

Managing seabird metapopulations in the Mediterranean: constraints and challenges*

DANIEL ORO

Institut Mediterrani d'Estudis Avançats IMEDEA (CSIC-UIB), Miquel Marqués 21, 07190 Esporles, Mallorca, Spain.
E-mail: d.oro@uib.es

SUMMARY: In recent times metapopulation models have contributed important insights to conservation, and they have inspired field studies that focus on collecting key data on demography and movement. Seabirds are suitable models for studying ecological processes in metapopulations because they breed in discrete local populations (i.e. colonies) both in space and time. However, in the Mediterranean, seabird colonies mostly show conservation problems at an ecosystem level, linked to human activities (e.g. fisheries, tourism, industrial pollution) and the resulting loss of habitat and deterioration of habitat quality. From a conservation point of view, it is crucial to study transfer processes in seabird metapopulations (i.e. emigration, immigration and colonisation) in order to propose management measures. Conservation agencies should always take into account these processes and the spatial factor involved in metapopulation dynamics. However, it is difficult to estimate demographic parameters at a metapopulation level because of technical and financial constraints. In addition, there is a need to act at large geographical scales, since seabirds are wide-ranging species, which operate in ranges beyond political boundaries and far greater than those encompassed by traditional management practices.

Key words: metapopulation, conservation, dispersal, transfer processes, management policies, research, rescue effect, multi-site capture-recapture models, Mediterranean.

RESUMEN: LA GESTIÓN DE LAS METAPOBLACIONES EN EL MEDITERRÁNEO: LÍMITES Y DESAFÍOS. – La modelización de metapoblaciones ha aportado importantes avances en la ecología de la conservación, y ha inspirado trabajos de campo centrados en la recogida de datos sobre demografía y movimiento entre poblaciones. Las aves marinas son modelos apropiados para estudiar procesos ecológicos en metapoblaciones ya que crían en poblaciones locales discretas (i.e. colonias) tanto en el espacio como en el tiempo. En el Mediterráneo, además, las colonias de aves marinas suelen presentar problemas de conservación al nivel de ecosistema, principalmente relacionados con las actividades humanas (p. ej. pesquerías, turismo, contaminación) que han resultado en una pérdida y/o deterioro de hábitats de calidad. Desde el punto de vista de la conservación, es crucial estudiar los procesos de transferencia en metapoblaciones de aves marinas (i.e. emigración, inmigración y colonización) para proponer medidas de manejo. Las agencias de conservación deberían tener siempre en cuenta estos procesos y el factor espacial involucrado en la dinámica de las metapoblaciones. No obstante, es difícil estimar parámetros demográficos a nivel metapoblacional a causa de las limitaciones técnicas y económicas que normalmente supone. Además, es indispensable actuar a una elevada escala geográfica, pues las aves marinas son muy móviles, y desarrollan sus funciones más allá de las fronteras políticas, a una escala mucho mayor de la que se ha considerado tradicionalmente en los esfuerzos de gestión.

Palabras clave: metapoblación, conservación, dispersión, procesos de transferencia, criterios de gestión, investigación, efecto rescate, captura-recaptura, Mediterráneo.

INTRODUCTION

“A volcanic island, for instance, upheaved and formed at the distance of a few hundreds of miles

*from a continent, would probably receive from it in the course of time a few colonists...” (Charles Darwin, *On the Origin of Species*)*

Conservation agencies mostly focus their work on the management of populations, mostly of rare

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and endangered species, but also of others considered as pests. Although colonisation and the fact that populations are connected by emigration-immigration processes (i.e. dispersal) have been known since very ancient times, they have been traditionally considered in isolation by wildlife conservationists and managers. Environmental policies are typically limited in space by administrative boundaries, imposing a narrow vision compared to an ecological picture of the situation.

This is especially true for birds, and among them for seabirds, which show high flight mobility and in turn very high dispersal capacities. Furthermore, seabirds breed in discrete populations in space, called local populations or most commonly colonies. When movement and genetic mixing among these local populations or patches occurs, and when these patches can be re-established following extinction, they constitute a metapopulation, or a population of populations. Seabirds form “natural” metapopulations, whereas other groups form extensive continuous populations that become “artificial” metapopulations after habitat fragmentation (see below).

The metapopulation approach comes up when space is introduced into the traditional approach to population ecology (Tilman and Kareiva, 1997; Hanski and Gilpin, 1997; Bascompte and Solé, 1998). During the 1960s, the dynamic theory of island biogeography (MacArthur and Wilson, 1967) first contributed to this new bi-dimensional framework of population ecology and conservation biology. Levins (1969, 1970) first coined the term metapopulation, and developed the first theoretical framework on this new topic. The two approaches are conceptually and formally similar because they assume unstable local populations and allow for demographic equilibrium at the regional scale. Nevertheless, while island biogeography has received less attention over time, interest in metapopulation approach has been greatly increasing in recent times (Hanski and Gilpin, 1997). Many of the advances in metapopulation theory have been the result of its application to conservation ecology, focusing on species rather than communities and associated with fragmentation of habitat under the spread of human activity (McCullough, 1994). The two keys to the metapopulation idea converge in conservation ecology: populations are distributed discretely in space, and several patches have a certain probability of extinction.

