Management of spatially structured populations: a case study

Karin Johst, Roland Brandl

Synopsis
We investigate the impact of management strategies on local and global dynamics of a spatially structured population by modelling the dynamics of black-headed gulls (*Larus ridibundus*). Due to the increase of the population during the last 40 years a reduction of population size has been suggested several times. Our results demonstrate that differences in the level and in the mode of the dispersal strategy can cause significant differences of management impacts. However, detailed knowledge of the dispersal strategies of species is rare. Therefore it will be an important task for further studies to fill this gap.

Modellierung, Populationsdynamik, Dispersion, Management, Lachmöwe, räumlich strukturierte Populationen

Modelling, population dynamics, dispersal, management, black-headed gull, spatially structured populations

1. Introduction

Many species live in spatially structured populations, that is they are subdivided into subpopulations connected by dispersal. There are several approaches to model the dynamics of spatially structured populations. Often details of the local dynamics and of dispersal are ignored and dynamics is described by the number of occupied habitat patches, local extinctions and colonizations. However, there are situations where this approach provides insufficient information for an understanding of the system (HANSKI 1991, BUCKLEY & DOWNER 1992, HASTINGS 1993). Sometimes detailed models are necessary to describe the dynamics of spatially structured populations in a more realistic way. Thereby one is forced to give up the elegant formalism of general patch models and has to turn to case studies. We investigate the dynamics of spatially structured populations of the black- headed gull (*Larus ridibundus*).

In the last decades black-headed gull became superabundant (ISENMANN & al. 1989). In Bavaria the number of breeding pairs increased from about 10000 pairs in 1950 to 40000 in 1990 (HEINZE 1992). This increase in population size has been caused by the improvement of food supply in the wintering areas and in the vicinity of the colonies (PFEIFER & BRANDL 1991). Due to the strong increase of populations management strategies have been discussed to reduce population size (VAUK & PRÜTER 1987). Apart from the general discussion concerning the pros and cons about the management of wildlife populations, the efficiency of most management strategies is unknown, especially in spatially structured populations. We developed a model for the dynamics of gull colonies coupled by dispersal, which takes into account detailed local dynamics and habitat heterogeneity (JOHST & BRANDL 1994). We will use this model to show that the efficiency of a particular management strategy depends on the dispersal strategy.

2. Model

Our model is described in JOHST & BRANDL (1994), therefore we give only a short summary. Biological details about behaviour, faunistics and ecology of black-headed gulls are given in GLUTZ & BAUER (1982) and GORKE (1989).

2.1 Local dynamics

We divide the year into a wintering season and a breeding season. The breeding season itself is again subdivided into two parts. During the first part the gulls arrive at the colony and occupy – if possible – a nest site within the colony (BRANDL 1987). Black-headed gulls are known to show some degree of colony fidelity (RITTER & FUCHS 1980, HEINZE 1992). Therefore we assume that after returning from the wintering areas gulls attempt to breed in the same colony as in the preceding year. Thus, fledgelings return first to the colony of their birth and thus some gulls may breed during their whole life in their birth colony. Furthermore during this first part of the breeding season an exchange of individuals between the colonies may cause some redistribution across the different colonies. After the search for breeding sites and possible dispersal the actual breeding starts. Within this second part of the breeding season gulls lay 3 eggs and commonly 1–2 nestlings survive. After breeding adults and fledged gulls leave the colonies and migrate to their wintering areas.

Population growth is affected by two carrying capacities. The first and most important one is the availability of breeding sites, called colony size K_S. K_S differs between the colonies according to the environmental situation and imposes an upper limit to the population size of a particular colony. If the number of potential breeding pairs is larger than K_S then some gulls cannot find a breeding site and become non-breeding floaters. These floaters are not lost for the system, we assume that they try to find a breeding site in the next year. As long as the number of breeding pairs is well below K_S, breeding is not disturbed by aggressive behaviour. However, if the number of breeding pairs approaches K_S, aggressive behaviour causes an increasing loss of eggs and small chicks. Therefore we introduce a density-dependent mortality of nestlings into the model.

