

# Key talks from the Biomove Symposium 2018

## Session 1: From individuality to biodiversity

### **Keynote: Individual variation in dispersal: Key to eco-evolutionary dynamics in populations and communities**

**Dries Bonte, *University of Ghent***

#### **Movement ecology as a field**

See for a broad introduction in the literature: Chesson (2000), Nathan *et al.* (2008), Jeltsch *et al.* (2013). Movement is a behaviour within the scope of Tinbergen's Four Questions. It is hierarchically structured, and links habitat patches, and is important in understanding population processes. Behaviour including movement is assumed to be optimal — leading to the question, what are the fitness consequences of movement? For example, Salguero-Gómez *et al.* (2016) show that plant traits and dispersal are related, with evidence for bet-hedging. See also Clobert *et al.* (2009), Bonte and Doherty (2017).

#### **The evolution of dispersal in meta-populations**

Related work is to be found in Van Belleghem *et al.* (2015), Hanski and Mononen (2011), I. and Hanski (2009), and Bonte *et al.* (2014); all asking the question of whether dispersal has fitness benefits, especially in fragmented landscapes. For more work see Cheptou *et al.* (2017). In experimental evolution, the question is, how does evolution in dispersal evolve? See Fronhofer *et al.* (2014). The result is that dispersal itself doesn't evolve, but other traits do; see De Roissart *et al.* (2016) for a study with three different simulated landscapes.

#### **Evolution at range fronts**

See Van Petegem *et al.* (2018), Van Petegem *et al.* (2016) for an overview of conditional dispersal. What feedbacks might we expect in such populations? Pardikes *et al.* (2017), Tack *et al.* (2015), and Hillaert *et al.* (2018) provide interesting reading related to informed and un-informed movement, which is related to the predictability of a landscape. One general idea is that reshuffling in a population kills evolution, or leads to a loss of information (i.e., a loss of informed individuals). Work related to this is found in Bonte and Bafort (2018).

## **Talks**

### **What's your move? Movement as a link between personality and spatial dynamics in animal populations**

**Orr Spiegel, *Tel Aviv University***

Speaking about the link between movement, personality, and evolution. A central assumption in animal movement and telemetry has been that all individuals of a species are essentially 'clones', or identical, but individuals matter. Personalities or behavioural types are often sub-optimal as plasticity is limited (Sih *et al.* 2004; see Lloyd-Smith *et al.* 2005; Réale *et al.* 2007, 2010; Dingemanse and Wolf 2010; Korsten *et al.* 2013). Why do individuals differ? Three possible causes: 1. Method — how you measure matters, 2. Proximate mechanisms, and 3. Ultimate mechanisms.

Animal search can be a behaviour and evolve a reaction norm. The intensity of local search can be a response to the clumpedness of resources, and behavioural type should determine habitat preferences. This can be tested with a simulation model of biased correlated random walk agents, in which the only difference between agents foraging in a landscape with clumped resources is 'giving-up time'. This affects home range size and structure. This can also be captured by a social network, such as a proximity based social network from tracking data. When resources are uniformly distributed, 'slow' (*meant as with high giving up time; in knots we could think of these as less exploratory - prg*) individuals are likely to interact very little with other 'slow' individuals, while fast individuals would move more and thus have higher sociality scores (*edge weights in a social network*). The opposite is likely in a scenario with more clumped patches (see Duckworth and Badyaev 2007; Aplin *et al.* 2013). Variation in the environment (variability, clumpedness) determines which neighbours an individual ends up with. Knowing the system well is imperative to determine the sensitivity of social networks to distance, and make reasonable assumptions about interactions/sociality. Null model testing of social networks is important (Farine and Whitehead 2015; Farine 2017).

## **Spatially structured trait variation between individuals may lead to biodiversity in heterogeneous, disturbed environments**

**Thomas Banitz, UFZ Leipzig**

Individual differences may be thought of as intra-specific trait variation (ITV) (Bolnick *et al.* 2011; Moran *et al.* 2016; Hart *et al.* 2016), and ITV can be structured or unstructured. Spatial structure of ITVS can be studied using a spatially explicit IBM. If there is no structure to ITV, trait values differ between species, or if they are the same between species, they change at different values. In a structured ITV scenario, disturbances of different kinds may be responsible (recurrent, non-random, or clumped). Clumped disturbances may allow species co-existence via dispersal differences see Banitz *et al.* (2008); *somewhat unclear talk - prg*.

