
Population Dynamics – Session 2

Multi-scale density-dependent dispersal in spatially structured populations

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In spatially structured populations, dispersal is context-dependent and related both to local conditions (within patches) and to the metapopulation as a whole. Density-dependence experienced at different scales likely plays a role in initiating dispersal and determining dispersal success. This multi-scale density-dependence has hitherto received little attention despite its potential to produce spatiotemporally heterogeneous dispersal rates and fundamentally alter predictions about metapopulation dynamics and persistence. We developed a spatially explicit metapopulation model to quantify dual-scale density-dependence using data from a metapopulation of water voles *Arvicola amphibius* in Assynt North West Scotland where those rodents grow up to 300 g, live in small colonies and occupy 8% of the 860 km waterway network with slow flowing water and vegetated banks. Average dispersal was large scale with a colonization halving distance of 4.14 km. The per capita probability that a dispersal event resulted in successful establishment, or prevented extinction via the rescue effect, was higher for juveniles living in source patches with larger population sizes, i.e., consistent with positive local density-dependent emigration, and higher in years when the number of occupied sites in the metapopulation was lowest, i.e., consistent with negative regional density-dependence. In model simulations, multi-scale density-dependent dispersal induced increased variability in metapopulation dynamics and hence increased extinction risk. This was offset by increased dispersal success in low occupancy years. Thus, negative density dependent dispersal at the metapopulation scale partly counters the heavily destabilising impact of positive density dependence at the local scale. We suggest that metapopulations can only persist where those influences counter each other.

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Coupling agent-based with equation-based models to study spatially explicit megapopulation dynamics

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Taking the spatial heterogeneity of real landscapes into account in population dynamics remains extremely difficult. We propose combining equation based modeling (EBM) and agent-based modeling (ABM) to overcome the difficulties classically raised. ABM allows describing entities that act according to specific rules evolving on various scales. However, a large number of entities may lead to computational difficulties (e.g. for populations of small mammals such as voles, that can exceed millions of individuals). Here, EBM handle aged-structured population growth and ABM represents the spreading of voles on large scales. Simulations applied to the spreading of a montane water vole population showed that our hybrid model is quite efficient in representing the reality observed and might help to highlight some key parameters during population expansion. This paves the way for further developments, including the introduction of density-dependent parameters (predation, diseases, etc.) capable of triggering population declines in an explicitly spatial context.

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The Bruce effect revisited: is pregnancy termination in female rodents an adaptation to ensure breeding success after male turnover in low densities?

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Pregnancy termination after encountering a strange male, the Bruce effect, is regarded as a counterstrategy of female mammals towards anticipated infanticide. While confirmed in caged rodent pairs, no verification for the Bruce effect existed from experimental field populations of small rodents. We suggest that the effect may be adaptive for breeding rodent females only under specific conditions related to populations with cyclically fluctuating densities. We investigated the occurrence of delay in birth date after experimental turnover of the breeding male under different population composition in bank voles (*Myodes glareolus*) in large outdoor enclosures: one-male-multiple-females (n=6 populations/18 females), multiple-male-multiple-females (n=15/45), and single-male-single-female (MF treatment, n=74/74). Most delays were observed in the MF treatment after turnover. Parallel we showed in a laboratory experiment (n=205 females), that overwintered and primiparous females, the most abundant cohort during population lows in the increase phase of cyclic rodent populations, were more likely to delay births after turnover of the male than yearborn and multiparous females. Taken together, our results suggest that the Bruce effect may be an adaptive breeding strategy for rodent females in cyclic populations specifically at low densities in the increase phase. Then isolated, overwintered animals associate in MF pairs. During population lows infanticide risk and inbreeding risk may then be higher than during population highs, while also the fitness value of a litter in an increasing population is higher. Therefore, the Bruce effect may be adaptive for females during annual population lows in the increase phases, even at the costs of delaying reproduction.

