

Modelling the size and distribution of protected areas for nomadic birds: alaudidae in the Nama-Karoo, South Africa

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Abstract

Nomadic larks in the semi-arid Nama-Karoo, South Africa, depend on patches of temporally suitable habitat for breeding. These patches occur where rain has recently fallen, where there has been growth and seeding of grasses, and where invertebrates are locally abundant. They are also attractive to domestic livestock which may constitute a threat to successful breeding by the larks. Since rainfall in the Nama-Karoo is unpredictable in time and space on a regional scale, it is difficult *a priori* to select protected areas for such nomadic birds. As a first approach, we present a spatio-temporal model for estimating the survival of flocks in relation to different configurations of protected areas. The results show that neither one large protected area nor a high number of small protected areas provide the optimal solution. This is due to the impact of various spatial effects which affect the probability of a flock finding a suitable breeding area. These effects are identified and discussed. Furthermore, we are able to reproduce and explain the present spatial abundance of the larks on a regional scale with our model. The model is intended to complement and define the field studies needed to determine practical parameters more precisely. © 1998 Elsevier Science Ltd. All rights reserved

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1. Introduction

The protection of nomadic birds in a spatially and temporally varying environment presents a difficult conservation problem. Our investigations described here are based on empirical knowledge of nomadic, granivorous larks (Alaudidae) in the Nama-Karoo, South Africa. Sclater's lark *Spizocorys sclateri*, Stark's lark *Eremalauda starki*, greybacked finchlark *Eremopterix verticalis* and blackeared finchlark *Eremopterix australis* are common in the Nama-Karoo (Dean et al., 1992; Maclean, 1993; Dean, 1995), breeding in large numbers in areas where sufficient rain has recently fallen and where grasses have grown and set seed (Maclean, 1970, 1996). The grasses provide not only food for the adult larks, but also nest material and

sheltered nest sites at the bases of tufts. Since seeds can be found everywhere, adult larks can survive throughout the Karoo. However, the young are fed mainly on arthropods, of which the harvester termite *Hodotermes mossambicus* is probably the most important (Maclean, 1970; Dean et al., 1992), and which is most abundant where rain has recently fallen (Coaton, 1958).

Though the spatial and temporal distribution of rain follows general rules on a regional scale, the actual rainfall is to a great extent randomly distributed on a smaller spatial and temporal scale. Consequently the grass patches, which correlate to sufficient rainfall, are similarly patchy and randomly distributed (Acocks, 1953; Hoffman and Cowling, 1987), and suitable sites for nesting are therefore much more restricted.

The semi-arid Karoo is used mainly for the pastoral farming of small domestic livestock, namely Merino sheep, Dorper sheep and Angora goats (Dean, 1995), for which grass patches are also attractive. If a grass

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patch is grazed, it becomes unsuitable for breeding. This is due to the loss of nest material, sheltered nest sites and the concomitant drop in the abundance of arthropods for feeding the young. Successful breeding is not observed in such affected areas (W. R. J. Dean, pers. observ.). Studies underline the need for protected areas to reduce the long-term impacts of land use on the avifauna (Dean, 1995). Although this threat is not yet acute, conservation measures must be taken now in order to avoid severe damage in future before it is too late. Note in this context that Sclater's lark and blackeared finchlark are respectively endemic and near-endemic species of the Karoo. We believe that conservation biology should not be confined to crisis management but should also plan for the future, especially if problems can be foreseen as in the present case. The redistribution of landed property is imminent in the Nama-Karoo, and therefore now is the time for land to be acquired for protection.

The obvious thing to do would be just to fence in an area to prevent the entry of livestock for grazing. But because of the unpredictable rainfall in space and time, it cannot be guaranteed that a sufficient rain event leading to a suitable breeding site will occur there in the near future. Therefore, it would seem logical to set up several protected areas at different places to increase the chance of getting one protected grass patch. The problem then arises of *how* to select these areas. Since grass patches are necessary for breeding (and not for the general survival of adult larks), areas protected from grazing by domestic livestock are not isolated islands of suitable habitat in an area of unsuitable habitat, and thus some of the views presented in the SLOSS debate (see Soulé, 1986) do not apply. It is not clear from the outset where such areas should be situated, or what size and number they should be to best 'catch' rain events. Does a scattered configuration of several small protected areas benefit the nomadic larks more than a few large protected areas? What effects play a key role and should be considered in conservation management?