Under Levins’ classical model, a metapopulation is distributed over spatially disjunct sites of suitable

habitat (e.g. seabird colonies on islands) called “patches” separated by a “matrix” of inappropriate habitat. In this model, habitat patches were all of equal size and quality, and dispersal probabilities among patches were equal. Nevertheless, Harrison (1991, 1994) pointed out that this model was too simple to explain the complexity of most populations in nature. Heterogeneity in patch quality is usually high, some patches (high quality ones) attracting more individuals than others (low quality ones). This asymmetrical dispersal at metapopulation level can cause extinction in low quality patches (i.e. local extinction), while some high quality empty patches can be occupied by immigrants (i.e. local colonisation). The extinction-colonisation ratio will determine the persistence of a metapopulation over time. In recent years, metapopulation theory has developed spatially realistic models that are more useful for telling wildlife managers and researchers what to measure in the field (see Hanski and Gilpin, 1997; Hanski, 1999 and references therein).

Suitable habitat is probably the key parameter for the persistence of local populations and metapopulations. Although for most organisms habitat destruction has three components (i.e. loss of habitat, increasing fragmentation and wear of habitat quality), for seabirds loss of habitat implies fragmentation because local populations are already fragmented in space. Human settlements on islands have caused many extinctions (including Mediterranean seabird species such as shearwaters, see for instance Alcover, 1989) caused by direct predation, loss of habitat and its deterioration through introduction of predatory species such as carnivores, snakes or rats.

In the Mediterranean region, many seabird species arouse some conservation concern. There are at least three endemic species, the Levantine shearwater *Puffinus yelkouan*, the Balearic shearwater *P. mauretanicus* and Audouin’s gull *Larus audouinii*, the last two considered critically endangered and vulnerable respectively, following IUCN criteria (Oro *et al.*, 2003). In addition, some other species show conservation problems at a more local level due mainly to the low availability of suitable breeding habitats and consequently to the low number of local populations. The yellow-legged gull *L. cachinnans michahellis*, a large and predatory species, breeds syntopically in most of the suitable patches where other breeding Mediterranean seabirds occur, and is commonly considered a pest

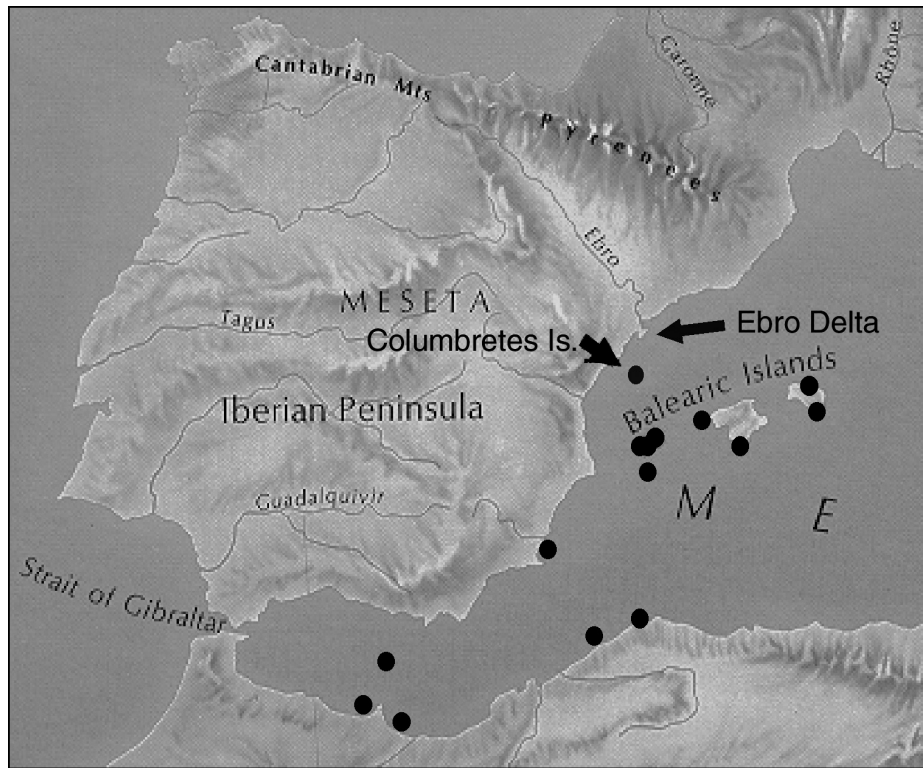


FIG. 1. – Actual distribution of the main local populations of Audouin's gull at the western Mediterranean metapopulation. Two neighbouring patches cited in the text, the Ebro Delta and the Columbretes Islands, are highlighted.

(Vidal *et al.*, 1998; although see Bosch, 2000). All these species have been included in conservation action plans, some of them at a multinational level, to guarantee their future, and these plans include research directed towards the understanding of their population dynamics. The persistence of these Mediterranean seabirds depends heavily on the availability of suitable patches to reproduce, which has been dramatically reduced owing to human settlements in one of the most crowded areas of the world. Thus, it is crucial to improve our knowledge of metapopulation dynamics, that is, the function of dispersal and recolonisation of locally extinct patches for these seabird species. I illustrate here two study cases within the framework of metapopulations for the conservation of Mediterranean seabirds: one is the rare and vulnerable Audouin's gull, which has shown a rampant increase in its metapopulations after protection of breeding patches, and another is the yellow-legged gull, whose numbers are being controlled through culling programmes in many Mediterranean countries. I also show the research tools that can be useful for studying metapopulation dynamics, mainly population counts and capture-mark-recapture techniques, and the intrinsic constraints related to them.

THE AUDOUIN'S GULL CASE

The population structure of Audouin's gull in space fits perfectly with the metapopulation concept (Fig. 1). The western Mediterranean metapopulation is spatially structured, and dispersal among local populations is relatively well known (Muntaner, 1997; Oro and Pradel, 1999; Oro *et al.*, 2000; Oro and Ruxton, 2001). This knowledge has been achieved by means of the use of two important field research tools in conservation ecology: counts of active nests at breeding patches and an extensive ringing programme, which included marking chicks and resighting adults at colonies. This ringing programme has allowed researchers to estimate demographic parameters that are crucial for the study of metapopulation dynamics, such as survival, recruitment and dispersal (both natal and breeding) probabilities.