Gulls are central-place foragers and the maximum distance they can travel away from the nest is around 20 km (GORKE & BRANDL 1986), beyond 20 km the energy balance of the foraging flight for a breeding bird becomes negative (BRANDL & GORKE 1988). This radius affects the number of gulls which can successfully forage around the colony. This number is measured in pairs and denoted as K_F. When the number of breeding pairs is well below K_F food supply is sufficient. When the number of breeding pairs approaches K_F, food is in short supply and imposes an increasing mortality on the nestlings. Adult mortality is assumed to be density independent during the breeding season and during winter. This mortality was chosen to yield an overall mean life expectancy of 4 years.

2.2 Environmental setting

In our model we define a set of 10 colonies of different size (K_S) that mimic the distribution of colony sizes found in Bavaria. K_S ranges from small (K_S = 50 breeding pairs) to large values (K_S = 15000 breeding pairs). The landscape around of the colonies determines the capacity K_F. We assume K_F to be equal for all colonies. From our experience we estimated K_F to be around 8000 breeding pairs (Fig. 1). We define »large colonies« as colonies where food supply is limiting ($K_S > K_F$), »medium-sized colonies« where $K_S \approx K_F$ and »small colonies« where only nest site availability is limiting ($K_S < K_F$).

2.3 Dispersal strategies

As already mentioned we define dispersal as the exchange of breeding pairs between the colonies during the first part of the breeding season. Dispersal rules used by black-headed gulls and the interaction between the actual ecological situation and dispersal are unknown. Field investigations suggest a certain degree of colony fidelity, which can be taken into account by

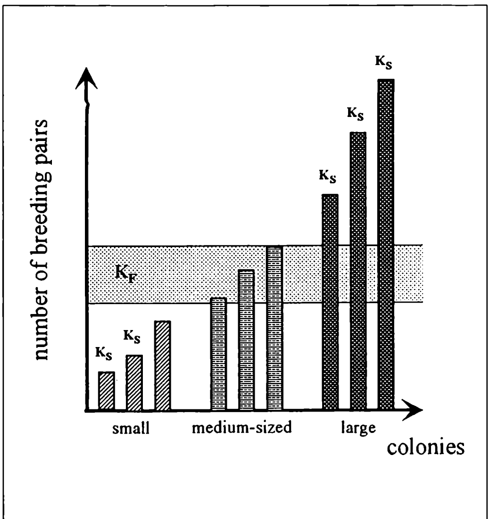

Fig.1
Sketch of the environmental setting used for the simulations. The capacity K_S determines the number of available nest sites at a colony, the capacity of food supply is called K_F. Capacity K_F was assumed to be equal for all colonies.

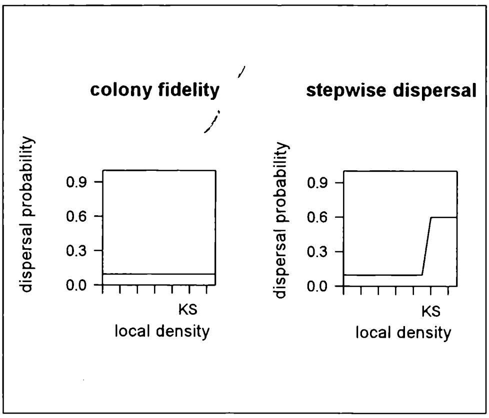

Fig. 2
The two dispersal strategies used in our model. Density independent dispersal is characterized by a very small probability to change the colony, even when nest sites are in short supply. Density dependent dispersal is characterized by colony fidelity as long as the number of available breeding sites is sufficient. When nest sites are in short supply, that is the number of potential breeding pairs approaches K_S, then the probability to change the colony is steeply increasing.

two total different dispersal strategies, a density independent and a special density dependent one.

Figure 2 shows these two dispersal strategies. Density independent dispersal is characterized by a very small probability to change the colony independent of the density, that is the number of potential breeding pairs already present at the colony. Thus, also when nest sites are in short supply the gulls do not change their colony. This dispersal strategy is called strategy of pure colony fidelity. Because it is biologically unreasonable to assume that dispersal is completely impossible we assume a small probability of 0.10.