Models may provide initial insight into this problem. We present a conceptual simulation model (Wissel, 1992) as an initial approach to the protection of nomadic birds. We identify the factors and processes that may be essential, and provide guidelines for the size, number and spatial arrangement of protected areas that could support the survival of the birds. Although the model has been developed for nomadic larks in the Karoo, the model could be applied to birds in other comparable semi-arid ecosystems.

2. Description of the model

The first part of the model describes the spatial and temporal patterns of suitable breeding areas. In a sec-

ond step, we develop an individual-based model incorporating survival and reproduction for the population dynamics of the larks.

2.1. Modelling patterns of rainfall and grass patches

As a framework for the model to generate the pattern of suitable breeding areas (i.e. the dynamic grass-patch mosaic caused by patchy rainfall), we used the following Karoo-specific empirical facts (Venter et al., 1986):

1. The mean rainfall is about 170 mm per year with a high variability (c. 20–50%).
2. Summer rainfall is patchy (isolated showers) and predominantly occurs in the eastern Karoo (where over 40% of the annual amount falls during the summer).
3. During the winter, extensive weather fronts drifting more regularly from the west bring widespread low precipitation. Winter rainfall is predominantly in the western Karoo (where over 40% of the annual amount falls during the winter).
4. Between the summer and winter rainfall zones there is a zone of between-seasons rainfall, where rain may fall at any time of the year, but generally most often in autumn and spring.

For the model, an area of the Nama-Karoo $175 \times 175 \text{ km}^2$ is divided into 50×50 squares (fields) each $3.5 \times 3.5 \text{ km}^2$. The mean size of a rain patch is equal to one field. The time-step used in the model is one week, so that the rain patterns produced with the model in one time-step should be seen as the summary of rain events in the previous week.

This large-scale pattern of the rainfall known from empirical data is incorporated into the present model. On the smaller scale of one week and one field, the likelihood and amount of rainfall has been determined using probabilities. One rain event is characterized by assigning a random value indicating the amount of rainfall to one field in the grid chosen at random. Patchy rainfall in summer is simulated in one time-step for each north-south strip in the 50×50 field grid (one strip has the width of one field). Many rain events are simulated in accordance with this procedure until a given amount of rainfall per north-south strip is achieved. These amounts (per strip), and the shapes of the random distributions for the location and intensity of one rainfall event, are derived from the empirical facts given above. Similarly, the winter rain scenario is simulated for each time-step by determining the extension of a weather front and amount of rainfall. Fig. 1(a) shows a typical scenario generated by the model for one time-step during between-seasons rainfall. In the west there is an extended weather front, while in the east typical patchy rain patterns occur.

The amount of rain necessary to stimulate grass growth must be above a certain threshold (Maclean,