The Ebro Delta and the Columbretes Islands colonies are two neighbouring local populations with large differences in habitat quality (e.g. Oro *et al.*, 1996): the Ebro Delta is a large and good breeding habitat, with a high food supply due to the oceanographic features off the colony and the high availability of foraging habitats (see Oro, 1998 and

TABLE 1. – Ecological features of two neighbouring local populations of Audouin’s gull in the western Mediterranean: the Ebro Delta (high quality patch) and the Columbretes Islands (low quality patch) (see Fig. 1). Data from Oro *et al.*, 1996; Oro, 1998; Martínez-Abraín *et al.*, 2003). Distances are approximate and show an average estimate.

Parameter	High quality patch Ebro Delta	Low quality patch Columbretes
Surface	2400 ha	19 ha
Habitat	Flat sandy dunes	Steep volcanic rocks
Distance to main prey (clupeoid fish) spawning areas	10 km	60 km
Distance to main opportunistic resource (fishing boats)	20 km	40 km
Distance to accessory foraging areas	15 km	85 km
Secondary foraging resources	Interspecific kleptoparasitism and predation; dunes, rice fields, olive tree crops, dumps	None
Abundance of predatory yellow-legged gull (ratio with Audouin’s gulls)	0.27	1.25

references therein), whereas the Columbretes colony is comparatively a low quality habitat, with very limited suitable breeding habitats and foraging resources and a relatively high number of interspecific competitors (Oro *et al.*, 1996; Martínez-Abraín *et al.*, 2003) (see Table 1). The Ebro Delta was colonised recently and shows a high population increase, whereas the Columbretes were colonised much earlier and show a more fluctuating population dynamics (Oro *et al.*, 1996). In 1994, a carnivore (a European badger, *Meles meles*) entered the Ebro Delta colony and caused high predation losses on nests, affecting both eggs and chicks. A capture-recapture analysis (see Oro *et al.*, 1999) showed that as a result, a large breeding failure affected thousands of birds, and many of them dispersed from the colony, this dispersal being permanent and not temporary. Where did these individuals go? Did they move to the neighbouring colony of the Columbretes Islands? Did this breeding dispersal cause any effect on local population dynamics at the

Ebro Delta? The population dynamics of the two colonies in the year after the badger event shows different trends for each colony: while at the Ebro Delta a slight increase was surprisingly recorded, at Columbretes a large increase occurred (Fig 2). If we had only the counts of nests at the Ebro Delta colony we would have concluded that no dispersal occurred since the population continued to increase as in previous years. Nevertheless, the count of nests at the Columbretes and especially capture-recapture models, showed that there was a clear breeding dispersal of individuals from the Ebro Delta to the Columbretes (see also Oro *et al.*, 2000). Analysis of data from the Ebro Delta showed that other demographic components such as local recruitment and even immigration probably compensated for the breeding dispersal of a large number of individuals (an average of 10%, this percentage larger for younger breeders than for more experienced birds, see Oro *et al.*, 1999). Figure 3 shows the demographic relationship between the two

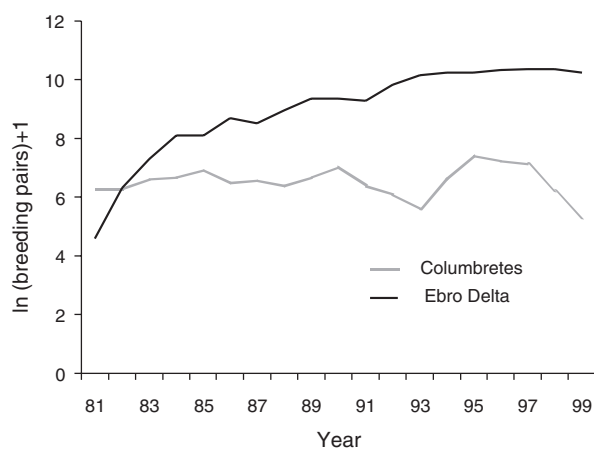


FIG. 2. – Local population growth at two neighbouring colonies of Audouin’s gull in the western Mediterranean: the Ebro Delta (solid line) and the Columbretes Islands (dashed line).

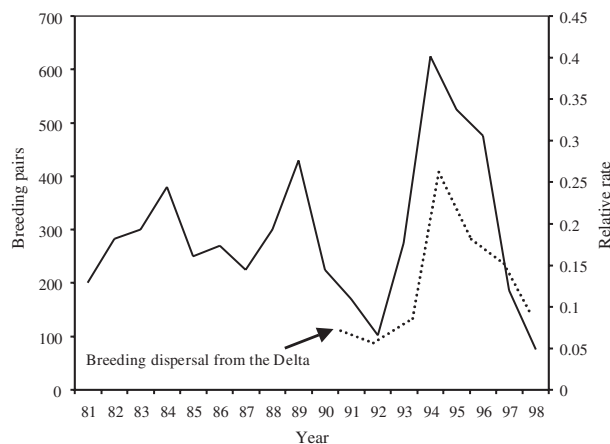


FIG. 3. – Number of Audouin’s gull pairs breeding at the Columbretes Islands (solid line) during the last two decades and relative rate of dispersal (dashed line) from the neighbouring colony of the Ebro Delta.