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The long-haired rat (*Rattus villosissimus*): an ecosystem disrupter in arid Australia

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Species in the genus *Rattus* are well-known as pests in agricultural systems. In natural ecosystems they can have strong top-down effects on vegetation through seed predation and seedling herbivory. However, the broad ecosystem impacts of population outbreaks of *Rattus* species are not well understood. We examined this issue for the long-haired rat (*Rattus villosissimus*) in a region of arid Australia with highly unpredictable rainfall. The species is the largest extant rodent in arid Australia (body mass: 150 g). The long-haired rat is not resident in the study area in the western Simpson Desert, rather population outbreaks occur every 25-30 years. We sought to describe and assess the full range of ecological interactions that occurred during a population outbreak that ran from June 2010 to December 2012. The long-haired rat outbreak resulted in a series of novel ecological interactions; these interactions had not been observed during the periods when the rat was not present. The interactions that were observed included; 1) long-haired rat predation on smaller mammals (body mass <100 g) especially other rodents; 2) invasion by the rats in to refuge habitat of the nationally vulnerable plains mouse (*Pseudomys australis*), and 3) feeding and associated damage to the nationally vulnerable keystone tree species *Acacia peuce*. In addition, long-haired rat burrow construction resulted in large volumes of soil redistribution and the presence of rats produced a spike in rodent biomass that was over twice that during irruptions where the rat was absent. The sporadic occurrence of the long-haired rat and the intensity and spatial scale of the novel interactions indicate that it can be considered a disruptive factor in the functioning of the Simpson Desert ecosystem.

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The role of food availability in life history traits and population dynamics of the edible dormouse (*Glis glis*) in pine dominated forest

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The distribution and the predictability of food resources are important ecological factors influencing reproduction and life history tactics of many animal species. It is especially important for specialized seed predators like the edible dormouse, which can skip reproduction in years with low seed availability. Whereas the majority of studies were conducted in beech or oak dominated forests the present study was conducted in pine forest, with Scots pine (*Pinus sylvestris*) as the dominant tree species (above 90%). In a field experiment we tested the hypothesis that the presence of high caloric food from spring to autumn affects life history tactics and population dynamics of dormouse. Therefore, in years 2014 – 2016 on two experimental plots, we provided hazelnuts as a supplementary food from spring to autumn, whereas two other study plots remained without any additional food as control plots. Supplemental feeding did not affect reproduction, body condition nor population dynamics of dormice. Moreover, we did not observe differences in number of offspring or their sex ratio. However, in one year (2015) additional food elevated body mass of adult females but in next year (2016) it caused the weight loss of females. This illustrates that high-calorie food in itself may not be the only factor responsible for the condition of individuals, their reproduction and population dynamics in this rodent species, contrary to other studies. Additionally, during the autumn time, we discovered that additional food decreased relatedness between dormice which shared the same nestbox, which indicates that increased food availability reduced the competition among individuals during the autumn period.

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Does anticipatory reproduction exist?

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Anticipatory reproduction is the controversial mechanism of population regulation by which the animal reproduces before the actual ripening of its main forage and the juveniles begin independent feeding during the period of maximal food abundance. The primary object in studies of such mechanisms is the edible dormouse (*Glis glis* L., 1766). The intensity of its reproduction is regulated according to two different principles: in the species' optimum range the changes in reproductive activity of males play the main role, and in the peripheral population of the Zhiguli Mountains, reproductive regulation occurs through mass embryonic resorption in females. In 2016–2017, studies of the species' reproduction were conducted in the Zhiguli population. For comparison, in 2017 a study of reproduction of the yellow-necked mouse (*Apodemus flavicollis*, Melchior, 1834) was realized. It was found that mating of the dormouse begins long before the growth of acorns. At the beginning of their maturation, the vast majority of dormice females are already pregnant. The resorption or birth of juveniles depends on the proportion of green acorns in female nutrition during the period of gestation. In the yellow-necked mouse at the very beginning of acorn growth oestrus occurs, and during the ripening of acorns the entire reproduction cycle from the mating to the reaching of puberty by the young is observed. In both species, by the time the acorns are completely ripe and fall, the juveniles become independent. Thus, at least in two species anticipatory reproduction in oak communities consists of rodents feeding on immature seeds during pregnancy and lactation, eliminating a delay between forage yield and rodent reproduction. Mechanisms similar to anticipatory reproduction can most likely be found in animals under two conditions: a long life cycle and reproduction that depends on the limited period of availability of the main forage.

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Small mammals in montane forests: not where, but when?