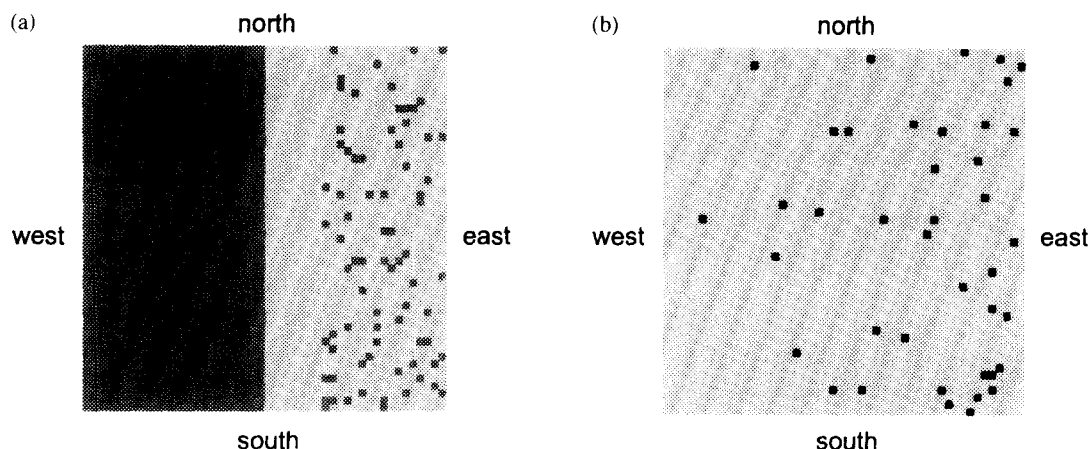


Fig. 1. (a) A typical scenario of one time-step for between-seasons rainfall generated by the model. In the west an extended rain front drifts across the Karoo while patchy rainfall occurs in the east; (b) a typical pattern of grass patches suitable for breeding by larks in summer. These patches are created by patchy rainfall (> 40 mm threshold) whose frequencies decline from east to west.

1970). In the model, the threshold rainfall for grass growth, and thus a suitable area for breeding for the larks, is 40 mm. Fig. 1(b) shows a typical grass patch pattern in summer when weather fronts are few and patchy rain clouds drift over the Karoo from east to west. We assume that these grass patches remain suitable for the larks to begin breeding for about two weeks after rain (two time-steps in the model) and that after this, conditions for initiating breeding will deteriorate.

2.2. Population dynamics

For the population-dynamics submodel we used the following input parameters (cf. Dean et al., 1992; Maclean, 1993, 1996):

1. the mean clutch size is two eggs;
2. about 30% of the young survive to become adults;
3. juveniles become adult at 39 weeks;
4. the mean lifetime of a bird is 3–5 years. We estimated that on average half of the birds die after 4 years and that the maximum age is 6 years.

These rules set the age-dependent probabilities in the model that one bird survives one time-step. In our individual-based model, the survival of each bird is simulated with these probabilities for every time-step.

If an area suitable for reproduction is found, the larks begin building nests and breeding. The period from the start of nest-building until the eggs hatch is about 16–17 days for all the study species (Dean et al., 1992). In general, the nestlings leave the nest after 7–10 days, and are fully fledged at the age of 15–20 days (Maclean, 1970, 1993). Overall, it takes about 34 days or about five weeks from the start of nest building until the young are fledged. At the end of this time the flock leaves the current patch to search for other patches. In our model, the young move with their parents and build

up juvenile cohorts in the flocks. We also limited the number of times that the birds could breed in a year to three.

To avoid unreasonably high numbers of individuals in the simulations, we consider limited growth for the birds by incorporating a rule that a flock consisting of more than 100 individuals should not reproduce until it becomes smaller by natural mortality. This simple rule can be justified because the purpose of our model is to obtain a general understanding of this conservation problem and not to provide a highly realistic description of population dynamics; it has no impact on the general conclusions of the model (see Discussion).

2.3. Searching for breeding areas

Larks would not immediately move with the scattered rain events because of a time lag of about two weeks between rain and the growth and seeding of grasses. The larks should be able to recognize whether a grass patch is suitable for breeding by the abundance of food, i.e. the 'quality' of a patch. If not, failed breeding events in inappropriate areas would be common, but this is seldom observed (W. R. J. Dean, pers. observ.). For the purposes of the model we assume that the larks breed exclusively inside protected areas and that patches in the unprotected matrix are completely grazed by livestock and therefore unsuitable for breeding.

The searching strategy for the birds was that a flock can see for a certain distance a (shown by broken line in Fig. 2). A corresponding square is denoted the *searching area*. If one grass patch suitable for breeding (filled squares in Fig. 2) is inside this searching area, the flock will move to it. If several patches are perceived by the flock, one of them will be chosen at random. If no potential breeding area is inside the searching area, any field inside the broken line square will be randomly

chosen. In this case, the flock cannot start breeding and tries to find an opportunity in the next time-step. This procedure is repeated for every time-step for non-breeding flocks.

The decisive parameter in this scenario is the distance a in Fig. 2. We set as standard value $a =$ four fields, i.e. each week a flock surveys an area of $(2a + 1) \times (2a + 1) = 81$ fields, corresponding to 992 km².

