

Twenty-two years a 'chair group': Guiding doctoral work between 1991 and 2013

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Much of my work as professor at Wageningen University has centred on supervising post-graduate students. In the fall of 2012, the seventy-fifth Ph.D. thesis was finished in my care was publicly defended (see attached list), and many other doctoral students are currently working on their thesis. Nearly all these beautifully produced theses fitted into an overall research plan aimed at understanding the ultimate questions in animal ecology, namely what determines the abundance and distribution of species.

We have concentrated on large herbivores, their food and the biotopes in which they live because of their impact on the landscape, the exciting feedbacks between vegetation and herbivores, and finally because of the potential for the use of knowledge on physiology and genetics gained from domestic livestock. But recently we worked more and more on the genetics of mammals and birds because modern genetics can answer questions that we only could dream about twenty years ago.

It should be noted that four dissertations do not follow a particular plan. *Franck Sterck* (1997 – the years mentioned refer to the year that the doctoral thesis was publicly defended) was supervised by me, with pleasure, because the Chair in forestry was vacant, while *Daan Vreugdenhil* (2003), *Fabio Corsi* (2004) and *Christiaan van der Hoeven* (2007) worked on theses that are of importance mainly for the practice of nature conservation planning. Such work is of importance, but conservation planning has never been a field that I wanted to develop in Wageningen. *Ton van der Have's* thesis (2008) on insects also did not fit a theme.

The first group of dissertations is about “understanding gains and losses of energy and nutrients in large herbivores”. Supervising in the present group started with the thesis of *Michiel WallisDeVries* (1994). He found that the performance of free-ranging large ruminants to a large extent could be understood if forage digestibility and nutrient concentrations are known. Apart from nitrogen, it appears as if phosphorus is much more important than we thought. *Sip van Wieren* (1996) took this further by comparing ruminants to hind-gut fermenters, such as horses, while *Hans de Jongh* (1996) included the marine dugong into the comparison. The simple-stomach dugong's behaviour can best be understood through the concentration and distribution of starch-rich food, and as rule it can be concluded that the key to comprehend decisions by herbivores is to understand the rate at which they acquire energy. In ruminants, this is the rate at which cell wall is

digested, which in its turn is often limited by the amount of nitrogen available for microbial breakdown, but in non-ruminants the rate at which energy becomes available is more directly associated with the rate at which soluble or non-soluble sources of sugar become available. Van Wieren worked closely with the Animal Husbandry Department at Wageningen, enabling proper experimentation. For free-ranging animals, most of the animal ecologists in our group would habitually have used optimal foraging theory and simple functional response curves to understand intake rate or energy acquisition rate, but our work on the exact relation between intake rate and vegetation shows the significance of fine-scale vegetation structure (*Michael Drescher* 2003). For this we used an experimental setup, habituated animals and close-up filming.

This we have taken further by looking into the exact relationship between body mass and functional response. *Nicol Heuermann* (2007) used close-up observations of differently-sized Canada geese, as did *Jasja Dekker* (2007) with domestic rabbits of different body masses. We then started research into energy expenditure (instead of energy acquisition) by large herbivores to further fill in the picture. In a landscape context, this entail developing images of so-called ‘thermal landscapes’ and experimentation with life-size models and studying how animals move in such landscape, as we studied with African elephant in the research of *Henjo de Knegt* (2010) and further developed by inserting thermologgers in African antelopes *Anil Shrestha* (2012).

The second line of research deals with the issue how and why food for herbivores is distributed over the landscape and how this affects the distribution of herbivores. Herbivores do not only make use of the uneven distribution of the food (*Michiel WallisDeVries* 1994), they also impact on that distribution. At first, we adhered to the traditional way of thinking that ‘vegetation succession’ can be retarded, or perhaps even reversed by herbivory, so we concentrated on traditional vegetation succession theory (*Frans Vera* 1997), but then we started realising that this impact proves to be much more complicated than we first believed, and we developed mathematical models to show that catastrophic behaviour may be typical of vegetation-grazing systems (*Max Rietkerk* 1998), which we then tested experimentally with four post-docs in the FLARE-programme (*Max Rietkerk, Frank van Langevelde, Johan van de Koppel and Lalit Kumar* in 2000 – 2002). We soon realised that fire may act as a ‘super-herbivore’, so we included this into the research programme (*Claudius van de Vijver* 1999). We tested the relation between fire and vegetation patterning in the Ph.D. research of *Thomas Groen* (2007), while *Eric Klop* (2009) studied the effects of burning on the distribution of antelopes in