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Community dynamics is a well documented topic concerning the ecology of small mammals, but very few studies have focused simultaneously on its temporal and elevational patterns. Here we report the multiannual dynamics of small mammal communities along an elevational gradient in relation to the habitat characteristics. During a five-year faunistic inventory in Retezat National Park, Romania we live-trapped small mammals in different forested and shrubby habitats at elevations between 770 m and 2,080 m. Because small mammal communities in mountains face more severe climatical and habitat-related limiting factors, we hypothesized that: 1. these communities undergo significant year-to-year changes; 2. elevation interferes with the patterns of community dynamics; 3. the effect of habitat selection is eclipsed by the temporal changes. We used ANOVA and partial constrained multivariate analysis with habitat factors, year, elevation, and their interaction as predictors and trapping site as covariate. All community metrics differed significantly among years. Species composition was predicted not only by year but also by its interaction with elevation, but not by elevation itself. The elevational pattern of the community dynamics shifted direction each year. The dominant rodent species, *Myodes glareolus* and *Apodemus flavicollis* showed opposite patterns, possibly as a strategy to avoid competition. Overall, their abundances were negatively correlated. Moisture, human disturbance and proportion of the conifers in the canopy were best predictors of species composition, but the variation explained was lower than that caused by the yearly changes. Human impact on montane habitats is currently increasing because of forest exploitation and the global warming will lead to decreased moisture and cover of conifers. Thus, the further study of the interaction of these habitat changes with the time is important in order to understand and predict their synergistic effects on small mammal communities, their mechanisms and consequences.

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Breeding versus survival: proximal causes of abrupt population decline under environmental change in a desert rodent

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The population dynamics of a desert-dwelling psammophilous rodent (the midday gerbil, *Meriones meridianus*) was shown to exhibit delayed step transition from the high-(1994-2002) to low-abundance (2003-2017) regime in response to gradual landscape change from desert to steppe caused by the drastic reduction of livestock in the rangelands of southern Russia after the collapse of the USSR in the early 1990s. We tested whether breeding and demographic parameters were correlated with the observed abrupt downward population shift. We found that reproductive activity (the percentage of breeding females, the number of litters per female, fecundity) did not vary with time or population regime. The number of young recruited per female also showed no trend, did not differ between periods of high and low population abundance, and did not depend on reproductive activity, suggesting that recruitment rate is determined by survival rather than reproduction. The only parameter that significantly varied with time and differed between periods was the sex ratio among mature individuals (SR=males:females) – it decreased with time and was as much as twice more female-biased during the period of low population abundance. However, SR was not related to any reproductive parameter, including the percentage of breeding females. We conclude that proximate reasons for abrupt population decline are not associated with the changes in breeding patterns or mate limitation caused by the Allee effect as was suggested (Tchabovsky et al. 2016), but relate to the increased mortality in the desert landscape fragmented by steppeization, which is expected to be higher for males as the mobile and the dispersing sex. (RFBR 16-04-00739)

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Habitat preferences and spatial distribution of lemmings in western Taimyr

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The lemmings in the Arctic tundra north of 73 °N have received little attention, because this region is remote and difficult to access. Habitat use and spatial distribution of two species of lemmings – Siberian lemming (*Lemmus sibiricus*) and collared lemming (*Dicrostonyx torquatus*), were studied during nine summer field seasons (June-August) in 1993-1995, 2002 and 2004-2008 at the west coast of Taimyr peninsula in the delta of the river Pyasina (74°10' N, 86°45' E). Lemmings were captured by three different methods: by snap-traps along permanent lines and in plots in the main types of habitats and by live-traps on a permanent plot in the dominant habitat types. We caught 492 Siberian and 73 collared lemmings. Snap-trap line surveys showed that each of the two species had its own preferred habitat. For Siberian lemming, it was the grass-sedge marshy tundra and rocks or stony fields with lichen-moss vegetation, for collared lemming it was the rubble polygonal dwarf-willow tundra. On the other hand, the plant community preferences partly coincided in the two species: both lemmings had a high abundance in the dominant plant community - polygonal-hummocky tundra. Habitat distribution of Siberian lemmings was considerably wider than that of collared lemmings. *Lemmus sibiricus* had a significantly wider spatial-ecological niche, measured as Simpson's index of habitat diversity. When both species coexisted on the same plot, Siberian lemmings were ousted into the moister habitats with a moss-sedge type plant cover. The spatial distribution of lemmings was patchier when the habitat diversity increased. The home range size decreased when the population density increased.