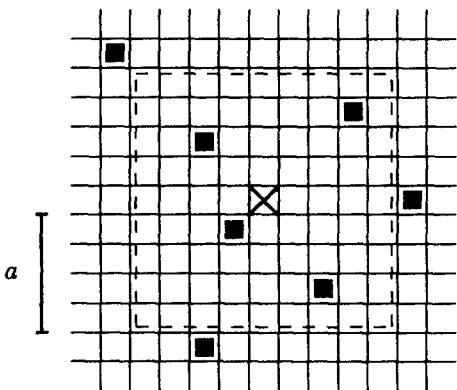


Fig. 2. Modelling the movements of lark flocks and the search for breeding areas. A flock (X) can see grassy patches (■) from a distance a , i.e. inside a *searching area* of $(2a + 1) \times (2a + 1)$ fields (indicated by the broken line). These patches are chosen first and foremost.

3. Results and interpretation

3.1. Spatial distribution of the birds

Over a period of 20,000 time-steps the model recorded how often a flock is present on each field in the 50×50 grid when potential breeding areas are not disturbed by livestock grazing. As noted above, the chance of a rain event generating a patch suitable for breeding is significantly higher during the summer than during the winter. Because of the statistical gradient of increasing rainfall from west to east during summer, there are on average more potential breeding sites in the east. One may argue that the birds are unable to perceive this large-scale gradient because of the small scale of their searching horizon for breeding areas (Fig. 2), since, in the model, this gradient is faded by stochastic noise. Therefore, one might expect the pattern of the presence of the flock in space over a long period of time to be equally distributed. However, the results shown in Fig. 3 differ from this hypothesis. Flocks are evidently more likely to be found in the east than in the west.

Thus, although the searching strategy for breeding areas does not exhibit a trend towards any single spatial direction (Fig. 2), the combination of this isotropic

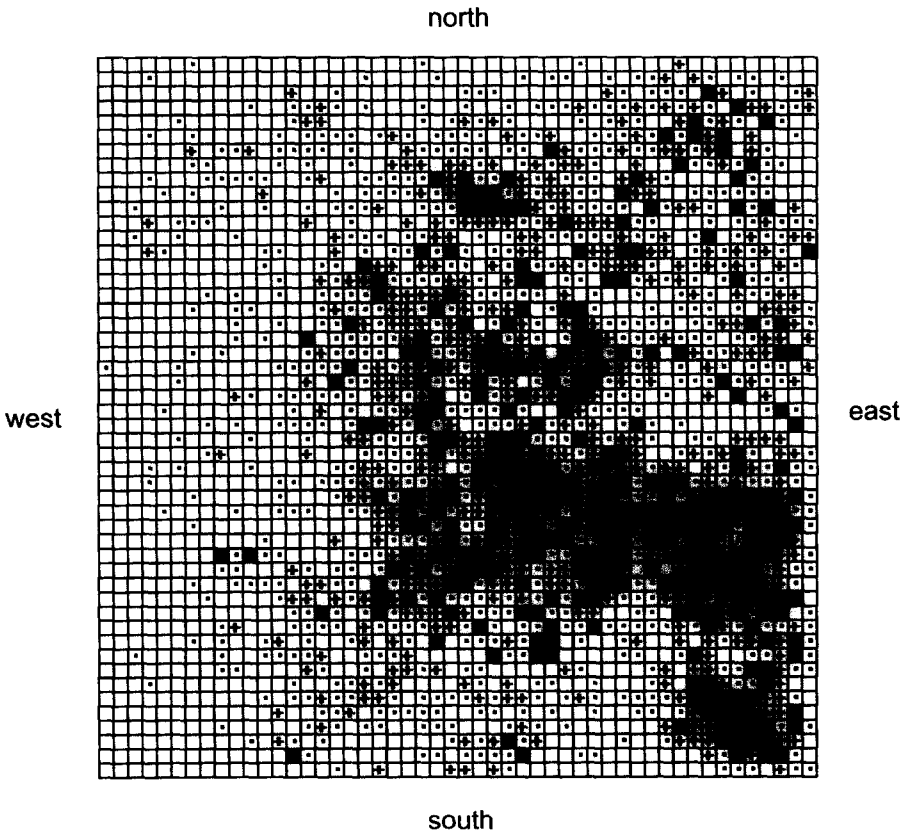


Fig. 3. The spatial distribution of the presence of one flock over a period of 20,000 time-steps. The position of the flock is recorded and each field is scored for the number of times used for a stay per time-step (plain white, 0–5; stippled, 6–10; +, 11–15; black, > 15 stays of the flock on the corresponding field).