## **Quantifying animal personalities from movement data: Repeatable among individual variation in wildlife studies**

**Anne Hertel, BiKF Senckenberg**

Behavioural types in populations can lead to individuals consistently selecting for certain habitat types. Using a definition of personality as repeatable among individual variation, a number of behavioural types can combine, and evolve non-independently, to form a behavioural syndrome. Quantifying personality in an animal population is difficult, especially in post-hoc studies.

42 female brown bears in Sweden were tracked over 1 – 7 years, and linear mixed models were used to separately relate different behavioural traits using the simple form behaviour ~ fixed effect + random effect (bear identity, year). Repeatability was quantified as  $r = (\text{variance among individuals}) \div (\text{variance among individuals} + \text{variance among years} + \text{residual variance})$ . The R package rptR provides confidence intervals for random effects. Syndromes were difficult to identify from this procedure, but there was a gradient of behavioural types which reflected human tolerance (Leclerc *et al.* 2016; Hertel *et al.* 2017).

## **Fencing solves human-wildlife conflict locally but shifts problems elsewhere: Modelling seasonal landscape connectivity for African elephants**

**Niko Balkenhol, University of Göttingen**

Landscape resistance is an important concept in movement ecology Zeller *et al.* (2012), and step selection functions can help quantify resistance from tracking data, using the method  $\text{resistance} = 1 \div \text{step selection probability}$ . 14 elephants (10 males, 4 females) were tracked at four hour intervals in the Greater Amboseli system over two years. Landscape resistance can either be averaged using a single value from a population-level step selection function, or take into account individual variability and seasonal effects by running individual and/or seasonal step selection function models and weighing the step selection probability of each point in the landscape by distance to the individual's home range centre.

This results in the finding that not all predictors matter to all individuals. The averaged resistance method and the individual variability method predict very different resistances (Osipova *et al.* 2018a, see 2018b).

## Session 3: Animal movement across scales

### Keynote: Animal movement across scales and the existence of syndromic guilds

Wayne Getz, *University of California, Berkeley*

#### The components of movement

The scales of structures and processes in animal movement are not well understood except for a few cases, such as the movement of the horse (*horses have five distinct movement modes, stationary, walk, trot, canter, gallop, that were only fully characterised after the advent of film cameras - prg*). Movement can be thought of as being made up of 'fundamental movement elements (FMEs)', a series of steps which can be scaled up to form a 'canonical activity mode (CAM)'. These FMEs and CAMs are best measured using accelerometer data for different parts of animal bodies in motion to characterise speed and other movement variables. FMEs can be scaled down to their individual mechanistic components, such as a single wingbeat, or other discrete action. Such subFME strings can be identified in accelerometer data, and scaled up to FME strings, which form recognisable movement patterns (such as flight). CAMs are typically one level higher, and comprise such behaviours as grooming, dispersal, translocation. 'Syndromic movement types (SMTs)' are made up of a mix of CAMs that identify a behavioural type at one or more (and possibly ever increasing) temporal scales.

#### Questions in movement

Questions in movement are scale-dependent. At the FME scale, questions focus on mechanism, such as mechanical efficiency or physiological processes. At the CAM scale, movement questions should focus on movement syndromes (Sih *et al.* 2004), where a movement syndrome is a suite of correlated movement patterns in one or more ecological contexts. Movement syndromes can be integrative, and can be continuous or discrete as variables. Classifying movement modes from tracking data can be done in a number of ways (Wittemyer *et al.* 2008; Patterson *et al.* 2009; see Nathan *et al.* 2012; Cizauskas *et al.* 2015; Gurarie *et al.* 2016; Abrahms *et al.* 2017) at different scales. This classification can then be used to answer questions arising from variation in animal phenotypes.

#### Syndromic guilds

In a 3 strategy movement model, three types emerge —  $\rho$ , which has a movement threshold based on local resource depletion ('tactical movement'),  $\alpha$ , which moves to avoid competition ('strategic movement'), and  $\delta$ , which is a mix of 'tactical' and 'strategic' movement types. Syndromic guilds with association based on movement types emerge in this model with otherwise identical agents. Introducing sex as a degree of freedom results in assortative mating (Getz *et al.* 2016), and this may be similar to previously known assortative mating based on 'magic' genes (eg. MHC). *Three questions were asked but not clearly answered: 1. Do movement strategies co-exist, or does the population converge on to one strategy in the model? 2. Is the movement type phenotypically plastic? 3. What would happen if a movement type were artificially removed from the model population, how would space use across the landscape change? - prg*