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The linkage between *Melocanna* bamboo flowering and rodent outbreaks: an empirical study from Chittagong Hill Tracts of Bangladesh

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In 2006 to 2010 rodent population outbreaks resultant from the 50-year cycle of bamboo flowering were reported in Mizoram, India, the Chittagong Hill Tracts, Bangladesh, and Chin State, Myanmar. The ecological dynamics between rodent population outbreaks and bamboo flowering were studied in Ruma Upazila of Bandarban district. Small mammal trapping (March 2009 to December 2011) in the villages of Basatlang, Munlai, Mualpi and Neweden was carried out to understand the dynamics of rodent populations in different habitats. The highest percentage of rodent species was captured at community households, followed by bamboo forests, crop fields and outside around villages. Ecological survey of bamboo flowering and bamboo seed fall in 2009 found that there were differences in partially rodent eaten seeds per square meter by month ($p=0.0001$) and a positive correlation between seed fall and partially eaten seeds ($r = 0.611$). In 2010 there was a positive correlation ($r = 0.417$) between seed fall and the number of rodent damaged seeds in response to cut, burned and normal bamboo forest. The study confirms that massive bamboo seed fall increases food availability for rodents, rodents do indeed eat bamboo seeds and the extended availability of seed leads to population outbreaks. Particularly *Rattus rattus* was able to breed for 4-5 months in the forest with animals migrating out in to farmers' fields as the bamboo seed germinated, causing crop losses of 80-100%. Shortening the time of rodent breeding was possible by cutting and/or burning the bamboo forest at the time of flower initiation as this led to a significant delay in seed production. Implementing large scale bamboo clearance could help prevent the development of population outbreaks or reduce their severity. Although farmers did not feel competent or knowledgeable about rodent management, their main coping strategy of planting earlier ripening rice crops in order to harvest before rodent outbreaks develop, is a sound strategy that should be encouraged during outbreak years. Research on increasing the yield of earlier ripening crops could help manage food insecurity during rodent outbreaks.

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Population dynamics and breeding patterns of multimammate rat (*Mastomys natalensi*, Smith 1832) in semi-arid areas in Tanzania

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The population dynamics and breeding patterns of Multimammate rat (*Mastomys natalensis* Smith 1834) in maize agro-ecosystems in semi-arid areas in Tanzania was investigated from March 2016 to February 2018 in the maize fields and fallow land. A capture mark release study was carried out with four 70 x 70 m grids and set at farmers' fields using live-trapping at a distance of 10 x 10 m apart for three consecutive nights. Rodent species captured were: *Mastomys natalensis*, *Lemniscomys rosalia*, *Lemniscomys zebra*, *Gerbilliscus vicinus*, *Pelomys fallax*, *Arvicanthis neumani*, *Thallomys paedulus* and *Acomys wilsoni*. *Mastomys natalensis* was the most abundant (>93%) of all species captured while other were in low number in both habitats. The highest population was observed from June to October indicating that was probably due to the influx of juveniles into the population. It was observed that the study area experiences a short rainfall season with extended breeding patterns for *Mastomys natalensis*. However, the highest percentage of reproductively active animals was found during April and the lowest level in September and October. We concluded that most females *Mastomys natalensis* are reproductively active when there is enough food and rainfall. It is recommended that there will be necessary to reduce breeding activity by preventing access to fresh vegetative food such as young sprouting grass.