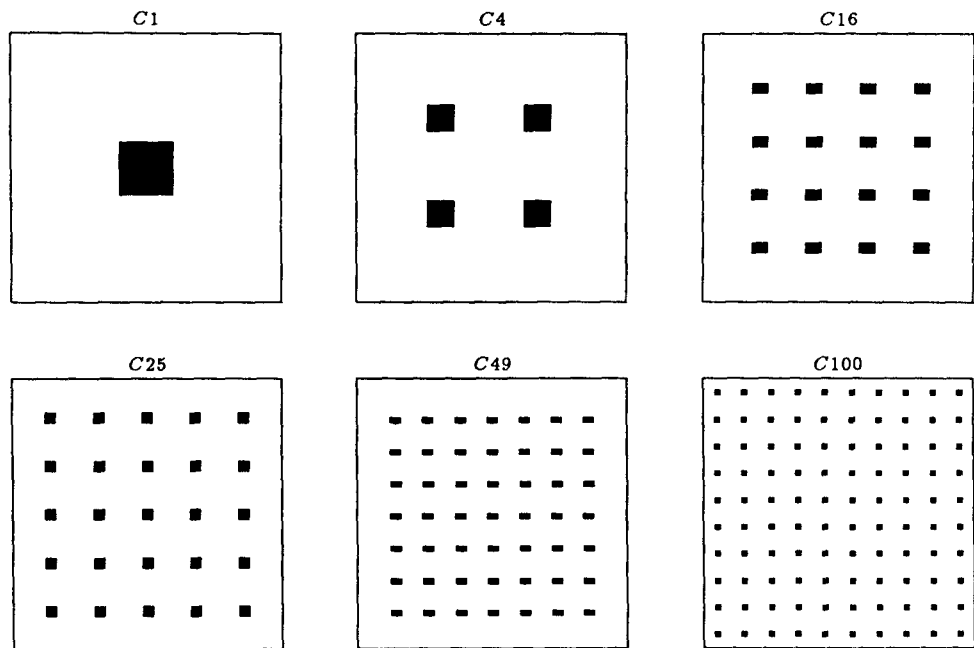


Fig. 4. The spatial arrangement of the configuration C1, ..., C100 of protected areas. Sizes of fragments are given in Table 1.

searching strategy, which works on a small scale, with a large-scale spatial gradient of frequencies of such breeding areas leads to the effect that the birds follow the gradient.

3.2. Optimising the selection of protected areas

Configurations of protected areas of nearly equal total size but of a different degree of fragmentation were investigated. Six configurations of protected areas of different numbers of fragments (C1,..., C100) are shown in Fig. 4 and described in Table 1. The index indicates the number of separate parts making up the total protected area in each configuration. The total size of protected areas in each configuration is about 100 fields (see last column in Table 1), which are equally distributed all over the grid.

Table 1
The size and fragmentation of the six configurations C1, ..., C100 (sizes of fragments and total area are in units of *fields*; 1 field = 3.5×3.5 km²; see description of the model). The spatial arrangement is shown in Fig. 4

Configuration	Number of fragments	Size of fragment (in fields)	Total size (in fields)
C1	1	10×10	100
C4	4	5×5	100
C16	16	2×3	96
C25	25	2×2	100
C49	49	1×2	98
C100	100	1×1	100

To compare the different scenarios of the six configurations, runs were made for each scenario to determine:

- 1. the mean number *N* of annual breeding events of one flock;
- 2. the mean survival time *T* of a flock starting with 50 adults and 50 juveniles.

For (1) the simulations run over 1000 years in order to establish statistically clear results; for (2) we made 1000 runs to obtain the average *T*.

