Research News

Population persistence in fragmented landscapes

James N.M. Smith and Jessica J. Hellmann

Many ecologists believe that fragmenting habitats into discontinuous patches disrupts the reproduction, survivorship and movement of animals. It has seldom, however, been possible to measure all these processes in one study. Recent work by Lesley and Michael Brooker on an Australian songbird, the blue-breasted fairy wren *Malurus pulcherrimus*, has achieved this elusive goal. Their new paper in *Wildlife Research* demonstrates that reduced connectedness among habitat patches lowers population recruitment to below break-even levels.

It is almost an article of faith among conservation biologists that dividing native habitats into discontinuous patches harms both flora and fauna [1]. Decreased habitat area can lower reproduction [2] and survival [3] in habitat fragments. Both butterflies [e.g. 4] and birds [e.g. 5] also experience difficulties in dispersing to isolated patches of habitat. Metapopulation models provide a framework for predicting how such populations might respond to habitat loss and fragmentation if their demography varies with fragment area and their ability to disperse over nonhabitat is limited [6]. In spite of these attractive and plausible ideas, populations in small habitat fragments often perform as well as those in larger areas [e.g. 7,8], thus casting doubt on whether habitat fragmentation is commonly detrimental. A new and unusually complete study of the blue-breasted fairy-wren *Malurus pulcherrimus* by Lesley and Michael Brooker [9], however, now provides evidence that poor connectivity does indeed lower recruitment to unoccupied patches below the level needed to replace mortality.

The Brookers' study is unique in that it examines fragmentation effects on reproduction and survival as well as on dispersal and recruitment in a landscape that is large enough to capture the longest natural movements. Most existing information on individual dispersers is biased towards short-range movements [10], and thus does not capture the whole range of behaviors. The Brookers examined individual dispersing birds over a wide area (320 km^2) from 1993 to 1998 and determined how individuals used the habitat and performed in the fragments of varying size and isolation. They report data on the occupancy of ~80 habitat patches, reproductive success within those patches and the probability of individual dispersal events between patches.

Their study organism is the sedentary blue-breasted fairy-wren, a species that is native to western Australia. This tiny (8 g) group-living wren inhabits patches of native vegetation that today account for only 7% of the landscape (the remaining is dedicated to grain and livestock production). The wren has several characteristics that make it ideal for tracking population performance across a wide area: it is conspicuous, readily marked, fairly common but not abundant, and it can be followed from its birthplace to where it breeds. Wrens live year round on small territories (2–3 ha) in fragments of native heath and eucalypt woodland. Social groups comprise a dominant male, a breeding female and up to three helpers, who are usually the female's offspring. Most movements of individuals involve yearlings or older helpers leaving their natal group and moving <2 km to form their own breeding pair or to join other existing groups. Hence, over the study area, both short- and long-distance dispersal can be observed. Individuals that establish a breeding territory rarely move to other locations except when a mated individual loses its partner.

The Brookers used three methods to deduce the viability of wren populations:
(1) careful mapping of wren distribution and dispersal across an extensive and highly fragmented landscape;
(2) detailed study of the reproduction and survival of color-banded wrens within fragments of varying size [11]; and
(3) simulation modeling of population growth rates in landscapes of varying composition and degree of connectivity [12]. These approaches enabled the authors to estimate whether an individual moving among patches in the landscape would be likely to locate a breeding vacancy, enabling them to identify groups of patches, or

Fairy-wren image © Princeton University Press

Fig. 1. The blue-breasted fairy-wren *Malurus pulcherrimus* study area. Blue patches are those areas that are grouped into well-connected neighborhoods (i.e. pairs of patches sharing a better than average likelihood of successful dispersal). Poorly connected patches marked in red had a lower than average probability of successful dispersal. Green areas represent native vegetation that is unsuitable as wren habitat (i.e. wrens never established territories there), but which is used by dispersing wrens. The fawn-colored intervening matrix is mostly tilled for agriculture.