# References

- Abrahms B, Seidel DP, and Dougherty E *et al.* 2017. Suite of simple metrics reveals common movement syndromes across vertebrate taxa. *Movement Ecology* **5**: 12.
- Aplin LM, Farine DR, and Morand-Ferron J *et al.* 2013. Individual personalities predict social behaviour in wild networks of great tits (*Parus major*) (A Sih, Ed). *Ecology Letters* **16**: 1365–72.
- Banitz T, Huth A, Grimm V, and Johst K. 2008. Clumped versus scattered: how does the spatial correlation of disturbance events affect biodiversity? *Theoretical Ecology* **1**: 231–40.
- Bolnick DI, Amarasekare P, and Araújo MS *et al.* 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology & Evolution* **26**: 183–92.
- Bonte D and Bafort Q. 2018. The importance and adaptive value of life history evolution for metapopulation dynamics. *bioRxiv*: 179234.
- Bonte D and Dahirel M. 2017. Dispersal: a central and independent trait in life history. *Oikos* **126**: 472–9.
- Bonte D, De Roissart A, Wybouw N, and Van Leeuwen T. 2014. Fitness maximization by dispersal: evidence from an invasion experiment. *Ecology* **95**: 3104–11.
- Cheptou P-O, Hargreaves AL, Bonte D, and Jacquemyn H. 2017. Adaptation to fragmentation: evolutionary dynamics driven by human influences. *Philosophical transactions of the Royal Society of London Series B, Biological sciences* **372**: 20160037.
- Chesson P. 2000. Mechanisms of Maintenance of Species Diversity. *Annual Review of Ecology and Systematics* **31**: 343–66.
- Cizauskas CA, Turner WC, Pitts N, and Getz WM. 2015. Seasonal Patterns of Hormones, Macroparasites, and Microparasites in Wild African Ungulates: The Interplay among Stress, Reproduction, and Disease (S Sreevatsan, Ed). *PLOS ONE* **10**: e0120800.
- Clobert J, Le Galliard J-F, and Cote J *et al.* 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* **12**: 197–209.
- De Roissart A, Wybouw N, and Renault D *et al.* 2016. Life-history evolution in response to changes in metapopulation structure in an arthropod herbivore (M Pfrender, Ed). *Functional Ecology* **30**: 1408–17.
- Dingemanse NJ and Wolf M. 2010. Recent models for adaptive personality differences: a review. *Philosophical transactions of the Royal Society of London Series B, Biological sciences* **365**: 3947–58.
- Duckworth RA and Badyaev AV. 2007. Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America* **104**: 15017–22.
- Farine DR. 2017. A guide to null models for animal social network analysis (R Freckleton and S Rands, Eds). *Methods in Ecology and Evolution* **8**: 1309–20.
- Farine DR and Whitehead H. 2015. Constructing, conducting and interpreting animal social network analysis (S Altizer, Ed). *Journal of Animal Ecology* **84**: 1144–63.
- Fronhofer EA, Stelz JM, and Lutz E *et al.* 2014. Spatially correlated extinctions select for less emigration but larger dispersal distances in the spider mite *Tetranychus urticae*. *Evolution* **68**: 1838–44.
- Getz WM, Salter R, Seidel DP, and Hooft P van. 2016. Sympatric speciation in structureless environments. *BMC Evolutionary Biology* **16**: 50.
- Gurarie E, Bracis C, and Delgado M *et al.* 2016. What is the animal doing? Tools for exploring behavioural structure in animal movements (L Börger, Ed). *Journal of Animal Ecology* **85**: 69–84.
- Hanski I and Mononen T. 2011. Eco-evolutionary dynamics of dispersal in spatially heterogeneous environments. *Ecology Letters* **14**: 1025–34.
- Hart SP, Schreiber SJ, and Levine JM. 2016. How variation between individuals affects species coexistence (T Coulson, Ed). *Ecology Letters* **19**: 825–38.
- Hertel AG, Swenson JE, and Bischof R. 2017. A case for considering individual variation in diel activity patterns (A Lindholm, Ed). *Behavioral Ecology* **28**: 1524–31.
- Hillaert J, Hovestadt T, Vandegehuchte ML, and Bonte D. 2018. Size-dependent movement explains why bigger is better in fragmented landscapes. *bioRxiv*: 264861.
- I. K and Hanski I. 2009. Heritability of and strong single gene (*Pgi*) effects on life-history traits in the Glanville fritillary butterfly. *Journal of Evolutionary Biology* **22**: 1944–53.