As starting conditions, the flock is set in the middle of the 50×50 grid. For each time-step the individual mortality and the rain scenario (i.e. the local distribution of the potential breeding areas) are simulated. Then the flock moves in accordance with the prescribed rules for the search for breeding areas, and the model records whether a suitable nesting patch is found. We thus obtain the mean number *N* of annual breeding events and the mean lifetime *T* of the flock by recording the time of extinction in every run.

In Fig. 5(a), we obtain a maximum for the configuration C25, i.e. 25 areas each of 4 fields (=49 km²) would give the optimum breeding habitat for the larks. This maximum value for *N* is about twice as great as for one large protected area in configuration C1. *N* decreases from C25 to higher fragmented configurations C49 and C100. As expected, the values of *N* for each configuration in Fig. 5(a) closely correlate with the corresponding values for the mean lifetime *T* in Fig. 5(b). From *T*=9.8 years in configuration C1, *T* increases to a maximum of *T*=32.6 years in C25. In comparison with Fig. 5(a), the maximum in Fig. 5(b) is much more distinct.

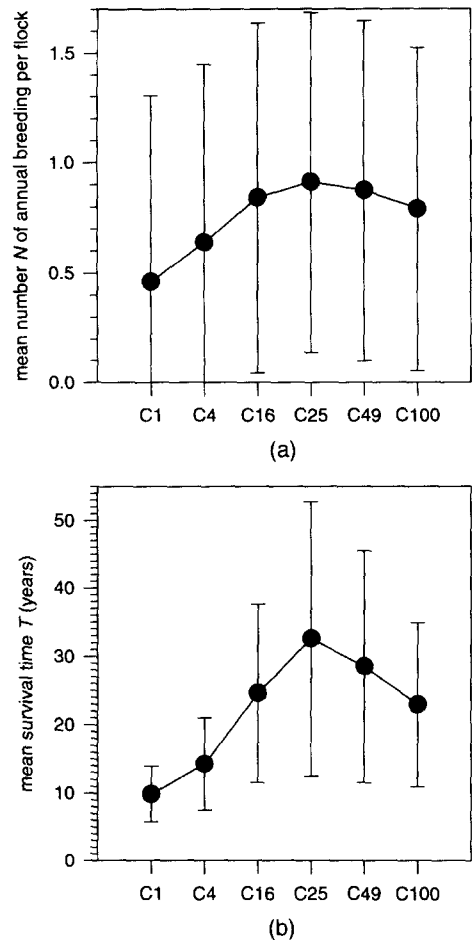


Fig. 5. (a) Annual breeding events ($N \pm \text{s.d.}$) per flock for the configurations C1, ..., C100 over a run of 1000 years (cf. last column in Table 2). The maximum in C25 is based on two counter effects depending on the degree of fragmentation (see Results and Interpretation); (b) Mean survival time ($T \pm \text{s.d.}$) over a set of 1000 runs of a flock initially consisting of 50 adults and 50 (non-breeding) juveniles. Note the similarity of the curve to Fig. 5(a), caused by the strong correlations between N and T .

3.3. Analysis

For each configuration C1,...,C100, Table 2 lists in detail the frequencies for the cases of $n=0,1,2,3$ annual breeding events of the flock for simulations made for (1) in the previous section to determine N . Comparing the frequencies for the case of one ($n=1$) or two ($n=2$) successful breeding events per year for C1,...,C25, it can be seen that fragmentation increases the frequencies for $n=1$ and $n=2$. In C49 and C100 the contribution of $n=1$ and $n=2$ is nearly constant or decreases while $n=0$ (no breeding in one year) becomes more frequent. On the other hand, $n=3$ is generally low and even decreases with fragmentation. Fig. 6 shows the configurations for C1 and C4. The broken line around each protected area indicates the area inside which a flock is in principle able to find a suitable grass patch, the distance between the filled squares and the broken lines being equal to the

Table 2
The frequencies for the cases of $n=0,1,2,3$ breeding events per year and flock for the configurations C1, ..., C100 gained by simulation over 1000 years. The last column shows the resulting mean value N in each case and is shown in Fig. 5(a)

Configuration	$n=0$	$n=1$	$n=2$	$n=3$	N
C1	718	158	70	54	0.460
C4	549	291	134	26	0.637
C16	384	418	172	26	0.840
C25	326	460	192	22	0.910
C49	353	441	187	19	0.872
C100	387	449	153	11	0.788

range of vision a in Fig. 2. We call the area(s) within the broken line the *catchment area(s)* whose total size is larger in more fragmented configurations. This explains why the mean numbers N of annual breeding events initially rise with increasing fragmentation (see last column in Table 2). In more fragmented areas, there is a higher probability that a flock is inside the catchment area of any protected area and that it can find a patch for successful breeding.

