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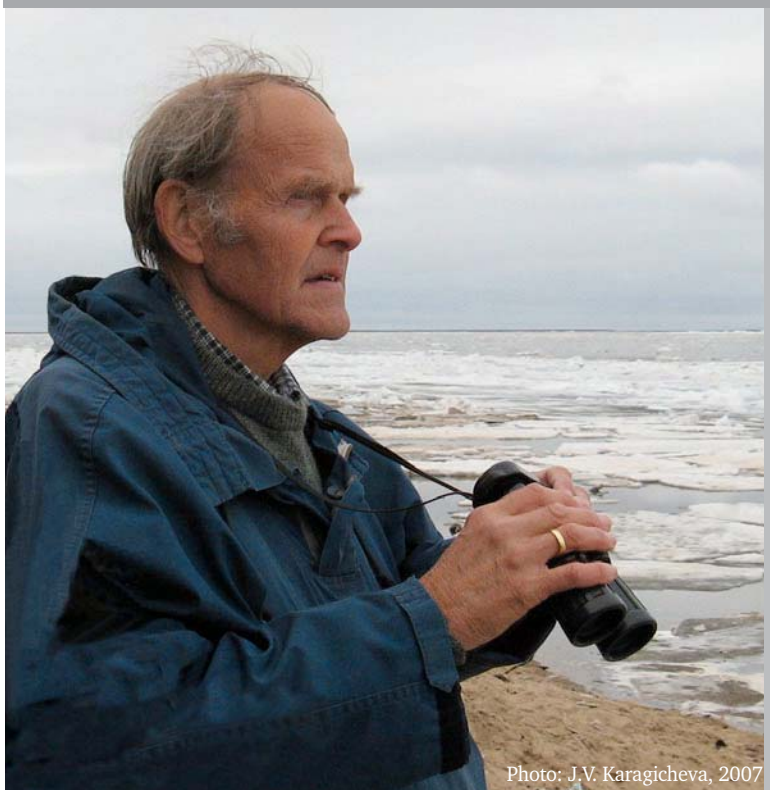


Photo: J.V. Karagicheva, 2007

Sailing without the captain; we are ship-shape thanks to his legacy

Rudolf Herman Drent (1937 – 2008)

We have lost Rudi Drent. He died on 9 September 2008, aged 71 years. It is hard to believe that we will not see him anymore. We miss the stimulating discussions, his sharp analysis of ecological problems, his vision and kind personality. Rudi Drent was an outstanding authority in ecology both in The Netherlands and beyond with few equals. With his sharp insight and intelligence, he educated the current generation of bird ecologists and he used his enthusiasm to stimulate students in ecology in The Netherlands and abroad to contribute to this fascinating field.

Drent was born in 1937 in Los Angeles and studied biology in Vancouver at the University of British Columbia (1954–1961). Stimulated by Lars von Haartman and Miklos D.F. Udvardy, he became interested in sea bird ecology. For his Master's thesis, he studied the breeding ecology of the Pigeon Guillemot on Mandarte Island (1959–1960), the island where his friend Frank Tompa did his famous work on the Song Sparrow. Drent published his own work on guillemots in *ARDEA* in 1965 (53: 99–160). It is a detailed behavioural and ecological study that incorporated many of the topics that he and his students have addressed in the course of his career. He discussed colony structure, behaviour, incubation period and rhythm, lay date and clutch size, thermoregulation, nestling growth and diet, body temperature, CO_2 production, energy expenditure and homoiothermy. From this work it is already apparent that Rudi was an excellent field biologist and naturalist and that he also was able to communicate the excitement of his findings clearly in his writings. He saw the uniqueness of Mandarte Island and together with Frank Tompa and Peter Grant, stimulated Jamie Smith to take up the Song Sparrow study when he came to Vancouver.