colonies, which are clearly connected by transfer processes, via emigration and immigration. The badger event also showed that dispersal is not constant and directed always to the same patches, and that it can show fluctuations, depending on local environmental conditions, mainly food and protection against predators, which in turn determine productivity. The situation of a high quality patch (the Ebro Delta) receiving immigrants from the low quality patch (the Columbretes Is.) (Oro and Ruxton, 2001) reversed in 1995 due to a stochastic and detrimental event at the former site. The two populations are not at demographic equilibrium, since density dependence is not yet acting at the Ebro Delta. Nevertheless, this shift in source-sink roles between the two populations due to dispersal pulses caused by stochastic events probably prevents extinction at the low quality patch (Holt, 1997; Stacey and Taper, 1992). This result also suggests the existence of strong rescue effects in metapopulations (Brown and Kodric-Brown, 1977), a phenomenon that is normally difficult to test due to the difficulty of following individuals between patches (Stacey *et al.*, 1997). Some management measures frequently used in conservation are the re-establishment of extinct populations (i.e. reintroductions) and the reinforcement of the number of local populations (i.e. introductions). This is being attempted with Audouin's gull in the western metapopulation, where a new local population is trying to be formed at Benidorm Island using management tools such as conspecific attraction (decoys) and hacking of chicks coming from other colonies (see also Martínez-Abraín *et al.*, 2001). In the Mediterranean, we know from the fossil records that reduction of suitable patches for breeding seabirds is probably an ancient process related to the human colonisation of islands and marshes. This phenomenon has severely increased in the region during the last 5 decades due to tourism pressure (the Balearic Islands, for instance, receive more than 10 million visitors per year), although it has been recently buffered at least partially through the protection of most of the remaining patches, allowing some cases of successful recolonisation and increase in numbers. Audouin's gull is a neat example of this, and represents one of the most strikingly successful examples of the recovery of an endangered species. In the late 1960s, this species was probably the most endangered gull in the world, with a total population estimated at only 600 pairs scattered in small colonies throughout Mediterranean coasts.

During the 1980s, protection of sites stopped severe causes of population limitations (such as egg collecting or other human disturbances), but the crucial change was the protection of a site, the Ebro Delta, where the species was not present as a breeder, and where only a few pairs of yellow-legged gulls and terns bred at that time. The patch unveiled as an extremely high quality patch in terms of availability of both food and suitable nesting sites, and allowed the establishment of a colony that has become the largest in the world in a few years, gathering more than 60% of the total world population. The recovery of Audouin's gull in the western Mediterranean is a clear example of the role played by dispersal or emigration in the metapopulation context (Oro and Pradel, 1999; Oro and Ruxton, 2001) and of a success in conservation biology. The species is now far from extinction levels although one of its main threats is that more than 80% of the total world population breeds in only three colonies, all sited in the western Mediterranean metapopulation (Oro *et al.*, 2000). Dispersal capacities together with reproductive abilities following a more generalist foraging ecology (Oro, 1998) make Audouin's gull a good coloniser, enabling it to persist and recover from a bottleneck situation once protection of suitable patches was guaranteed (see also McCullough *et al.*, 1994).

It is important to point out again that the Ebro Delta was almost an empty patch when it was protected, and that most of the conservation measures and criteria for protecting sites worldwide use the number of rare species occupying these sites. However, these criteria seldom take into account that

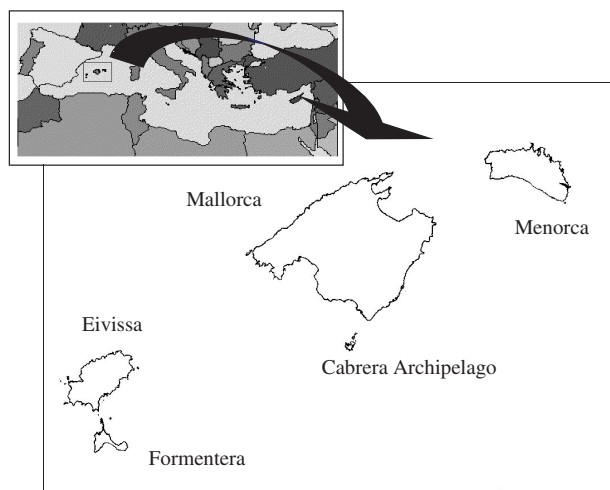


FIG. 4. – Map of the Balearic Archipelago showing the main islands and the Cabrera Archipelago, where the only National Park is found.