Cameroon. Our state-and-transition models to understand vegetation dynamics (resulting in a publication in *Science*) can also be used for both temperate and tropical areas: the dynamics of very nutrient-rich grazed swamps in Western Europe show the same behaviour (*Theo Vullink* 2001). While we got more and more interested in the alternative states of trees or grasses (leading to a publication in *Nature*), we then realised that trees may both compete with grasses and facilitate them. This we had researched through the work of *Fulco Ludwig* (2001); we found that trees can act as nutrient pumps, thus affecting especially the N/P ratio in grass and thus the digestibility. At present, we take this further by a new research project by *Edward Kobi* (2013) who experimentally changed the tree density in an area, while *Priya Koduganti* (2013) delved much deeper into the nutrient 'giving-and-taking' between trees and grasses.

Linked to this is the issue how seeds can germinate and seedlings can establish in a grass-layer (*Paul Loth* 1999). This we took further through the work of *Cornelis van der Waal* (2010), *Mhosisi Masocha* (2010), *Tessema Kelkay*(2011), *Eduardo Barbosa* 2013) and post-doc *Kyle Tomlinson* (ending 2013). We further worked on rodents, because in savannas they may perhaps be crucial for further understanding the establishment of woody species (*Nicole Hagenah* 2006) and we may use methodologies which we used in rainforest (*Patrick Jansen* 2003), but at present we do that mainly in oak forests in the Netherlands (work of *Lennart Suselbeek*). A hot topic in future will be competition but also facilitation (published in *Nature*). We have started this type of work already (see *Heuermann and Dekker*, referred to above; but also *Dries Kuijper* 2004). The research in exclusion experiments by *Joris Cromsigt* (2006) is only a beginning, and we have taken this to great heights in Welgevonden Private Game Reserve in the Plains Project.

These lines of research, namely the one on how and why herbivores select their food and the one on how food is distributed over the landscape, came together in the research of *Margje Voeten* (1999) who investigated how migratory behaviour of wildebeest and zebra in East Africa can be understood. For this we also needed to know more about herbivore population development over time, which was investigated by *Wilbur Ottichilo* (2000) for the Masai Mara in Kenya, by *Shem Mwasi* (2002) for Lake Nakuru National Park (also in Kenya), and *Mohammed Said* (2003) for the whole of East Africa. Our work on resulting herbivore assemblages resulted in another paper in *Nature*. In this type of work, we came to rely more and more on remote sensing, as also evidenced by the work of *Boniface Oindo* (2001). Modern remote sensing techniques coupled to new statistical methods give startling possibilities to investigate landscape features that are

apparently important for herbivore distributions: an unexpected (and not understood) relationship is the one between elephant density and landscape scale (*Amon Murwira* 2003). Pivotal appears to be the work of *Fulco Ludwig* (2001) referred to above, who related herbivore densities and performance to the aforementioned P/N ratios under trees. In the now finished TEMBO- programme in Timbavati a number of postgraduate students further work on this: *Cornelis van de Waal* (2010) conducted large scale fertilization experiments in a natural savanna to investigate the roles of nutrients on tree/grass co-existence, while *Yolanda Pretorius* (2009) investigated how herbivores react to these nutrient additions; *de Henjo de Knegt* (2010) modelled large scale herbivore distribution based upon small-scale foraging decisions. *Claudia Pittiglio* (2012) investigated movements of elephant in this TEMBO-programme in South Africa, and *Shadrack Ngene* (2010) did the same in Kenya.

Remote sensing also now enable us to map the distribution of plant communities (*Xuehua Liu* 2001; *Chacon Moreno* 2007) or even that of individual plant species, as was shown by *Chaichoke Vaiphasa* (2006), and even map food quality – whether the distribution of plant nutrient concentrations (*Onisomo Mutanga* 2004) or the distribution of antifeedants in plants (*Jelle Ferwerda* 2005). *Nicky Knox* (2010), took this further in the TEMBO-programme. We invested much time in understanding the possibilities of hyperspectral remote sensing and automatic species recognition in many different ecosystems through the work of *Moses Cho* (2007), *Marleen Noomen* (2007), *Mohammed Sobhan* (2007), *Guofeng Wu* (2008), *Jane Bemigisha* (2008), *Rosbanak. Darviszadeh* (2008). In the work of *Tiejun Wang* (2009) we even went a step further because there we also looked at the thermal niche of mammals. I think we have now explored this well enough, and we now concentrate again more on the animals themselves.