Drent chose The Netherlands to study for his PhD degree (1962–1967), the country in which his father was born. Gerard Baerends, Professor of Zoology at the University of Groningen, was working at unravelling the organisation of behaviour in birds. He and his group made detailed quantitative studies on the incubation behaviour of the Herring Gull. Functional analysis of incubation using the approach that Drent had

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started in his guillemot studies deepened their insights of the consequences of variation in incubation behaviour. The teaming-up of Baerends and Drent led to Drent's dissertation on '*Functional aspects of incubation in the Herring Gull*' (1967). This work shows how powerful the combination of observation, measurement and experiment is in unravelling functional aspects of behaviour. The essential role of quantifying observations is emphasized in Goethe's poem that Drent choose to prefix his thesis:

Bewährt den Forscher der Natur
Ein frei und ruhig Schauen
So folge Messkunst seiner Spur
Mit Vorsicht und Vertrauen

A nice detail from the thesis follows. By measuring the rotation of the eggs around the long axis both in the nest and in a water dish, his work showed that the breaks in parental incubation when they reposition the eggs enabled gravity to position the egg according to the asymmetry of its own weight. Parents did not 'turn' the eggs but enabled the egg to find its own position! Because of the weight asymmetry of the chick in the egg, chicks would pip at the upper side of the egg, ensuring there was air to breath and allowing communication to the parent that the eggs were hatching. Energetic cost–benefit analysis that was to become such a central part of his research is already recognizable in his thesis. Drent estimated energetic incubation costs for the parent using cooling curves of the eggs at different ages. Actual measurements of CO_2 production of the eggs were performed by Nel Drent, who later became his wife. These data were used to quantify energy expenditure of the egg.

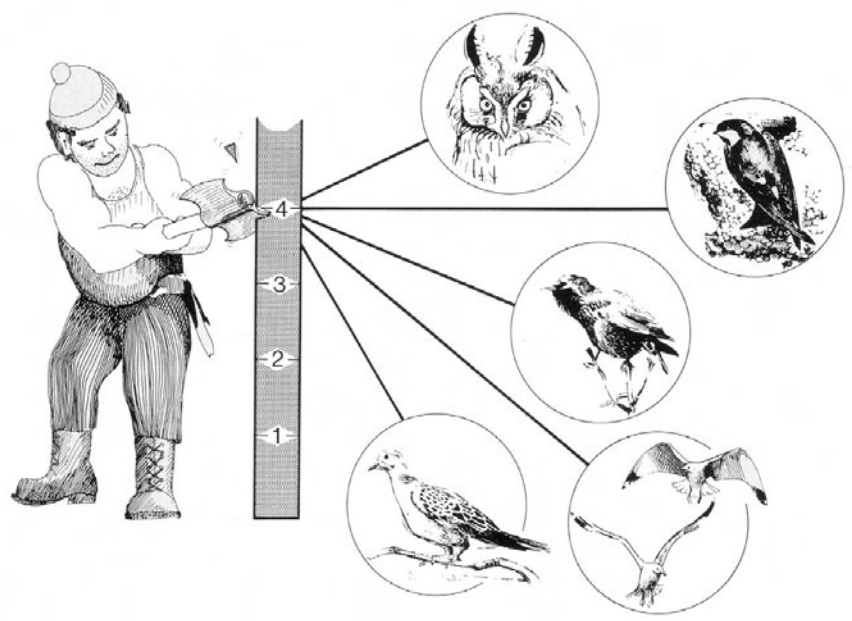
Drent went back to Vancouver after his thesis defence, now as a married man. He took up his work at Mandarte Island on the Pigeon Guillemot using cameras and balances to quantify diet and growth in more detail than previously. Logistically, the work on Mandarte was attractive, because Drent's father after his retirement had bought a boat called 'Ilse' built for him by Niestern in Delfzijl, The Netherlands. With his father as captain of the boat, travel to and from Mandarte Island was facilitated! Drent took command of the Ilse later, and she was used over many years to record monthly counts of waterbirds in the Lauwersmeer and for expeditions collecting shellfish in different parts of the Wadden Sea and the Baltic with his sons Jan and Hugo.

Drent developed a close friendship with John Krebs in Vancouver. Krebs had just finished his thesis on territory and breeding density in the Great Tit and both became Associate Professor of Ecology at the University of British Columbia. Krebs' experimental study showed, contrary to Lack's idea, that breeding numbers were limited by territorial behaviour, not by food supply. Throughout their entire careers Drent and Krebs kept in close contact as both were interested in foraging behaviour. While Krebs concentrated on experimental work on foraging in the laboratory, Drent emphasized field studies, describing how wild animals exploited their natural food supplies and conducting experiments wherever possible. It was during this time that the field now called evolutionary ecology originated, a mix between the ethology as mastered by Baerends and Tinbergen and ecology. The organization of behaviour was not the prime goal anymore; instead the ecological consequences of behaviour became a more central question. The economics of patch and prey choice were hot topics in those early days.