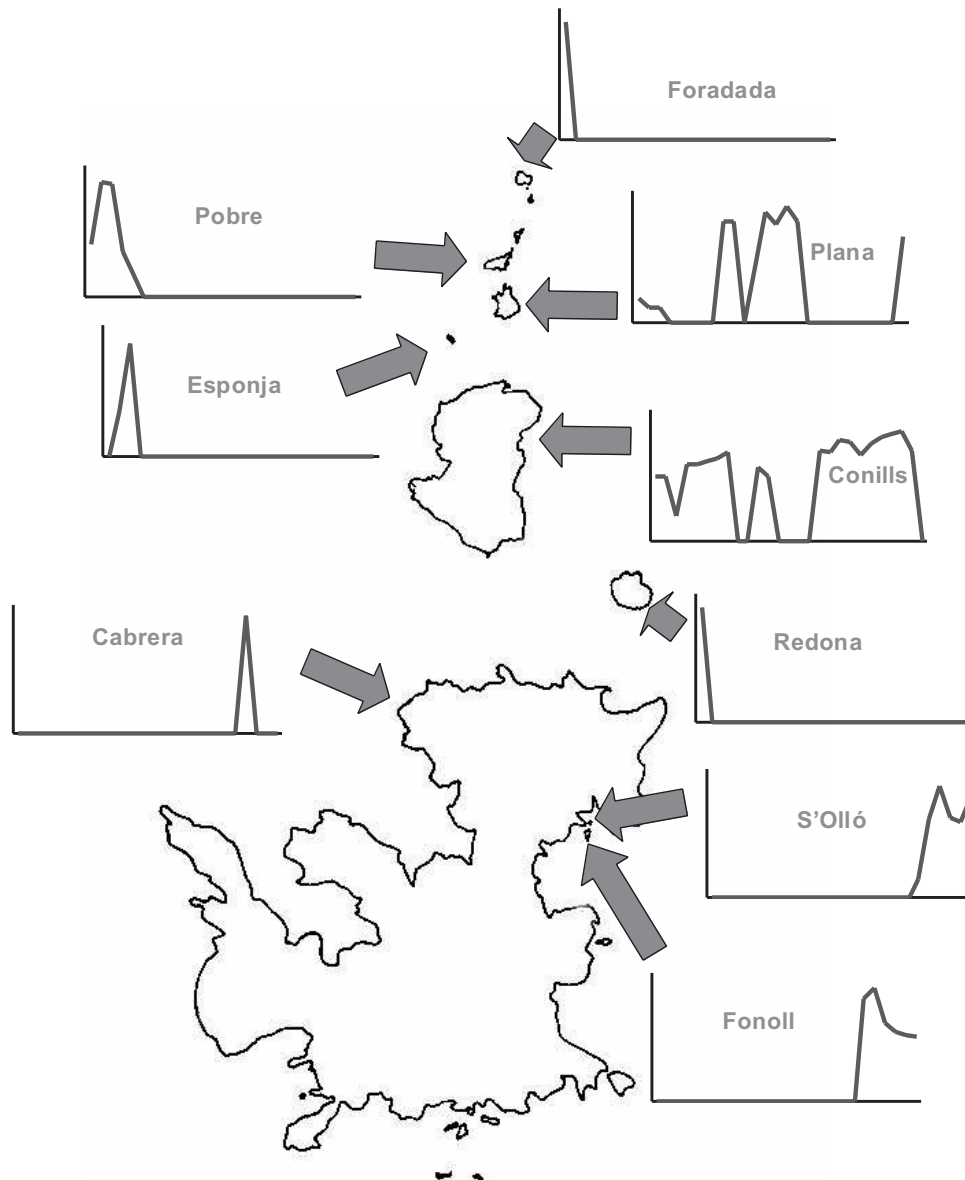


FIG. 5. – Map of the Cabrera Archipelago (Balearic Islands) showing the local population growth rate (all at the same scale) for each of the islands and islets occupied at least once. All curves range since 1974 to 2000, while the number of breeding pairs is shown at log scale (+1).

empty patches are probably empty not because they are unsuitable, but because human activities have precluded their use by wildlife. Consequently, there is also a need to consider empty patches in most of the metapopulation models considered for conservation purposes, especially when the quality of patches is normally shaded by anthropogenic factors. Fortunately for conservation biology, metapopulation theory has highlighted the importance and value of small sites, which had a vague importance in the framework of the island biogeography theory.

At the small Cabrera archipelago (Balearic Archipelago, western Mediterranean) (Fig. 4), breeding site turnover of Audouin's gull is high (Oro and

Muntaner, 2000) compared to the traditional high breeding site tenacity of seabirds. Oro and Muntaner (2000) analysed the colony dynamics within the archipelago and showed that there is a clear demographic relationship among the 9 islets occupied at least once (Fig. 5). For instance, extinction at one of the two islands more frequently occupied (Plana) normally represented recolonisation of the other (Conills) (Fig. 5). Data on breeding numbers from the last 4 years also suggest that these transfer processes can also occur beyond the archipelago, and they represent the colonisation of new sites (author, unpubl. data). This dispersal has no evident causes, since no clear conservation problems are

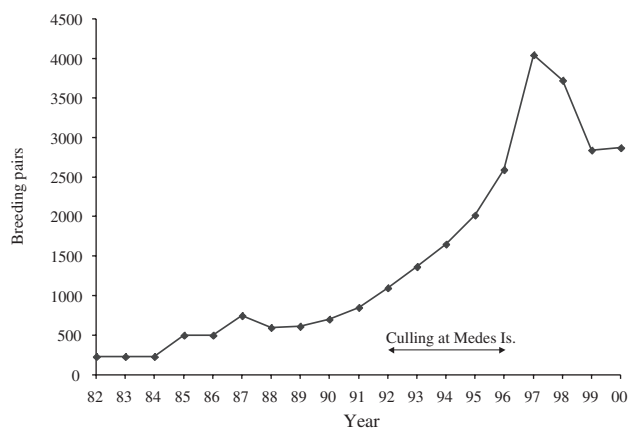


FIG. 6. – Number of yellow-legged gull pairs breeding at the Ebro Delta (western Mediterranean) during the last two decades. The years of culling affecting the colony of the Medes Islands are also shown.

affecting gulls at the archipelago. This poses a new conservation and management problem, since Cabrera is a National Park that is effectively protected, whereas islets around the Park are protected by law but human disturbance can be high. The same pattern of high extinction-colonisation rates is observed in the central and eastern Mediterranean metapopulations (N. Bacetti and HOS, unpubl. data), and this phenomenon also occurs within large colonies, where sub-colonies go extinct after some years and new patches are colonised (see Table 2). Little is known about the factors (proximate or ultimate) that determine these movements, although breeding success and failure probably influence the probability of patch extinction.