Conversely, highly fragmented configurations like C100 are not optimum. Although the total size of catchment areas is maximum (the larks can see at least one protected area from each point of the grid), the fragmentation reduces the probability that sufficient rainfall will occur exactly in the fragment near the flock because of the small size of this area.

Further analysis shows that the probability of three breeding events per year ($n=3$) decreases with increasing fragmentation of the spatial configuration (Table 2), and there is a marked difference in the proportion of the frequencies for one ($n=1$) and three ($n=3$) breeding events per year. In C1, $n=1$ is about three times more frequent than $n=3$, while in configuration C100 it is over 40 times more frequent. This is due to a ‘surface-effect’. If a bird has nested in a certain protected area it will search again for a new breeding opportunity. The smaller the protected area actually used, the greater the probability that it will cross its boundaries (perimeter–area relationship) in order to search for a new patch. In configuration C1, this effect has faded. If a flock has bred inside the large protected zone, it will move to and fro after breeding for the next few time-steps and very probably remain inside the protected area where new patches providing suitable habitat for reproduction can be found.

3.4. Variation of the model parameters

A sensitivity analysis of the model was performed. The most important parameters in the model are the mean amount of annual rainfall (170 mm) (which has a strong impact on the mean number of actually available breeding areas) and the searching distance a (see Fig. 2)

(which is correlated with the chance that a flock can find breeding areas). Variation of these two parameters (rainfall and a) shows the obvious influence on the survival times or on the mean number N of annual breeding events per flock. Because these two parameters only change the probability that a flock will find a patch suitable for breeding, the *relative* values of N for the different configurations do not essentially change. Consequently, such configurations as C25 in Fig. 5 remain optimal even when a is varied. For example, a smaller value of a = two fields (instead of a = 4) of the searching distance for a flock (cf. Fig. 2) means that the flock has a lower range of vision and consequently the catchment areas are smaller. As expected, the results of these simulations are qualitatively the same as in Fig. 5 (a maximum in C25), but on a lower level (N is reduced by about 50%). Therefore, varying these parameters does not change the general results discussed above.

4. Discussion

Our main concern was to investigate the impact of the fragmentation of protected areas on the survival of the larks shown in Fig. 5(a) and (b). The shape of these curves can be accounted for by the occurrence of two counter-effects. First, the more fragmented the configuration, the higher the probability that the birds can find a protected area because of the increasing total size of the catchment areas (Fig. 6). This increases the likelihood of a suitable breeding area being found inside the protected areas. Second, the more fragmented the configuration, the less likely it is that sufficient rain will fall in such a fragment, and that it can support a second breeding season ('surface-effect'; see above). Depending on the degree of fragmentation of a configuration, one or the other effect is dominant, leading to the maximum shown in Fig. 5(a) and (b).

To assess the important role of the surface-effect, one should note that protected zones do not constitute

islands where survival is exclusively possible; the birds can also survive outside protected areas for a long time without breeding. Such boundaries do not represent natural obstacles. The birds will leave a protected area without realizing that they are entering an unprotected area where the chance of successful breeding is reduced by livestock grazing. In this sense, there is no special attraction for the larks to enter or to stay in protected areas. Therefore, the surface-effect partly offsets the advantages of large catchment area-sizes in a highly fragmented design of protected areas.

The curve in Fig. 5 shows that a certain degree of fragmentation in the design of protected areas is necessary to best adapt to the extreme stochasticity of the ecosystem. Creating protected areas could be done by acquiring land and fencing in these areas to prevent the entry of livestock for grazing. Now, let us assume we have a certain budget for conservation management and that the costs of land are proportional to its size. The results in Fig. 5 indicate that the money would be spent much more effectively if we acquired not one large area but several plots measuring about $10 \times 10 \text{ km}^2$ scattered over a large regional range, because this increases the size of catchment areas. But if these fragments are too small, the surface-effect cancels out the advantages of fragmentation and our money is not optimally invested.