In 1972, Drent was invited by Baerends to come to Groningen. Drent took up the position (Lector in Animal Ecology 1972–1984, Professor in Animal Ecology 1984–2008) and contributed to students' field studies that were in progress at the time, starting with the work of B.S. Ebbinge and K. Canters who studied how Barnacle Geese exploited the new food supply in the Lauwersmeer, which had been recently reclaimed from the sea. Drent's overall objective was to quantify the energy budgets of Barnacle Geese in the wild. The biological station of the University of Groningen, 'de Herdershut' on the island of Schiermonnikoog was an ideal basis for small student camps where the aim was to determine how the geese exploited their food supply in winter. By combining observations throughout the day on foraging activity, bite frequency and size, estimates of dropping intervals, weights of faecal pellets, and analysis of indigestible markers in food on offer and in droppings, Drent showed it was possible to make estimates of daily uptake of food. During these sojourns, Drent taught the students in the field which questions to ask and how to get the answers. And he made the plots of the newly collected data every evening.

Drent valued ornithology in its widest sense. He joined in, and was responsible for, monitoring studies of monthly bird counts in the Lauwersmeer (from 1973–2008) and in the Dollard (1972–2008). He was an inspiring president of the Netherlands Ornithologists' Union during almost his whole career in The Netherlands (1974–2003), enabling amateurs and professionals alike to communicate their latest findings at meetings. He was a master in the way he led these meetings and in his short, enthusiastic and concise

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Maximum sustained working level of parent birds tending nestlings, expressed as metabolizable energy per day (DME) in multiples of BMR (basal metabolic rate). The data refer to *Asio otus* (Wijnandts, in prep.), *Delichon urbica* (Bryant & Westerterp, this symposium), *Sturnus vulgaris* (Westerterp, in progress), *Larus glaucescens* (Drent & Ward, in prep.) and *Streptopelia risoria* (Brisbin 1969) and cluster at approximately 4 BMR, the working level of heavy labour by human standards (Brody 1945).

One of the key figures in 'The prudent parent', 1980.

summaries of the day's research findings. Drent realised the importance of both a national (*LIMOSA*) and an international ornithological journal (*ARDEA*) to the development of ornithology in The Netherlands, which offered the possibility of publishing results in one of our own journals and it also placed The Netherlands on the international ornithological map.

In 1975, Serge Daan joined the research group of Drent. Having a background in circadian rhythms, Daan gave added impulse to work on parental investment, a research topic that was started by Drent with the work on annual energy budgets in Long-eared Owls (H. Wijnandts) and on foraging decisions in Starlings (J.M. Tinbergen). Both studies included factors that limited family size. Daan initiated a field study of the European Kestrel (D.J. Masman) using a similar approach to that of Drent. The appointment of Daan was a great success because these two outstanding researchers teamed up to write their famous article '*The prudent parent: energetic adjustments in avian breeding*' in 1980 (Ardea 68: 225–252) providing both empirical and theoretical insights of parental investment at an apposite moment. The authors discuss the energetics of reproduction in the context of how the parent adjusts its effort to maximize the lifetime output of young. Parental trade-offs in relation to the seasonal decline in offspring survival, the concept of capital and income breeders and the empirical finding that parents of different species worked at similar energetic levels of around four times the basal metabolic rate during chick rearing was central to the idea that parents might monitor their own energy expenditure in order to adjust their effort to maintain the optimal working capacity. This paper became a classic work and has been very influential in subsequent ornithological studies. At a personal level, Drent and Daan were competitors, a phenomenon more easily observed when two great men are in the same group. Yet, research discussions were open and many students profited from the exchanges. Drent's insights of human nature helped to make this period a great success.