Audouin's gull is among the species that have a specific Action Plan of the European Union. Several international meetings have allowed researchers and conservation agencies to put forward different strategies for managing and conserving the species at multinational level. After broadening the ringing programme to other countries (Italy, Greece, France) we already know that birds can disperse to breed in very distant colonies, crossing artificial boundaries such as political frontiers. Thus, there is a need to act at large geographical scales, since seabirds are wide-ranging species which operate on extents far greater than those encompassed by traditional management efforts (e.g. Wiens 1994). With Audouin's gull distributed along Mediterranean coasts, it is clear that an effort is necessary to improve our knowledge of northern African local populations and our communication with African conservation agencies to include most of the colonies in monitoring and conservation programmes (Oro *et al.* 2000).

THE YELLOW-LEGGED GULL CASE

Yellow-legged gulls have been monitored during the last decade at some of the main breeding colonies in the eastern Iberian Peninsula. Counts of nests and some ringing (much less intensive than the programme carried out on Audouin's gull) have also allowed researchers to study the metapopulation dynamics of this species. The yellow-legged gull is considered a pest in the western Mediterranean (Vidal \neq 1998), although several studies fail to find any population decrease or extinction of smaller and threatened seabird species owing to interference competition (Bosch, 2000; Martínez-Abraín *et al.*, 2003). In 1991, only 710 pairs of yellow-legged gull bred at the Ebro Delta (see Fig. 1). At that time, some neighbour colonies and metapopulations held breeding numbers of several thousand pairs (Aguilar *et al.*, 1994; Bosch *et al.*, 2000). The largest colony is that of the Medes Islands, ca. 270 km from the Ebro Delta colony, where more than 14,000 pairs bred in 1991. From 1992 to 1996 a culling programme carried out by the local conservation agency killed more than 25,000 breeding adults, and Bosch *et al.* (2000) showed that this culling not only succeeded in reducing local population to less than 6000 pairs, but also caused dispersal (both natal and breeding) to other colonies. It is very likely that at least some of these dispersers recruited into the Ebro Delta colony, where population increased greatly during these years (see Fig. 6), and stabilised after the cessation of culling operations at the Medes Islands. At this site, numbers are recovering rapidly now that culling has stopped (M. Bosch, unpub. data), probably as a result of high recruitment rates, at both local (natal recruits) and non-local (immigrants) levels, to a patch where competition for resources had been lowered by human manipulation of population numbers. Even though yellow-legged

TABLE 2. – Extinction/colonisation ratio of sub-colonies within the Ebro Delta colony of Audouin's gulls during 1997-2001. Sub-colonies are groups of nests that occupy discrete patches, in this case sandy dunes covered by vegetation. Extinction and colonisations during 1997 were estimated from censuses carried out in 1996, when 14 dunes were occupied.

Year	Number of sub-colonies	Extinction (%)	Colonisation (%)	Ratio
1997	18	28.57	44.44	0.50
1998	32	9.38	53.12	0.10
1999	40	7.50	27.50	0.22
2000	41	31.71	29.27	1.06
2001	35	48.8	42.9	1.33

gulls seem less mobile than Audouin's gulls, this study showed that individuals move to other colonies as a consequence of human disturbances, that is, as a result of impoverishment of habitat quality. The results also suggest that individuals react to changes in patch quality over time and space, moving from low to high quality patches. The goal of the culling programme was to reduce gull disturbances to humans and other wildlife, especially to other protected bird species in surrounding habitats, where some pairs of herons and waterbirds breed. Nevertheless, although the goal of reducing numbers was achieved (at least temporarily), the conservation problem was moved to a distant colony where more than 25,000 pairs of waterbirds (including herons, seabirds, waders and flamingos) breed, and where concern about a larger yellow-legged gull local population has increased in recent years.

CHALLENGES OF MEDITERRANEAN SEABIRD METAPOPOPULATIONS

In the last decade, there has been a very exciting positive feedback between conservation ecology and metapopulation theory, expressed in many excellent pieces of work reviewing this relationship (e.g. Doak and Mills, 1994; Fahrig and Merriam, 1994; Harrison, 1994; Hanski and Simberloff, 1997) and several books (e.g. McCullough, 1994; Hanski and Gilpin, 1997; Hanski, 1999). Although seabird metapopulations in the Mediterranean are very difficult to study because they are isolated populations connected by migration processes (see below), they become the natural choice of metapopulation studies. Only a few works have been published, mostly on Audouin's gull, but unpublished data on transfer processes among local populations have been collected in recent years on some other species such as Cory's shearwaters, Balearic shearwaters, yellow-legged gulls and slender-billed gulls (Martínez-Abraín *et al.*, 2002). These species show very different life-history strategies and represent a challenge in the study of metapopulations; in addition, most of them are endangered and show a very high conservation need. Metapopulation ecology is expected to make predictions about the biological and ecological consequences of habitat destruction and its effects on loss of biodiversity. In some areas of high human development (industrial but mostly from tourism) such as the Mediterranean region, these predictions will be crucial for the future of its seabirds and the landscapes they occupy.

The study of seabird metapopulations should stimulate conservation ecologists to gather data that are crucial for the development of effective management strategies: dispersal among sites, fecundity and survival rates that might vary from site to site, population size-dependent extinction risk and enhanced colonisation of empty patches. Furthermore, the seabird model can sometimes be very useful for testing theoretical concepts and models such as the source-sink model, the rescue effect, the shifting balance in metapopulation genetics, predator-prey interactions, metacommunity dynamics and the role played by conspecific attraction in metapopulation dynamics.

