1992. Family Phoenicopteridae (flamingos). Pp. 507–526 *in* del Hoyo, J., Elliott, A. & Sargatal, J. (eds.) *Handbook of the birds of the world*, vol 1. Lynx Edicions, Barcelona.

IUCN. 2018. The IUCN Red List of threatened species. Version 2018-2. www.iucnredlist.org (accessed 10 July 2021)

Jander, R. 1975. Ecological aspects of spatial orientation. *Ann. Rev. Ecol. Evol. Syst.* 6: 171–188.

Johnson, A. & Cézilly, F. C. 2007. *The Greater Flamingo*. T. & A. D. Poyser, London.

Kennedy, J. S. 1985. Migration, behavioral and ecological. Pp. 5–26 *in* Rankin, M. A. (ed.) *Migration: mechanisms and adaptive significance*. Univ. of Texas Press, Austin.

Ketterson, E. D., Fudickar, A. M., Atwell, J. W., Grieves, T. J. 2015. Seasonal timing and population divergence: when to breed, when to migrate. *Curr. Opin. Behav. Sci*. 6: 50–58.

ISSN-2513-9894 (Online)

Ketterson, E. D. & Nolan, V. 1990. Site attachment and site fidelity in migratory birds: experimental evidence from the field and analogies from neurobiology. Pp. 117–129 *in* Gwinner, E. (ed.) *Bird migration*. Springer Verlag, Berlin.

Kroodsma, D. E., Sánchez, J., Stemple, D. W., Goodwin, E., da Silva, M. L. & Vielliard, J. M. E. 1999. Sedentary life style of Neotropical sedge wrens promotes song imitation. *Anim. Behav.* 57: 855–863.

Kumar, A. & Rana, S. 2021. Population and conservation threats to the Greater Flamingos *Phoenicopterus roseus* (Aves: Phoenicopteriformes: Phoenicopteridae) at Basai Wetland and Najafgarh Jheel Bird Sanctuary, Haryana, India. *J. Threat. Taxa* 13: 18894–18898.

Leu, M. & Thompson, C. W. 2002. The potential importance of migratory stopover sites as flight feather molt staging areas: a review for Neotropical migrants. *Biol. Conserv*. 106: 45–56.

Lohmann, K. J. 2018. Animal migration research takes wing. *Current Biol*. 28: 952–955.

Mascitti, V. & Bonaventura, S. M. 2002. Patterns of abundance, distribution and habitat use of flamingos in the high Andes, South America. *Waterbirds* 25: 358–365.

McCulloch, G., Aebischer, A. & Irvine, K. 2003. Satellite tracking of flamingos in southern Africa: the importance of small wetlands for management and conservation. *Oryx* 37: 480–483.

Milner-Gulland, E. J., Fryxell, J. M. & Sinclair, A. R. E. 2011. *Animal migration: a synthesis*. Oxford Univ. Press.

Moreno-Opo, R., Ould Sidaty, Z. E., Baldó, J. M., García, F., Ould Sehla Daf, D. & González, L. M. 2013. A breeding colony of the Near Threatened Lesser Flamingo *Phoeniconaias minor* in western Africa: a conservation story of threats and land management. *Bird Conserv. Intern*. 23: 426–436.

Newton, I. 2003. Geographical patterns in bird migration. Pp. 211–224 *in* Berthold, P., Gwinner, E. & Sonnenschein, E. (eds.) *Avian migration*. Springer Verlag, Berlin & New York.

Newton, I. 2006. Advances in the study of irruptive migration. *Ardea* 94: 433–460.

Newton, I. 2010. *The migration ecology of birds*. Elsevier, Cambridge, UK.

Nice, M. M. 1941. The role of territory in bird life. *Amer. Midl. Nat.* 26: 441–487.

Noble, G. K. 1939. The role of dominance in the life of birds. *Auk* 56: 253–273.

Parasharya, B. M., Rank, D. N., Harper, D. M., Crosa, G., Zaccara, S., Patel, N. & Joshi, C. G. 2015. Long-distance dispersal capability of Lesser Flamingo *Phoeniconaias minor* between India and Africa: genetic inferences for future conservation plans. *Ostrich* 86: 221–229.

Petersen, E. de S., Chesini-Rossi, L. & Petry, M. V. 2015. Records of vagrant bird species in Antarctica: new observations. *Mar. Biodivers. Rec*. 8: 1–6.

Pretorius, M. D., Leeuwner, L., Tate, G. J., Botha, A., Michael, M. D., Durgapersad, K. & Chetty, K. 2020. Movement patterns of lesser flamingos *Phoeniconaias minor*: nomadism or partial migration? *Wildl. Biol*. 3. doi:10.2981/wlb.00728.

Price, E. R., McFarlan, J. T. & Guglielmo, C. G. 2010. Preparing for migration: the effects of photoperiod and exercise on muscle oxidative enzymes, lipid transporters, and phospholipids in white-crowned sparrows. *Physiol. Biochem. Zool*. 83: 252–262.

Pütz, K., Schiavini, A., Raya Rey, A. & Lüthi, B. H. 2007. Winter migration of Magellanic penguins (*Spheniscus magellanicus*) from the southernmost distributional range. *Marine Biol*. 152: 1227–1235.

Ramenofsky, M., Campion, A. W., Pérez, J. H., Krause, J. S. & Németh, Z. 2017. Behavioral and physiological traits of migrant and resident white-crowned sparrows: a common garden approach. *J. Exp. Biol*. 220: 1330–1340.