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Effects of stream proximity on trails of *Cuniculus paca*: a 20 year survey

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The Paca (*Cuniculus paca*), found from Mexico to Brazil and Paraguay, is one of the largest rodents in the world (5-14 kg). The species is hunted for its valued meat throughout its distribution area. Pacas use burrows that have multiple entrances and exits, with at least one leading to a water source. The latter is used both to escape from predators as well as in reproductive behavior. Given the foregoing, the density of pacas and their trails should therefore theoretically be higher nearer sources of water. We walked a trail leading away from a stream and recorded the number of paca trails at 50 m intervals for 600 m, and every 10 m along an elevation gradient. This count was conducted over the span of 20 years (1997–2017), at the Alberto Manuel Brenes Biological Reserve, San Ramón, Costa Rica, specifically along the Palmito trail (10° 13.14 N, 84° 35.79 W). The number of paca trails decreased with distance from water in 2017 ($y = -0.024x + 7$, $R^2 = 0.82$). We found seven trails at 50 m from water, five at 100 m and three at 150 m. Besides that we found only one additional trail, 250 m from water. The relationship between trail number and elevation was also significant, but not as strong ($y = -0.018x + 17.67$, $R^2 = 0.44$). There is therefore a clear relationship between distance from water and elevation at the site. The highest distances from water were found in 2007 and the largest number of trails in 2010 (10 trails at 50 m). The smallest number of trails was found in 2005, all within 200 m of water. The pattern has been consistent throughout the years: the number of paca trails always is greatest nearer the stream, although numbers and distances varied, perhaps due to climatic factors.

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It's a trap: effective methods for monitoring mouse populations in Australia

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Feral house mice cause substantial economic damage to grain crops in Australia, particularly during house mouse plagues. Populations are monitored to detect changes in abundance and to use in models to forecast likely mouse outbreaks. However, it is not possible to use live-trapping (the "gold standard") for assessing mouse abundance at a large number of monitoring sites spread across southern and eastern Australia. A range of alternative methods was tried to assist the grains industry with strategic decisions to reduce crop damage. The aim of this work is to determine which survey methods could provide useful, affordable information across a large area. Monitoring of mouse populations was conducted at representative grain farms using (1) live trapping at long-term ("benchmark" sites (n=3), (2) mouse chew cards and active burrow counts (n=110 farms), and (3) qualitative information networks with growers, grower groups and advisors (n=12 regions). Monitoring was conducted over 5 years through low, medium and high abundance conditions. Live trapping provided the most useful, but most expensive, information. There was wide variability in chew card and active burrow counts much of which was unlikely to be due to differences in mouse abundance. When alternative food was abundant, mice did not use chew cards. When crop biomass was high, it was difficult to detect active burrows. Live trapping supplemented with data from chew cards and active burrows remains the best approach to monitor a wide range of sites. We are now exploring development of automated recording systems to signal changes in mouse activity in fields. These systems will need to be compared against data from live trapping sites over a range of conditions. It is likely that live-trapping will need to be used for the foreseeable future to provide useful information such as breeding condition and population abundance, required for the forecast models.

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Study on the evolutionary ecology of small herbivorous mammals: life history strategy of plateau pika (*Ochotona curzoniae*)

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Life history research lies at the heart of evolutionary ecology. It studies the complex relationships in the living process, which can help us understand the evolution theory and analyze and predict population dynamics. After studying life history of plateau pika, an endemic herbivorous small mammal habituating in the Qinghai-Tibet Plateau, the following results are reported: 1. General life history features of plateau pika. 2. The similarities and differences of life history features between plateau pika and boreal pika. 3. Survival features of plateau pika in life history 4. Reproductive features of plateau pika 5. The body growth rule of plateau pika and its growth model. The growth model of juveniles is: $dm/dt=6.5266 \cdot m^{0.75} - 12.1787 \cdot m$. 6. Trade-off between life history features. 7. The fitness level of plateau pika in Mammalia. A life history feature table and a life history strategy analysis table of 65 mammal species belonging to 9 Order have been compiled according to their life table data, among which the fitness indexes of 46 species have been calculated. The fitness index of plateau pika is ranked 43rd, only higher than those of bank vole (*Myodes glareolus*), chimpanzee (*Pan troglodytes*) and African elephant (*Loxodonta africana*). The fitness index of plateau pika ($r=0.1125$) was lower than that of boreal pika (*Ochotona princeps*) ($r=2.172$). The survival rate is the main factor influencing fitness. 8. The dynamics of plateau pika population. The density of plateau pika population in three years was calculated with a computer program compiled in Turbo C language, according to Jolly-Seber method. The dynamics of plateau pika population was coincident with the low intrinsic population growth rate ($r=0.1125$), i.e. plateau pika population was stable.