The concept of metapopulations has greatly influenced both conservation biology and ecology, and conclusions about management and conservation have changed since space has been introduced in the studies of population dynamics. The spotted owl breeding in old forests in North America is a nice example of this (e.g. McCullough, 1994). More research is still needed to assess the potential contribution of metapopulation theory to seabird conservation. In contrast to other organisms, there is an important social aspect in seabird population and metapopulation dynamics. The present metapopulation theory does not really deal with seabird ecology satisfactorily. In the current models and conceptual framework, the population extinction rate may rise (especially in small patches) when the emigration rate is very high, but in seabirds there appears to be the extra complication that birds at a colony may decide to move as a group elsewhere (e.g. Oro and Muntaner, 2000; see also Table 2). This poses interesting challenges for modelling, going beyond the usual scenarios of source-sink dynamics and conspecific attraction, since this has been a largely unexplored feature. Nonetheless, even though there might be such group dispersal affecting extinctions and colonisations, the point still remains that a network of sites of sufficient quality and located sufficiently close to each other is needed for a viable metapopulation. Presumably the risk of catastrophic extinction is reduced if the birds are distributed among several sites.

CONSTRAINTS OF MANAGING SEABIRD METAPOPOPULATIONS

As stated above, there are two main tools for studying metapopulation dynamics of seabirds in the field: estimation of the number of breeding pairs

through census techniques; and estimation of demographic parameters such as survival and dispersal through mathematical modelling using capture-mark-recapture procedures.

Both tools have several restrictions that make it difficult to estimate some of these parameters. Counting breeding numbers is especially difficult for Procellariiformes, which normally breed in inaccessible sites such as burrows or caves in cliffs. This task becomes even harder when we have to estimate the size of several local populations to estimate transfer processes among them, since this may involve large geographical areas with hard fieldwork conditions. For Laridae, colonies are more conspicuous and the restriction here is the number of people involved to count nests at large colonies and to reduce investigator disturbance and time spent at colonies. Moreover, these species may show a high colonisation-extinction rate of patches, which involves more effort in surveys to locate new patches every year.

When one is estimating demographic parameters, ringing is a time-consuming task that has to be planned to prevent disturbances to birds, both chicks and adults. Recapturing marked birds (through direct capture as with Procellariiformes or through resight from a distance of rings engraved with a code, as with gulls or terns) poses an additional and even more serious constraint, since it is more time-consuming than ringing. The difficulties are greater when we deal with a group of populations, both for ringing and recapturing, since this involves more fieldwork effort. Finally, capture-recapture models or matrix models used to simulate population trajectories also at a metapopulation level (Caswell, 2001) need some expertise and mathematical background. Multi-site capture-recapture models, which allow researchers to estimate dispersal probabilities (Lebreton *et al.*, 1999), need large sample sizes of recaptures at local and non-local level to ensure that the parameters (whose numbers are much larger than at uni-site models) can be estimated with some precision. This is why there are so few studies estimating dispersal probabilities in birds and in seabirds in particular (e.g. Spindelov *et al.*, 1995). When all these constraints are met (which commonly occurs in the Mediterranean region), I suggest that efforts should focus on carrying out estimations of local population sizes over time at a regional scale, which can give us an idea of the dynamics of a metapopulation and a conservation diagnosis. Even at this level, difficulties in obtaining funding arise,

and financial constraints commonly preclude the estimation of the most useful parameters for a metapopulation conservation approach.

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REFERENCES

- Aguilar, J.S., G. Fernández and J. Mayol. – 1994. Dinámica de la población de *Larus cachinnans michahellis*. Doc. Tècn. Cons., 23: 81-130. Conselleria d'Agricultura i Pesca, Palma de Mallorca.
- Alcover, J.A. – 1989. Les aus fòssils de la cova de Ca Na Reia. *Endins*, 14-15: 95-100.
- Bascompte, J. and R.V. Solé. – 1998. *Modeling spatiotemporal dynamics in ecology*. Springer, New York.
- Bosch, M. – 2000. *The ecology of the yellow-legged gull Larus cachinnans in the Medes Islands*. PhD thesis. Universitat de Barcelona, Barcelona.
- Bosch, M., D. Oro, F.J. Cantos and M. Zabala. – 2000. Short term effects of culling on the ecology and population dynamics of a yellow-legged gull colony. *J. Appl. Ecol.*, 37: 369-385.
- Brown, J.H. and A. Kodric-Brown. – 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, 58: 445-449.
- Caswell, H. – 2001. *Matrix population models: construction, analysis, and interpretation*. Sinauer, Sunderland.
- Doak, D.F. and L.S. Mills. – 1994. A useful role for theory in conservation ecology. *Ecology*, 75: 615-626.
- Fahrig, L. and G. Merriam. – 1994. Conservation of fragmented populations. *Cons. Biol.*, 8: 50-59.
- Hanski, I.A. – 1999. *Metapopulation Ecology*. Oxford University Press, Oxford.
- Hanski, I.A. and M.E. Gilpin. – 1997. *Metapopulation Biology*. Academic Press, San Diego.
- Hanski, I.A. and D. Simberloff. – 1997. The metapopulation approach, its history, conceptual domain and application to conservation. In: I.A. Hanski and M.E. Gilpin (eds.), *Metapopulation biology*, pp. 5-26. Academic Press, San Diego.
- Harrison, S. – 1991. Local extinction in a metapopulation context: an empirical evaluation. *Biol. J. Linn. Soc.*, 42: 73-88.
- Harrison, S. – 1994. Metapopulations and conservation. In: P.J. Edwards, R.M. May and N.R. Webb (eds.), *Large-Scale Ecology and Conservation biology*, pp. 111-128. Blackwell, Oxford.
- Holt, R.D. – 1997. On the evolutionary stability of sink populations. *Evol. Ecol.*, 11: 723-731.
- Lebreton, J.-D., T. Almeras, and R. Pradel. – 1999. Competing events, mixtures of information and multistratum recapture models. *Bird St.*, 46: S39-S46.
- Levins, R. – 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entom. Soc. Amer.*, 15: 237-240.
- Levins, R. – 1970. Extinction. In: M. Gerstenhaber (ed.), *Some Mathematical Questions in Biology*, pp. 77-107. American Mathematical Society, Providence.
- MacArthur, R.H. and E.O. Wilson. – 1967. *The theory of island biogeography*. Princeton Univ. Press.
- Martínez-Abraín, A., C. Viedma, N. Ramón and D. Oro. – 2001. On the potential role of philopatry and conspecific attraction as