Furthermore, the spatial distribution of the birds concluded from Fig. 3 leads to the hypothesis that protected areas in the eastern part of the Karoo will be most efficient in ensuring the long-term survival of the larks, since they are predominantly present in this region.

We assumed in our simulations that the larks cannot breed outside the protected areas because the grazing pressure may be so high that any grass patch would immediately become unusable for breeding. In actual fact there may nevertheless be a small chance for successful breeding outside protected areas, because some areas may not be utilised by livestock. In the simulations, however, we want to present a worst-case scenario.

Our aim was to design a model as an initial approach to the problem of protecting nomadic birds, where changing spatio-temporal patterns of patches suitable for breeding determine the frequency and success of breeding. One fundamental problem of such a model is that not all known factors of a system can be included. For instance, in the model presented here, different qualities of breeding areas and the splitting and coalescing of flocks are not considered. Another problem is that precise data about this ecosystem are limited. General trends may be known, but there is for instance (to our knowledge) no detailed recording of patterns of grass patches in space and time on a regional scale that could be taken as validation for our model of grass-patch dynamics. Under these conditions, a model cannot

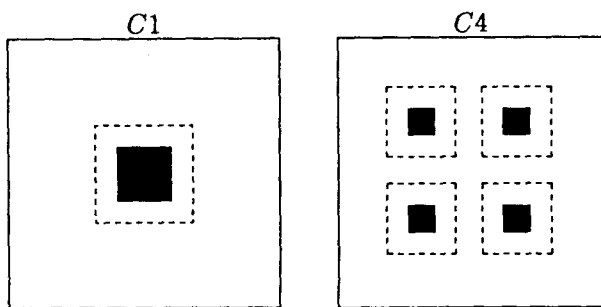


Fig. 6. The *catchment area(s)* in the configurations C1 and C4. The broken line indicates the area inside which a flock is able to see a potential breeding area inside the protected area (filled squares). The total size of the catchment areas increases with the degree of fragmentation (C1: $18 \times 18 = 324$ fields, C4: $4 \times (13 \times 13) = 676$ fields).

make exact quantitative predictions, but it still provides a tool to obtain an understanding of the system's dynamics and of the main factors important for conservation. Here we concentrate on the consequences for reproduction success and mean lifetime of a flock under several protection scenarios. Therefore, the results gained reveal *fundamental* effects that become significant for the design of protected areas (see the interpretation of the two counter-effects in the section 'Analysis'). They help us to analyse and understand the complex system and point out the facts that must be considered in order to design a successful protection strategy.

Long-term prognoses such as mean lifetimes of populations are not checkable. However, one way of assessing the quality of our model is to obtain results that are not directly dependent on the model inputs and that can be validated. Our model produces a pattern of the spatial distribution of one flock moving in accordance with the assumed moving strategy (see section above, Fig. 3). The result that the flock is more frequently present in the eastern parts over a long period of time is equivalent to the statement that a higher proportion of the lark populations can be found mainly in this region, a situation that in fact occurs in the Karoo (W. R. J. Dean, pers. observ.). This can be taken as a hint that the rain model and the submodel for the searching strategy for breeding sites are sensible and simulate reality well.

The initial results generated by the model are comprehensible and reasonable and help to understand the system. As this model describes the main processes and factors fairly approximately, the quantitative details of the results cannot be taken literally. For example, the value of the survival times (Fig. 5(b)) should not be regarded as 'true'; nor is it asserted that the spatial configuration C25 of protected areas (Fig. 4) will in fact be the optimum of all possible protection strategies. But nevertheless, our model reveals the importance of the trade-off between the surface-effect and the effects based on the total size of catchment areas leading to the existence of a maximum in C25 (Fig. 5). In this way, the model provides a measure which allows us to *compare* the efficiency for protection of different configurations of protected areas.

Further field investigations, e.g. on mortality rates and factors determining population densities of larks, and on the patterns of grass patches in time and space, are necessary to produce a better data base for modelling and for practical conservation measures.

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