Based on the premise that energy could be the relevant currency for the bird to make its decisions and that in the field it was possible to measure both energy income and expenditure, Drent decided to quantify goose energetics (1978, Verh. Orn. Ges. Bay. 23: 239–264). The expeditions to Spitsbergen (1975) were first undertaken by B.S. Ebbinge, together with the English group from the Wildfowl and Wetlands Trust (M. Owen, J. Black). Drent and some of his team joined for long happy summers, and their visits led to the development of a full-grown research program. These expeditions enabled Drent to escape the continuous administrative burden of the University, at least for some time each year, and to participate in the important empirical work. What fascinated Drent and his students was how the geese managed to breed in the High Arctic. How much reserves did they build up on the wintering grounds and did the variation in reserves at departure predict breeding success? Or was it the food in the Arctic that played a central role in determining success? Were the geese in-

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deed capital breeders? Many hours of observations were recorded, especially on Brent Geese, to estimate the body reserves of colour-ringed individuals based on their abdominal profile. Similar observations were made to determine family size of these known individuals when the birds returned south along the flyways to the wintering grounds. Indeed, geese with higher reserves upon departure for the north were more likely to produce offspring than birds with a low level of reserves (1995, J. Avian Biol. 26: 105–113; 1998, Norsk Polarinst. Skrifter 200: 175–193). Experimental work on family size also revealed that in Barnacles large families did better because of their competitive advantage over smaller families (1999, J. Anim. Ecol. 68: 753–768).

Studies in conjunction with the plant ecologist Jan P. Bakker on the availability and exploitation of vegetation as a food resource on the salt marshes of Schiermonnikoog became an increasingly important research topic in the 1980s and 1990s. The studies showed there was a strong interaction between goose and hare foraging. Hares facilitated goose feeding, yet they also competed for plant resources. As the research progressed, a more long-term view developed over how the salt marshes of Schiermonnikoog would change and affect herbivore activity. In an ageing marsh, marine clay deposition changes nutrient availability and thereby enhances vegetational succession and plant species establish that are not exploitable by small grazers. Can small grazers slow down the process of succession? The conclusion emerged that they can, but they cannot stop it (2000, Ecography 23: 60–69).

The details of the foraging process particularly interested Drent. He was fascinated by the possibility that geese timed their repeated foraging visits to a particular sward in order to maximize their own intake rate. While estimating carrying capacity of salt marshes and cultivated areas, many generations of students took detailed measurements on cycles in goose visitation and plant regrowth in swards of *Plantago maritima, Festuca rubra* and *Puccinellia maritima* (H.H.T. Prins, R.C. Ydenberg, J. Prop, M.R. van Eerden, C. Deerenberg, B. Spaans, J. Stahl, D. Bos A.J. van der Graaf). The evidence shows that geese exploit their vegetation at optimal intervals, but the question how geese can prevent others from cheating by visiting a patch just before the local group return is still unresolved.

In the 1980s, we thought that Brent flew non-stop from the wintering grounds of Schiermonnikoog to their Arctic breeding grounds. When it became possible to visit the Russian tundra and thus the breeding grounds of Brent Geese (Ebbinge, 1990) and also the breeding grounds of Barnacle Geese, it became clear that Brent did not fly directly to their breeding grounds. They arrived much later than expected, stressing the importance of stopover sites. With the development of new bird tracking techniques, it was now possible to study what actually happened during the migration. At this time Drent realised the significance of the beloved green wave hypothesis (1978, Verh. Orn. Ges. Bay. 23: 239–264) that structured the work of the next generation of PhD students. The idea was that geese followed the wave of spring growth of the forage northwards in order to profit from maximal digestibility of high quality forage during migration and in addition time their hatching so that the goslings could profit from the spring growth in the Arctic and achieve a high intake of nutrients. In collaboration with plant ecologist J.P. Bakker, Drent and his students put the green wave hypothesis to test linking it with the potential effects of global warming on the timing of the digestibility peak of the vegetation along the flyway. The work was based on an experimental approach (2006, Ardea 94: 567– 577). Research on the migration of birds and geese, in particular, became more and more prominent. Inspired by the research findings of his friend T. Alerstam in Lund, Drent became more and more interested in the energetics of migration, a field already developed by two of his former PhD students M. Klaassen and T. Piersma. Many models estimating stopover ecology of geese and swans have been formulated, of which it has become clear that a non-stop flight to the breeding areas is unlikely. This led to the work on stopover ecology on the White Sea coast and the Russian tundra in which Drent took an active part up to 2007. The program was possible because Drent and his team joined the big expeditions organized by M.R. van Eerden (RIZA). The work on Kanin and in later years on the northern part of the Pechora delta was difficult, but profited from their Russian friends, particularly Konstantin Litvin and his students from the Bird Ringing Centre Moscow.

