Book Reviews

Herbivores as mediators

Herbivores as mediators of their environment. The impact of large and small species on vegetation dynamics. E.S. Bakker 2003. PhD thesis. Wageningen University, Wageningen, The Netherlands. 184 pp. ISBN 90-5808-878-2.

This PhD thesis deals with three herbivorous mammals (cattle, rabbit (*Oryctolagus cuniculus*) and common vole (*Microtus arvalis*)) and their impact on vegetation and vegetation constituents of a cool temperate alluvial grassland system (Junner Koeland). Quite some impact determinants are treated, such as plant consumption, treading, burying activity (gap creation), defecation, nutrient redistribution, endozoochory, (perceived) predation and herbivore interactions. Those who expected a book on mammals will be disappointed, only one of the chapters departs from the animal as response variable, all the others actually have vegetation and its constituents as responding subject. But as such many aspects are covered, none of them exhaustively though.

One result of this PhD thesis will be remembered in particular: the present-day underestimation of the possible impact of common voles on a grassland system. Not many biologists will ever have estimated the daily energy expenditure (DEE) of a vole population at any time period during the year to be equal to the DEE of cattle (with a density of 0.4 individuals per ha) in the same environment. Nonetheless, both appear to have an entirely different impact on the grassland environment: the effect of cattle grazing excludes common voles entirely from the grassland system and leads to a compositional and structural constancy of the vegetation, which is never reached with common vole grazing without cattle and rabbits.

What further remains as a general feeling after reading this PhD thesis, is the difficulty to deal with the complexity of field conditions. The field experiments are difficult to replicate and hardly ever lead to clear-cut conclusions. The author often needs to leave questions unanswered, because of the variability in weather and habitat conditions and population dynamics of both wild herbivores. On the other hand, she proofs the absolute necessity of field experiments: ecological questions can hardly be simplified to univariate experiments, ignoring the multivariate interactions. These are well documented in this PhD thesis. The apparent leitmotiv here is the importance of herbivore size.

The impact of different-sized herbivores on recruitment opportunities for subordinate herbs in grasslands

From a field experiment it is concluded that gap creation (colonization opportunity) plays a crucial role for the non-dominant (subordinate) plant species in a grassland system. It was found that cattle disperse much larger amounts of germinable seeds via their dung than rabbits do. Through their burying activities, rabbits on the other hand create bare soil and might be far more important for gap creation than cattle, and, hence, for colonization opportunities for plants. Artificial disturbance improved germination success for the four model plant species (*Prunella vulgaris, Ranunculus acris, Trifolium pratense, Plantago lanceolata*, perhaps not exactly the most critical plant species in nature conservation; selection criteria are not given) that were tested. Cattle are recognized as better seed dispersers, while rabbits are more important as creators of disturbance, necessary for germination and mainte-

nance of plant species-richness in a grassland ecosystem. Hence, different herbivores have different impact on colonization/extinction ratios of plants.

The interactive effects of grazing and litter on grassland plant diversity

In a second contribution to the estimation of herbivore impact on colonization and extinction rates of plants, emphasis is given on the importance of the litter decomposition cycle under grazing. In a nicely designed three-year long exclosure experiment it is proven that large herbivore grazing diminishes (not surprisingly) bio- and necromass accumulation significantly, creating favourable light conditions for plant colonization. Litter removal alone did not effect species richness significantly. Much emphasis is given on the favourable light conditions at soil level, but regrettably other determinants, such as available space and possible soil development are not taken into consideration. It remains unsolved why voles do not have the same impact on bio- and necromass removal and thus on favouring light conditions for colonization, given the general conclusion that the vole population has a daily energy expenditure close to that of the cattle grazing the area.

Compositional constancy in grazed plant communities increases with herbivore size