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Box 1. Population growth rates in well-connected and poorly connected habitat fragments

We calculated finite population growth rates of blue-breasted fairy-wrens *Malurus pulcherrimus* for the principle example used by the Brookers (see main text) using the following formula (Eqn I) [a]:

$$\lambda = S_f + (N_y * S_y) \quad \text{[Eqn I]}$$

where S_f is the mean survival rate of adult females modeled for all fragments using the relationship between annual rainfall and survival, N_y is the number of female offspring produced (assuming half of all young were female) from each set of habitat patches in the landscape, and S_y is the survival rate of female fledglings from the time of dispersal to when they joined groups as breeders, also estimated using data on rainfall. To contrast population performance across differing levels of connectedness, we use the parameters from the well-connected neighborhood and contrast them with the values for the same patches if they were poorly connected (Table I). The well-connected neighborhood has $p = 0.55$. In the corresponding poor neighborhood, $p = 0.32$. The probability of successful dispersal within the neighborhood, p, was estimated using simulation (see text).

Table I. Population growth rates in well-connected and poorly connected habitat fragments

	S_f	N_y	S_y	λ
Well-connected neighborhood				
Large remnant (144 ha)	0.67	0.70	0.46	0.99
Medium remnant (67–78 ha)	0.67	0.89	0.46	1.08
Small remnant (4–28 ha)	0.67	1.07	0.46	1.16
Neighborhood comprising 1 large, 3 medium and 6 small fragments	0.67	0.83	0.46	1.05
Poorly connected neighborhood				
Large remnant (144 ha)	0.67	0.70	0.32	0.89
Medium remnant (67–78 ha)	0.67	0.89	0.32	0.95
Small remnant (4–28 ha)	0.67	1.07	0.32	1.01
Neighborhood comprising 1 large, 3 medium and 6 small fragments	0.67	0.83	0.32	0.94

Wrens should therefore experience an average population growth of 5% annually when the neighborhood is well connected, and should decline by 6% annually when it is poorly connected. When the performance in the poorly connected neighborhood is compounded over successive generations, wren populations there will tend to go extinct.

Reference

a Zanette, L. (2000) Fragment size and the demography of an area-sensitive songbird. *J. Anim. Ecol.* 69, 458–470

'neighborhoods,' in which birds tend to search for breeding sites (Fig. 1).

The Brookers' data show that demographic performance is similar across a range of fragment sizes. Birds reproduce better in smaller fragments, but survive slightly less well there. Poorer reproductive success in large fragments is caused by the Horsfield's bronze-cuckoo *Chrysococcyx basalis*, a specialist brood parasite of fairy-wrens, which cannot persist in small habitat patches. Hence, wrens in small patches suffer no cost of brood parasitism [11].

More importantly, however, their data suggest that habitat connectedness affects individual movements and the establishment of breeding territories. Neighborhood patches with a high degree of connectedness (i.e. pairs of patches where the probability of successful dispersal in random-walk simulations, p, exceeded the average value of 0.4) had high rates of survival from fledging to territory establishment. Movements among such well-connected patches accounted for 91% (89/98) of all movements observed in the study. For example, in one well-connected neighborhood with $p = 0.55$, the observed post-dispersal survivorship was 38.4% (114 of 297 fledglings survived). However, poorly connected fragments (with simulated probability of movement, $p < 0.4$) had significantly lower rates of post-dispersal survivorship. For example, in one poorly connected area, $p = 0.32$, the observed post-dispersal survivorship was only 23.6% (13 of 55 fledglings). The Brookers use these and other parameters to estimate that 4% of individuals die during dispersal in this well-connected neighborhood and 18% die in the poorly connected area. Hence, a smaller fraction of dispersing birds successfully establishes new breeding territories in poorly connected relative to well-connected neighborhoods.

Comparing rates of dispersal, reproduction and survival in the two neighborhood types, the authors estimated that, although all remnants together produce enough yearlings to replace breeder losses, populations in poorly connected neighborhoods experience greater dispersal losses and net population declines (Box 1). Thus, it is the direct effect of fragmentation on bird movements, rather than the effect of fragment size on individual performance within patches, which is the key demographic variable. In other words, connected neighborhoods sustain populations by preventing disperser loss, but the size of patches *per se* is secondary to persistence.