Rappole, J. H. 2013. *The avian migrant: the biology of bird migration*. Columbia Univ. Press, Boston, MA.

Rendón, M. A., Rendón-Martos, M., Garrido, A. & Amat, J. A. 2011. Greater flamingos *Phoenicopterus roseus* are partial capital breeders. *J. Avian Biol*. 42: 210–213.

Romano, M., Barberis, I., Arengo, F., Caselli, A., Minotti, P., Morandeira, N., Contreras, M., Uraoka, T., Polla, W., Cruz, N. & Milano, C. 2011. Seasonal variation of Andean and Chilean Flamingos in lowland wetlands of central Argentina. *Flamingo* 18: 12–13.

Rose, P. E. (ed.) 2020. *Flamingo: Newsletter of the IUCN SSC Flamingo Specialist Group* e3: 1–91. http://www.flamingo-sg.org/wp-content/uploads/2021/01/Flamingo-2020-complete.pdf (accessed 12 January 2021).

Runge, C. A., Tulloch, A., Hammill, E., Possingham, H. P. & Fuller, R. A. 2015a. Geographic range size and extinction risk assessment in nomadic species. *Conserv. Biol*. 29: 865–876.

Runge, C. A., Watson, J. E. M., Butchart, S. H. M., Hanson, J. O., Possingham, H. P. & Fuller, R. A. 2015b. Protected areas and global conservation of migratory birds. *Science* 350: 1255–1258.

Sanz-Aguilar, A., Béchet, A., Germain, C., Johnson, A. R. & Pradel, R. 2012. To leave or not to leave: survival trade-offs between different migratory strategies in the greater flamingo. *J. Anim. Ecol*. 81: 1171–1182.

Senner, N. R., Morbey, Y. E. & Sandercock, B. K. 2020. Flexibility in the migration strategies of animals. *Front. Ecol. Evol*. 8: 111. doi:10.3389/fevo.2020.00111.

Shaffer, S. A., Cockerham, S., Warzybok, P., Bradley, R. W., Jahncke, J., Clatterbuck, C. A., Lucia, M., Jelincic, J. A., Cassell, A. L., Kelsey, E. C. & Adams, J. 2017. Population-level plasticity in foraging behavior of western gulls (*Larus occidentalis*). *Mov. Ecol*. 5: 27. doi:10.1186/s40462-017-0118-9.

Simmons, R. E. 1996. Population declines, viable breeding areas, and management options for flamingos in southern Africa. *Conserv. Biol*. 10: 504–514.

Simmons, R. E. 2000. Declines and movements of Lesser Flamingos in Africa. *Waterbirds* 23: 40–46.

ISSN-2513-9894 (Online)

Somenzari, M., Amaral, P. P., Cueto, V. R., Guaraldo, A. C., Jahn, A. E., Lima, D. M., Lima, P. C., Lugarini, C., Machado, C. G., Martinez, J., Nascimento, J. L. X., Pacheco, J. F., Paludo, D., Prestes, N. P., Serafini, P. P., Silveira, L. F., Sousa, A. E. B. A., Sousa, N. A., Souza, M. A., Telino-Júnior. W. R. & Whitney, B. M. 2018. An overview of migratory birds in Brazil. *Pap. Avuls. Zool., São Paulo* 58: e20185803.

Svensson, L., Mullarney, K., Zetterström, D. & Grant, P. J. 2010. *Collins bird guide*. Second edn. HarperCollins, London.

Teitelbaum, C. S. & Mueller, T. 2019. Beyond migration: causes and consequences of nomadic animal movements. *Trends Ecol. Evol*. 34: 569–581.

Ugarte-Núñez, J. & Mosaurieta-Echegaray, L. 2000. Assessment of threats to flamingos at the Salinas and Aguada Blanca National Nature Reserve (Arequipa, Perú). *Waterbirds* 23: 134–140.

Wijesundara, C. S., Wanniarachchi, S., Hettiarachchi, T., Galappaththi, S., Weerawardhana, A. & Rajkumar, P. 2018. Population size and movements of the Greater Flamingo (*Phoenicopterus roseus*) in the Jaffna peninsula, Sri Lanka: results from a long-term study. *Ceylon J. Sci.* 47: 373–378.

Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A. & Gwinner, E. 2003. Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proc. Roy. Soc. B* 270: 2383–2388.

Winger, B. M., Barker, F. K. & Ree, R. H. 2014. Temperate origins of long-distance seasonal migration in New World songbirds. *Proc. Natl. Acad. Sci. USA* 111: 12115–12120.

Winkler, D. W., Billerman, S. M. & Lovette, I. J. 2020. Flamingos (Phoenicopteridae), version 1.0. *In* Billerman, S. M., Keeney, B. K., Rodewald, P. G. & Schulenberg, T. S. (eds.) *Birds of the world*. Cornell Lab of Ornithology, Ithaca. https://doi.org/10.2173/bow.phoeni1.01.

Xu, Y., Si, Y., Takekawa, J., Liu, Q., Prins, H. H. T., Yin, S., Prosser, D. J., Gong, P. & de Boer, W. F. 2020. A network approach to prioritize conservation efforts for migratory birds. *Conserv. Biol*. 34: 416–426.

Zaccara, S., Crosa, G., Vanetti, I., Binelli, G., Childress, B., McCulloch, G. & Harper, D. M. 2011. Lesser Flamingo *Phoeniconaias minor* as a nomadic species in African shallow alkaline lakes and pans: genetic structure and future perspectives. *Ostrich* 82: 95–100.

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ISSN-2513-9894 (Online)