A third line of research is also linked to this work, and that one focuses on the economic importance of wildlife.. This builds on earlier work in western Africa by *Hansson Njiforti* (1997), *Allard Blom* (2001), *Theodore Mayaka* (2002) and *Paul Scholte* (2005). I think that nature conservation increasingly depends on an economic cost-benefit analysis, but it is also clear that we cannot ignore the effects of humans on the structure of assemblages any more (*Fred de Boer* 2000), and thus we started cooperating with economists on this issue. The first thesis coming from this was the one by *Emmanuel Mwakiva* (2011) but more are soon to follow. Emmanuel studied the economic importance of elephant to landowners, whether they are private ones or communal ones.

During my professorship we also have guided research in nearly totally man-

made environments or in landscapes that were altered by man. *Ben Verboom* (1998) examined how edges between different vegetation structures are of importance to bats in the Netherlands, *Bas van Balen* (1999) elucidated the relation between forest fragments and assemblages of bird species on Java, *Claire Vos* (1999) investigated how Dutch frogs could survive due to connectivity between fragments, *Marcel Huijser* (2000) researched mitigating strategies for the survival of small mammals in fragmented landscapes, and *Ton Stumpel* (2004) did the same for reptiles and amphibians. *Irma Wynboff* (2001) took to this the ultimate level of nature management: she investigated how extinct species can be reintroduced in such a man-made landscape. In conservation biology, fragmentation together with bottle-necking is one of the most pressing problems and one of the most severe threats to the long-term survival of species. In Africa we investigated the genetic consequences of this, and selected as model species the African buffalo first through the work of a post-doc (*Paul Wenink* 1999) and later through the postgraduate work of *Pim van Hooft* (2001). This genetic type of work will be intensified in the near future at the chair group with two new Ph.D. students, for which cooperation with the Animal Genetics Group will be intensified. However, wild animals in future will not only be confronted with fragmentation or threatened by having to live in very small populations; they also will be menaced by competition from domestic herbivores, as was shown by *Charu Mishra* (2001). In fact current animal assemblage composition can be understood from the competition the species suffered with domestic livestock. This was further investigated by *Tsewang Namgail* in the eastern Himalayas (2009) and *Farshid Abrestani* in mainland India (2009).

Given time, where will all this work lead to? There are four issues I would like to see ‘solved’, namely,

(1) Can we better predict how and why individual animals move through the landscape so that we better understand where and why competition (or facilitation) occurs?

(2) Can we better understand the relation between food and the vital rates that determine animal population dynamics?

(3) Can we better understand the feedback loops between herbivory (and fire) so that we better can predict the different states a vegetation and associated animal assemblages can occur in.

(4) Can we contribute to One Health through the study of animal movements and animals as vectors of diseases?

These four questions are aimed at solving that key question of animal ecology, namely, what determines the abundance and distribution of (different) species? During my career I have chosen to focus this on a particular group of animals, namely herbivorous vertebrates. It is not that I think these are a particularly well-suited group to study these questions; I think these species are beautiful and appealing, and they occur in sufficient large numbers to make it likely that one can observe them. Moreover, they often have an impact on the landscape, which gives them additional importance in, for instance, nature conservation. I have thus taken up my old love again, and started working on waterfowl. There moderns insights can be linked to old questions, as was shown by *Robert Kraus* (2011) who discovered gene flow between species of ducks, *Ralf Kurvers* (2011) who did great work on personality of geese that may explain their way of group living, *Rudy Jonkers* (2011) who studied changing breeding patterns of barnacle geese in Europe, and *Yali Si* (2011) who delved into lateral transport of avian influenza from China to Europe. The linking theme there is moving ecology. We started working on that with *Geerten Hengeveld* (2007) but soon *Tom Huisman* will defend his thesis on this too. This is greatly fostered by an EU grant to develop new hardware and software for animal tracking (*E-Track*) and by our cooperation with Ron Ydenberg from Simon Fraser University, which also yielded a thesis defended by a man well in his seventies (*Dick Dekker* 2009). I hope his is a model for all of us who want to continue doing for a very long time what we love, namely, teaching, research and conservation.

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