Again within the framework of the alluvial grassland system of Junner Koeland, and with a herbivore-differentiated exclosure experiment, the impact of the three differently sized herbivores on vegetation compositional stability and the impact of nutrient addition was tested. When grazed by large herbivores (cattle + rabbit), plant species composition of the grassland was very stable during consecutive years, while it fluctuated strongly when exclusively grazed by both smaller herbivores (fluctuations were strongest with exclusive vole grazing). Very interesting for nature managers was the observation that local nutrient addition did not effect plant species composition significantly when vegetation was grazed by large herbivores, since those nutrient-enriched spots were highly preferred by the herbivores. Apparently, seasonal cattle grazing at a density of 0.4 heifer per ha, suppresses species composition fluctuations and promotes structural homogeneity, while exclusive small herbivore grazing enhances structural variation (expressing soil differentiation), while plant species richness increases less. However, one remains with the evident question, which of both is preferable from a nature manager's point of view, taking into consideration that structural diversity in space (perhaps less so in time) is assumed to be favourable for invertebrate diversity. In this respect, the author makes an important note on the fact that the conclusion that large and small herbivores control the vegetation differently depends on the scale of observation: "If the scale of observation was adjusted to herbivore size and for example the vegetation structure of several hectares was compressed to a few square meters, the grazing patterns created by cattle and voles may be very similar. At the landscape scale cattle may even create a structurally more diverse landscape because they prefer certain vegetation types and patches [while others are avoided]. This results in vegetation with a mosaic of high and low patches. Vole grazing on a landscape scale may result in structurally rather homogeneous vegetation, because vole grazing lawns are so small that they are hard to detect at a landscape scale".

Impact of herbivores on nitrogen cycling: contrasting effects of small and large species

Again within an exclosure experiment, in which consecutively cattle and cattle + rabbit were excluded from grazing, the effect of different herbivore combinations on nitrogen cycling was tested. First important conclusion is that cattle grazing (at a heifer density of 0.4 animals per ha) excludes voles almost entirely. Despite comparable daily energy expenditure of all three herbi-

vores given the respective animal densities in the system (peak densities of common vole are extremely high), the impact of the different herbivore combinations was quite different. Net annual in situ N-mineralization was higher in the small herbivore treatments (voles and voles + rabbits, respectively), while turnover of nitrogen was significantly lower under cattle grazing treatment.

Experimental manipulation of food quality and apparent predation risk in the European rabbit: bottom-up versus top-down control in a central-place foraging herbivore

After four chapters on response variables of herbivore grazing, we finally arrive at the herbivores themselves. In her field experiment, the author tries to differentiate between the impact of food quality and predation risk on the foraging behaviour of the European rabbit (*Oryctolagus cuniculus*). A very original and highly appreciated field experimental design, unfortunately with a low replication level, revealed that grazing intensity, not surprisingly, declined with increasing distance from the burrows, situated beneath thorny scrub of blackthorn (*Prunus spinosa*). Fertilizing vegetation increased rabbit foraging four times, and decreased the above-mentioned distance-to-burrow effect. Through more intense grazing close to the burrows, the rabbits increase food quality and facilitate themselves. More surprising was the effect of addition of predator scent (realised through addition of mink pellets as a substitute of potential polecat predation). Although it did not result in different *total* visitation rates by the rabbits, it did cause a significant change in diurnal feeding pattern. Without pellets the rabbit foraged predominantly during the night, while addition of mink pellets made them forage during daylight as well. In fact, no nocturnal foraging preference could be noticed anymore when pellets were added. This shift in activity pattern clearly points at an adaptation to increased perceived predation risk by mustelid predators, which are mainly nocturnal. The results further suggest that the improvement of food quality through frequent grazing and, hence, promotion of new shoot development, is a more important trigger than the accompanying improvement of visibility of the surroundings.

Ecological anachronisms in the recruitment of light-demanding tree species?

After exactly one chapter on one of the herbivores themselves, we return to their environment again. This last contribution deals with vegetation development on the longer time scale. We partly leave Junner Koeland to have a broader view on plant defences that evolved under predation pressure (e.g. thorns of blackthorn). Predation pressure has vanished partly (not forgetting present-day wild herbivores like roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*)) because of extinction of plant predators (aurochs (*Bos primigenius*), tarpan (*Equus caballus gmelini*)). In this context the hypothesis is tested whether grazing by their descendants (cattle, horse) could give evidence to the succession mechanism of shifting mosaics hypothesized by Olff et al. in 1999 and more or less introduced by Vera (1997, 2000). The question is reduced to the impact of both large grazers and the lagomorphic European rabbit on palatable pedunculate oak (*Quercus robur*) and seven thorny (i.e. “defensive”) shrub species. It is shown that oak can regenerate in the presence of large herbivores through spatial association with blackthorn. The palatable species can resist herbivores through association with the defended thorny shrub (so-called associative resistance). However, rabbit presence suppresses this facilitation process, since rabbits do eat oak seedlings and juveniles, whether growing underneath blackthorn scrub or not. Also blackthorn ramets are consumed by rabbit. Through study of consecutive aerial photographs one was able to associate blackthorn encroachment with temporal low rabbit density. Although the author states that the results give some evidence for the shifting mosaic theory, one might equally conclude that the presence of other herbivores than aurochs (cattle) and tarpan (horse), not improba-

ble in historical and pre-historical time (although European rabbit was introduced in the Middle Ages only) is not favouring the same succession theory.