- Jeltsch F, Bonte D, and Pe'er G *et al.* 2013. Integrating movement ecology with biodiversity research - exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology* **1**: 6.
- Korsten P, Overveld T van, Adriaansen F, and Matthysen E. 2013. Genetic integration of local dispersal and exploratory behaviour in a wild bird. *Nature Communications* **4**: 2362.
- Leclerc M, Vander Wal E, and Zedrosser A *et al.* 2016. Quantifying consistent individual differences in habitat selection. *Oecologia* **180**: 697–705.
- Lloyd-Smith JO, Schreiber SJ, Kopp PE, and Getz WM. 2005. Superspreading and the effect of individual variation on disease emergence. *Nature* **438**: 355–9.
- Moran EV, Hartig F, and Bell DM. 2016. Intraspecific trait variation across scales: implications for understanding global change responses. *Global Change Biology* **22**: 137–50.
- Nathan R, Getz WM, and Revilla E *et al.* 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences of the United States of America* **105**: 19052–9.
- Nathan R, Spiegel O, and Fortmann-Roe S *et al.* 2012. Using tri-axial acceleration data to identify behavioral modes of free-ranging animals: general concepts and tools illustrated for griffon vultures. *The Journal of Experimental Biology* **215**: 986 LP–996.
- Osipova L, Okello MM, and Njumbi SJ *et al.* 2018a. Using step-selection functions to model landscape connectivity for African elephants: accounting for variability across individuals and seasons. *Animal Conservation*.
- Osipova L, Okello MM, and Njumbi SJ *et al.* 2018b. Fencing solves human-wildlife conflict locally but shifts problems elsewhere: A case study using functional connectivity modelling of the African elephant (M Struebig, Ed). *Journal of Applied Ecology* **55**: 2673–84.
- Pardikes NA, Harrison JG, Shapiro AM, and Forister ML. 2017. Synchronous population dynamics in California butterflies explained by climatic forcing. *Royal Society Open Science* **4**: 170190.
- Patterson TA, Basson M, Bravington MV, and Gunn JS. 2009. Classifying movement behaviour in relation to environmental conditions using hidden Markov models. *Journal of Animal Ecology* **78**: 1113–23.
- Réale D, Garant D, and Humphries MM *et al.* 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical transactions of the Royal Society of London Series B, Biological sciences* **365**: 4051–63.
- Réale D, Reader SM, and Sol D *et al.* 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* **82**: 291–318.
- Salguero-Gómez R, Jones OR, and Jongejans E *et al.* 2016. Fast-slow continuum and reproductive strategies structure plant life-history variation worldwide. *Proceedings of the National Academy of Sciences of the United States of America* **113**: 230–5.
- Sih A, Bell A, and Johnson J. 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution* **19**: 372–8.
- Tack AJM, Mononen T, and Hanski I. 2015. Increasing frequency of low summer precipitation synchronizes dynamics and compromises metapopulation stability in the Glanville fritillary butterfly. *Proceedings Biological sciences* **282**: 20150173.
- Van Belleghem SM, Roelofs D, and Hendrickx F. 2015. Evolutionary history of a dispersal-associated locus across sympatric and allopatric divergent populations of a wing-polymorphic beetle across Atlantic Europe. *Molecular Ecology* **24**: 890–908.
- Van Petegem KHP, Boeye J, Stoks R, and Bonte D. 2016. Spatial Selection and Local Adaptation Jointly Shape Life-History Evolution during Range Expansion. *The American naturalist* **188**: 485–98.
- Van Petegem K, Moerman F, and Dahirel M *et al.* 2018. Kin competition accelerates experimental range expansion in an arthropod herbivore (T Coulson, Ed). *Ecology Letters* **21**: 225–34.
- Wittmeyer G, Polansky L, Douglas-Hamilton I, and Getz WM. 2008. Disentangling the effects of forage, social rank, and risk on movement autocorrelation of elephants using Fourier and wavelet analyses. *Proceedings of the National Academy of Sciences of the United States of America* **105**: 19108–13.
- Zeller KA, McGarigal K, and Whiteley AR. 2012. Estimating landscape resistance to movement: a review. *Landscape Ecology* **27**: 777–97.