The Brookers' work achieves what conservation biologists have long been seeking: quantitative evidence for the impact of habitat fragmentation on real-world populations. Most other studies have captured only individual components of the effects of fragmentation or measured net rates of dispersal and arrival at isolated habitat patches. For those of us working in landscapes that have been affected by humans (which describes nearly all of us), it is encouraging to see that intensive research in model landscapes can reveal the population dynamic consequences of habitat loss and fragmentation. The Brookers' study also reminds us that reliable conclusions come only from intensive study over several years. They have demonstrated that the way in which a landscape is structured, and the distribution of its habitat patches, affects the persistence of native species.

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Spatial dynamics of measles epidemics

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In a set of three new papers, Grenfell and collaborators lay bare measles dynamics in England and Wales over 50 years. They use a simple mechanistic model and current statistical techniques to analyse records of measles infections in every town and city, and show that measles dynamics, including the spatial spread of the disease, is astonishingly clockwork like, and the underlying processes are remarkably simple.

In the past two decades, population ecology has been developing a rich theoretical structure. However, testing this theory against real systems has proven more difficult. This is nowhere more apparent than in population dynamics in which spatial processes are important, if only because of the need for good data in both space and time. Three new papers on measles, by Bryan Grenfell and his co-workers, show how this can be done [1–3].

A key to the work of this group was Grenfell's earlier realization that the records of measles infections kept since 1944 in every city and town in England and Wales was a unique treasure trove of data. He and his group have since developed and analysed this data base to establish convincingly a mechanistic understanding of the spatial and temporal dynamics of measles. This work builds on a powerful history of measles research exploring spatial geography of infection [4], development of mechanistic models for the epidemiology and control of childhood infections [5–8] and recent forays into their nonlinear dynamics [9–11].

Measles is a highly infectious viral childhood disease. After infection, a latent period of about one week is followed by an infective period also lasting about a week, so the natural time scale of the disease is around two weeks. Before mass vaccination in the UK (1968), almost everyone was infected when first entering school [8,12]. In developed countries, measles is rarely fatal and recovery confers lifelong immunity.

The general pattern of measles dynamics in the UK, and its probable driving mechanisms, were originally modeled in seminal papers by Bartlett [5,6]. In large cities, infection rates undergo enormous cycles, with either annual or biennial peaks induced by the large influx of susceptible children at the start of school year. The disease spreads rapidly through the susceptible population, similar to a forest fire fed by a glut of fuel, then dissipates as the fuel is spent. However, there are always glowing embers in the forest – the disease is endemic (persistent) – because susceptible children are being added continuously at an adequate rate. Epidemics occur in smaller towns (<0.5 million people) when a spark from a nearby large fire (i.e. encounters between a local and an infected city child) ignites a local fire. These flare up but then collapse and often die out for lack of new fuel – measles goes extinct. Epidemics of measles in such towns are therefore sporadic and depend on re-introductions.

The outstanding contribution of Grenfell's group is to test many aspects of a quantitative, mechanistic understanding of the temporal and spatial processes that cause the dynamics just described. They do this by combining simple, but stochastic models, with creative time-series analysis, focused on many years of fortnightly data from towns and cities ranging in population from 10 000 to 3 million. Each of these general approaches has been used to analyse measles dynamics, but they have not been brought to bear in a unified way, and on a data set that so generously rewards this approach.

Bjornstad *et al.* [1] analyse data from 1944–1966, that is, before vaccination. They use a stochastic susceptible–infected–recovered (SIR) model, the time-series SIR (TSIR) model, that predicts the number of new infections during each two-week period on the assumption that infected and susceptible children mix at random. Thus, the expected number infected, λ_{t+1}, during the time interval between t and t+1, is proportional to the rate of encounter between infected (I_t) and susceptible (S_t) children. θ_t is the number of immigrants and B_t is the birth rate, at time t. The simplest deterministic version of the model is:

$$\lambda_{t+1} = \beta_s(I_t + \theta_t)S_t$$
$$S_{t+1} = S_t + B_t - I_{t+1}.$$

The per head transmission rate, β_s, is allowed to vary seasonally, and there is information on how the birth rate, B_t,

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