In the second density dependent dispersal strategy the gulls show colony fidelity as long as nest sites are sufficient. When nest sites are in short supply, that is the number of pairs in the colony approaches K_S, the gulls decide with a steep increasing probability to change their colony. This behaviour can be described mathematically by an approximate step function of dispersal probability with a step around K_S. Therefore it is called stepwise dispersal strategy. We assume that dispersal probability increases within a range of 10% around K_S from 0.10 to 0.60.

We consider each colony as equally well accessible by dispersing individuals. Thus, we ignore the spatial arrangement of the colonies, an assumption, which is valid for a mobile species like the black-headed gull.

3. Management

We selected two management strategies. First, a colony can be removed from the system by inundating or excavating all breeding sites. Second, breeding success can be reduced by destroying the eggs within the nests. We assess the efficiency of these two management strategies on population size by defining efficiencies E1 and E2, that is the relation between benefit and costs for each strategy. The benefit is defined as the reduction of the global population size by the management $\Delta N = N_{before} - N_{after}$. The costs depend on the type of the management. Of course the actual costs of removing a colony (A1) depend on the used machines and man power. It is beyond the scope of our paper to estimate A1. A very efficient strategy, however, of removing colonies in pond areas is to increase the water level of the fish ponds and thereby to innudate the colonies. This is simply done by manipulating the outflow of the pond and the costs are independent of pond area and colony size. Thus, we assume A1 to be roughly constant for all colonies and the efficiency of the first management strategy is defined as

$$E1 = \Delta N / A1 \qquad (1)$$

with A1 fixed at an arbitrary value.

The costs A2 of the second management strategy are assumed to be the number of breeding pairs, which must be managed. Thus, the efficiency of the second management is given by

$$E2 = \Delta N / A2 \qquad (2)$$

with A2 estimated quantitatively by the number of managed nests.

4. Results and Discussion

The dynamic behaviour of our model depends on the incorporated dispersal strategy. To demonstrate this we show in Fig. 3 two simulations. Both simulations

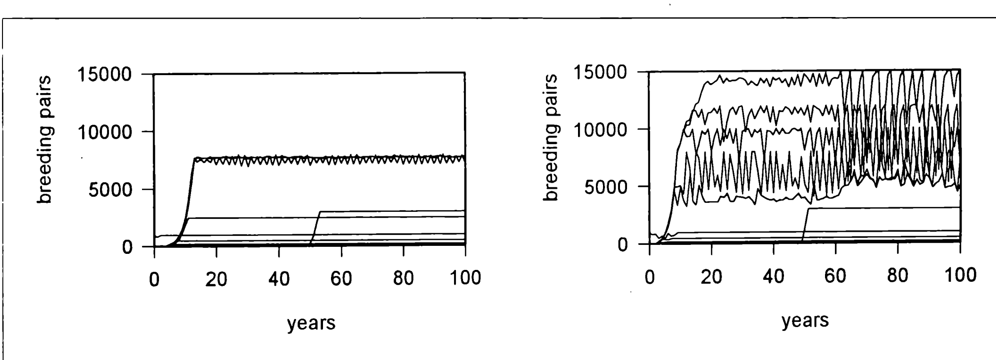

Fig. 3

Local dynamics of the 10 colonies in our model system coupled under the scenario of pure colony fidelity (left) and stepwise dispersal strategy (right). Note the different dynamics of both systems. At t=50 years a new, small colony is introduced. This altered environmental setting does not affect the dynamics of the other colonies within the scenario of pure colony fidelity, but may change the fluctuation pattern within the scenario of stepwise dispersal strategy.

were started with 1000 breeding pairs on a colony with K_S=1000 breeding pairs and after 50 years we introduced a new, small colony into the system. Within the strategy of pure colony fidelity colonies show a logistic growth to the capacities K_S and K_F, respectively. Within stepwise dispersal strategy, however, fluctuations of local population size of particular colonies are possible. These fluctuations arise because gulls decide independently to leave the colony and only when nest sites are in short supply (JOHST & BRANDL 1994). The altered environmental setting after 50 years does not affect the dynamics of the other colonies when the strategy of pure colony fidelity is assumed, but may change the fluctuation pattern within the stepwise dispersal strategy. We will show that these differences of the dynamic behaviour caused by the different modes of dispersal also affect the management efficiencies.