Maurice Hoffmann

Ghent University, Department Biology
Terrestrial Ecology Unit
Krijgslaan 281, S8
B-9000 Ghent, Belgium
e-mail: maurice.hoffmann@UGent.be

Het Walvisboek

Het Walvisboek. Walvissen en andere zeewezens beschreven door Adriaen Coenen in 1585. Redactie en inleiding Florike Egmond en Peter Mason, met commentaar door Kees Lankester 2003. Walburg Pers, Zutphen. viii-xvi, 208 pp. ISBN 90.5730.282.9.

Vier boeken heeft Adriaen Coenen(szoon) van Schilperoort gemaakt: het *'Grote Vis Boeck'* (in 1574 aan Willem van Oranje ten geschenke gegeven, en sindsdien spoorloos), het *'Visboeck'* (1577-1579; bevindt zich in de Koninklijke Bibliotheek te 's-Gravenhage), het *'Walvisboeck'* (1584-1585; in de bibliotheek van de Koninklijke Maatschappij voor Dierkunde in Antwerpen) en het *'Haringkoningboeck'* (in het Gemeentearchief van Keulen). Het betreft in alle gevallen manuscripten die tot nu toe nog nooit in druk zijn verschenen.

Adriaen Coenen werd in 1514 te Scheveningen geboren in een familie van vissers en is in zijn werkzame leven veilingmeester van de vismijn en groothandelaar in vis geweest. Vanuit zijn opvoeding en werk heeft hij een grote interesse gekregen in de mariene fauna en daar voor zichzelf veel aantekeningen en tekeningen van gemaakt. Dit materiaal vormde de basis van de genoemde manuscripten. Coenen stierf in 1587.

Bij Walburg Pers in Zutphen zijn nu de van tekst voorziene platen van het Walvisboeck gereproduceerd en van biologisch commentaar voorzien door de marien bioloog Kees Lankester. Het manuscript is van uitzonderlijk natuurhistorisch belang omdat er strandvondsten van marien gedierte en visvangsten met plaats en datum in worden beschreven. Coenen beschrijft gedetailleerd de allereerste marien-biologische waarnemingen van de Nederlandse kust. De originele tekeningen zijn een genoegen om te bekijken, de reproducties echter zijn van een fletse, nauwelijks acceptabele kwaliteit. Het boek bestaat uit twee delen. Het eerste deel omvat 58 bladen en het tweede 66 bladen. "Dat eerste boock" (1584) heeft als ondertitel: "*Van menich derleij walvisschen ende ander selseme groote wonderlijke visschen*". "Dat tweede boock" (1585) heeft als ondertitel "*Van veel vreemde zeemonsteren, veelderleij meereminnen, zeemans, zeebisschoppen, zeedraken, zeepaarden, zeeleeuwen, zeevossen, zeehasen, zeevarkens, zeeduvels, zeespinnen, zeenetelen, zeekarstangens, zeeridders, zeemonniken, zeekoijen, zeewolven, zeeapen, zeehonden, zeekaluen, zeekatten, zeemuijsen, zeeluijsen, zeekokommers ende noch meer andere vreemde onsiene en oneetbare vischen, cocodrillen, groote vremde schilpaddens"*.

Zoals uit deze titels blijkt, beschrijft Coenen fantasieschepsels, veelal overgenomen uit vertellingen en de toenmalige schaarse literatuur, maar daarnaast uit eigen waarneming ook gemakkelijk te herkennen bestaande soorten. Met name in het laatste ligt de grote kracht van het werk. De lezer kan zich in gedachten naar het 16de-eeuwse Nederlandse strand verplaatsen en zich een voorstelling van Coenen maken die aangespoelde walvisachtigen bekijkt, met zeepokken begroeide voorwerpen opraapt en bijzondere vissen in de manden van de Scheveningse vissers vindt. Hij beschreef en tekende zijn waarnemingen zeer nauwkeurig. Het manuscript zoals dat in Antwerpen aanwezig is telt 125 bladen, inclusief een uitvouwblad tussen de beide delen. In de nu verschenen uitgave zijn 23 bladen niet opgenomen, zonder dat de redacteuren in de tekst aangeven waarom dat zo is. In ieder geval zijn alle bladen uit het eerste deel gereproduceerd, en de 23 niet gereproduceerde bladen moeten dus in het tweede deel zitten. Een ander hinderlijk man-