- conservation tools in Audouin's gull. *Bird Cons. Intern.*, 11: 143-147.
- Martínez-Abraín, A., A. Sánchez and D. Oro. – 2002. Atlantic Cory's Shearwaters (*Calonectris diomedea borealis*) breeding in a colony of Mediterranean Cory's Shearwater (*C. d. diomedea*). *Waterbirds* 25: 221-224.
- Martínez-Abraín, J. González-Solís, V. Pedrocchi, M. Genovart, J.C. Abella, X. Ruiz, J. Jiménez and D. Oro. – 2003. Kleptoparasitism, disturbance and predation of yellow-legged gull on Audouin's gull in three western Mediterranean colonies. *Sci. Mar.*, 67(Suppl. 2): 89-95.
- McCullough, D.R. (Ed.) – 1994. *Metapopulations and wildlife conservation*. Island Press, Washington.
- McCullough, D.R., J.K. Fischer and J.D. Ballou. – 1994. From bottleneck to metapopulation: recovery of the Tule Elk in California. In: D.R. McCullough (ed.), *Metapopulations and wildlife conservation*, pp. 375-404. Island Press, Washington.
- Muntaner, J. – 1997. La Gaviota de Audouin *Larus audouinii* en las Islas Baleares y sus movimientos. *An. Orn. Bal.*, 12: 35-65.
- Oro, D. – 1998. Audouin's gull account. In: M.A. Ogilvie (ed.), *The Birds of Western Palearctic*, pp. 47-61. Oxford University Press, Oxford.
- Oro, D. and J. Muntaner. – 2000. La gaviota de Audouin en Cabrera. In: G.X. Pons (ed.), *Las aves del Parque Nacional marítimo-terrestre del archipiélago de Cabrera (Islas Baleares, España)*, pp. 95-112. GOB-Colecciones Técnicas del Ministerio de Medio Ambiente, Madrid.
- Oro, D. and R. Pradel. – 1999. Recruitment of Audouin's gull to the Ebro Delta colony at metapopulation level in the western Mediterranean. *Mar. Ecol. Progr. Ser.*, 180: 267-273.
- Oro, D. and R. Pradel. – 2000. Determinants of local recruitment in a growing colony of Audouin's gull. *J. Anim. Ecol.*, 69: 119-132.
- Oro, D. and Ruxton, G.D. – 2001. The formation and growth of seabird colonies: Audouin's gull as a case study. *J. Anim. Ecol.*, 70: 527-535.
- Oro, D., M. Genovart, X. Ruiz, J. Jiménez, and J. García-Gans. – 1996. Differences in diet, population increase and breeding performance between two colonies of Audouin's Gulls *Larus audouinii* during breeding seasons affected by a trawling moratorium. *J. Avian Biol.*, 27: 245-251.
- Oro, D., R. Pradel, and J.-D. Lebreton. – 1999. The effects of nest predation and food availability on life history traits in Audouin's gull. *Oecologia*, 118: 438-445.
- Oro, D., N. Baccetti, D. Boukhalfa, G. Eken, A. El Hili, V. Goutner, S. Karauz, C. Papaconstantinou, B. Recorbet and X. Ruiz. – 2000. Current breeding distribution and status of Audouin's gulls *Larus audouinii* in the Mediterranean. In: J. Sultana and P. Yésou (eds.), *Monitoring and Conservation of Birds, Mammals and Sea Turtles of the Mediterranean and Black Seas*, pp. 69-80. BirdLife Malta, Malta.
- Oro, D., J.S. Aguilar, J.M. Igual and M. Louzao. – 2003. Modelling demography and extinction risk in the endangered Balearic shearwater. *Biol. Conserv.*, 114 (in press).
- Spendlow, J.A., J.D. Nichols, I.C.T. Nisbet, I.C.T., H. Hays, G.D. Cormons, J. Burger, C. Safina, J.E. Hines and M. Gochfeld. – 1995. Estimating annual survival and movement rates of adult within a metapopulation of Roseate Terns. *Ecology*, 76: 2415-2428.
- Stacey, P.B. and M. Taper. – 1992. Environmental variation and the persistence of small populations. *Ecol. Appl.*, 2: 18-29.
- Stacey, P.B., V.A. Johnson and M.L. Taper. – 1997. Migration within metapopulations: the impact upon local population dynamics. In: I.A. Hanski and M.E. Gilpin (eds.), *Metapopulation Biology*, pp. 267-292. Ed. by Academic Press, San Diego.
- Tilman, D. and P. Kareiva. – 1997. *Spatial ecology*. Princeton University Press, Princeton.
- Vidal, E., F. Medail and T. Taton. – 1998. Is the yellow-legged gull a superabundant bird species in the Mediterranean? Impact on fauna and flora, conservation measures and research priorities. *Biod. Cons.*, 7: 1013-1026.
- Wiens, J.A. – 1994. Wildlife in patchy environments: metapopulations, mosaics and management. In: D.R. McCullough (ed.), *Metapopulations and wildlife conservation*, pp. 53-84. Island Press, Washington.