Figure 4 shows the efficiency E1 in relation to the size of the removed colony (small K_S=3000, medium-sized K_S=6000, large K_S=15000 breeding pairs). Of course one expects that the benefit ΔN increases with the size of the removed colony. Figure 4, however, demonstrates that within the strategy of pure colony fidelity this increase is quite small. The reason is that only a small number of individuals, which disperse from outside into a colony, affects the local dynamics. Thus, all colonies are more or less independent units and large colonies are limited by K_F, the food supply around the colony. Therefore many available breeding sites on these colonies remain unused and the removal of a large colony is less advantageous. Within the stepwise dispersal strategy small and medium-sized colonies generate a large number of emigrants, when they have reached K_S, and other colonies are supplied with immigrants. These immigrants allow the large colonies to exceed K_F. This makes it much more advantageous to remove a medium-sized or large colony within the scenario of stepwise dispersal compared to a scenario of pure colony fidelity.

Figure 5 shows the efficiency E2 in relation to two different scenarios to destroy eggs: firstly, in all small and medium-sized colonies egg number is reduced from 3 to 1 and secondly, all medium-sized to large colonies are managed. A2 differs between both scenarios, because the costs depend on the number of nests, which have to be handled. A2 increases with the size of the managed colonies. If ΔN increases in equal proportion to A2 then the efficiency E2 is a constant. This is the case within the strategy of pure colony fidelity. However, this picture changes, when a stepwise dispersal strategy is assumed. Then the scenario of managing all small to medium-sized colonies is more efficient than managing the large colonies. As already mentioned, within stepwise dispersal strategy small and medium-sized colonies generate a large amount of emigrants. Reducing the output of these colonies influences the whole system.

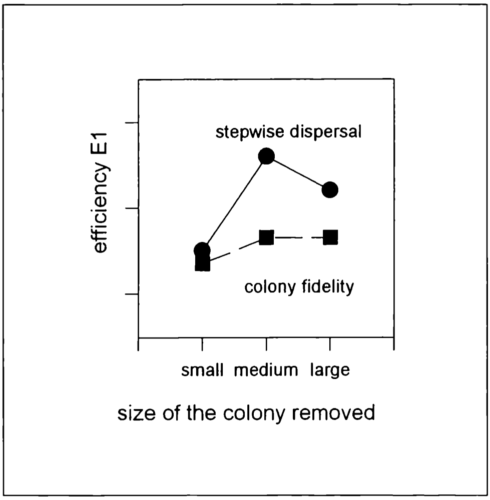

Fig. 4

Efficiency E1 of removing all breeding sites of a colony as a function of dispersal strategy and size of the colony removed. We present no tick labels for E1, because the curves provide only qualitative results.

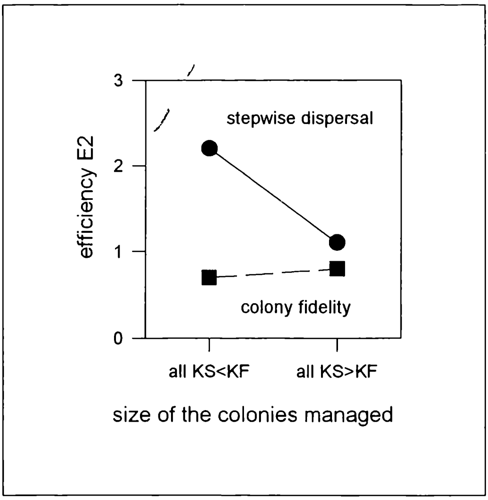

Fig. 5

Efficiency E2 of reducing the number of eggs of breeding pairs from 3 to 1 as a function of the dispersal strategy and size of the managed colonies either by managing all small to medium-sized colonies ($K_S \leq K_F$) or all medium-sized to large colonies ($K_S \geq K_F$).

5. Summary and conclusions

We investigate the impact of management strategies on local and global dynamics in spatially structured populations of the black-headed gull by model simulations. Our results demonstrate that differences in the type of coupling (different dispersal strategies) can cause significant differences in the impact of management strategies. Within the scenario of stepwise dispersal strategy management impacts will be more efficient compared to the scenario of pure colony fidelity strategy, but depend more sensitively on the selection of the managed habitats. Small and medium-sized habitats, often ignored within field studies, are important for the dynamics of our model system. Within stepwise dispersal strategy management plans must include these habitats to be efficient. Thus, an effective management in spatially structured populations depends on the dispersal strategies of the species. In nature conservation it is often assumed, that a successful management depends predominantly on the connectivity of the habitats. Our results suggest that this may be misleading. We need not only information about the general level of dispersal but also about the internal or external forces, which trigger the dispersal events. But a detailed knowledge of the dispersal strategies of species is rare. Therefore it will be an important task for further field research and theoretical investigations to fill this gap.

References

BUCKLEY, P.A. & R. DOWNER, 1992: Modelling metapopulation dynamics for single species of seabirds. – In: D.R. MCCULLOUGH & R.BARRET (ed.): Wildlife 2001: Populations. – Elsevier Applied Science: 563–585.

BRANDL, R., 1987: Warum brüten einige Vogelarten in Kolonien? – Beziehungen zwischen Koloniegröße, Nahrungsressource und Verhalten am Beispiel der Lachmöwe. – Verh.Orn.Ges.Bayern 24: 347–410.

BRANDL, R. & M. GORKE, 1988: How to live in colonies: foraging range and patterns of density around a colony of black-headed gulls Larus ridibundus in relation to the gull's energy budget. – Orn. Scan. 19: 305–308

GLUTZ VON BLOTZHEIM, U.N. & K.M. BAUER, 1982: Handbuch der Vögel Mitteleuropas. Vol.8/1, Akademische Verlagsgesellschaft, Wiesbaden

GORKE, M., 1989: Die Lachmöwe (*Larus ridibundus*) in Wattenmeer und Binnenland. – Diss. Univ. Bayreuth: 109 S.

GORKE, M. & R. BRANDL, 1986: How to live in colonies: spatial foraging strategies of the Black-headed Gull. – Oecologia 70: 288–290.

HANSKI, I., 1991: Single-species metapopulation dynamics: concepts, models, and observations. – Biol. J. Linn. Soc. 42: 17–37

HASTINGS, A., 1993: Complex interactions between dispersal and dynamics:lessons from coupled logistic equations. – Ecology 74: 1362–1372.

HEINZE, G., 1992: Die Bestandsentwicklung der Lachmöwe (*Larus ridibundus*) in Bayern von 1959–1991. – Dipl. Univ. Bayreuth: 106 S.

ISENMANN, P. & J.D. LEBRETON & R. BRANDL, 1989: The Black-headed Gull in Europe. – Acta XX Cong. Intern. Orn.: 2384–2389.

JOHST,K. & R. BRANDL, 1994: Modellierung der Populationsdynamik von Lachmöwen. – Verh. GfÖ. 23: 329–338

PFEIFER, R. & R. BRANDL, 1991 : Der Einfluß des Wiesenmahdtermins auf die Vogelwelt. – Orn. Anz. 30: 159–171.

RITTER, M. & E. FUCHS, 1980: Das Zugverhalten der Lachmöwe *Larus ridibundus* nach schweizerischen Ringfunden. – Orn. Beob. 77: 219–229.

VAUK,G. & J. PRÜTER, 1987: Möwen – Niederelbe-Verlag H. Huster Otterndorf/Niederelbe

Karin Johst, Roland Brandl
Umweltforschungszentrum Leipzig/Halle
Sektion Ökosystemanalyse
Permoserstr. 15
D-04318 Leipzig