Drent was broadly interested in all of the goose flyways around the globe and this interest stimulated research leading to world-wide collaborations and friendships with people like Tony Fox, Jesper Madsen, and Preben Clausen (NERI, Denmark), Gilles Gauthier and his group at Laval University in Québec and Bob Jefferies at the University of Toronto. This work, in combination with data of satellite transmitters and geolocators has greatly improved our knowledge on goose and swan stopover ecology (2007, J. Ornithol. 148: S501–S514; 2009, J. Anim. Ecol. 78: 63–72). Drent was a gifted communicator and he inspired many other ecologists especially goose scientists, as is evident from the website of the Goose Specialist Group. Here, people

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Early morning at Shoyna River, Kanin, Russia. Rudi Drent (second from left) and his Dutch-German-Russian field group, June 2002 (photo G. Eichhorn). Elena Gurtovaya (third from right) sadly died in January 2007.

from abroad, like Austin Reed, Jeff Black, Ian Patterson, Bob Jefferies, Fred Cooke, Olga Pokrovskaya, Hugh Boyd, Preben Clausen, Tony Fox, Barbara Ganter, Myrfyn Owen, Sean Boyd and Robert Rockwell, have reacted to the news of his death with personal reminiscences of Rudi and his achievements.

Drent's research interests were much wider than just goose studies. He stimulated J. Hulscher's work on the Oystercatcher and was an active discussion partner of L. Zwarts (RIZA), who had been interested in wader foraging and competition from his early twenties. This interest led B. Ens and M. Kersten, students working with Zwarts and Hulscher, to start PhD studies on Oystercatcher energetics and settlement decisions. This work produced the queue-hypothesis, an important insight that lifetime rather than annual reproduction counts in evolution. It may pay an Oystercatcher not to settle on a vacant poor territory, but to queue for a richer, occupied one (1995, Am. Nat. 146: 625–650). Drent was convinced that work on passerines was also important because it emphasized different aspects of avian biology and offered exciting research possibilities. As a board member of the Netherlands Institute of Ecology NIOO in Heteren, he became involved in the work of J.H. van Balen and J.A.L. Mertens that influenced his thinking, as can be judged from the role their work played in 'The prudent parent'.

Drent was very active in the management of the University of Groningen. His commitment as leader of his own Animal Ecology Group (1972–2002), the group 'Gedragsbiologie' (behavioural biology), the Faculty of Biology (1984–1986) and the Centre for Ecological and Evolutionary Studies (CEES, 1993–2002) was impressive. His stimulating vision on science, education and human nature made him a much appreciated director and colleague. When there was a difference of opinion he spent a lot of time and energy to convince his colleagues in order to reach consensus. He also convinced the University that it was necessary to renew the field station, the Herdershut on Schiermonnikoog (1983), for field work of a high standard to take place on the salt marshes and in the Wadden Sea. His strong opinion, however, did not always match with those of the faculty, and he had to spend a considerable amount of energy to survive. As an example, Drent did not think that it was a good idea to move the biology department away from Haren with all of its animal facilities. And ironically, it did not happen in his time…….

Drent could not bring himself always to do things that had to be done, often inconvenient for his colleagues. Undoubtedly, he always had a good reason. When he promised to do something, one had to read between the lines to predict what would happen, but if things went wrong he had an enormous talent to im-

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provise. We were very lucky that both the group and the CEES profited from the talents of Suus Bakker-Geluk, his secretary, who prevented many misunderstandings.

Throughout the country, Drent was involved in the activities of many work groups and committees, including BION (Dutch Organisation of Scientific Research), the Netherlands Arctic and Antarctic Programme, the Research School of Functional Ecology, and the Board of the NEVECOL (Netherlands Flemish Ecological Association). When Rudi was president of NEVECOL, it organised, in cooperation with the British Ecological Society, the 38th Annual BES Symposium in The Netherlands (1997) resulting in '*Herbivores: between plants and predators*' (1999, edited by H. Olff, V.K. Brown and R.H. Drent). He was member of many scientific committees, as of NIOO, Royal Netherlands Institute of Sea Research KNIOZ, Alterra, and the Biological Station 'Tour du Valat' in the Camargue, France.

How Drent was appreciated became clear when, in 2000, his students assembled a compilation of the work done with Drent in the honour of Drent's 40th PhD student ('*De onvrije natuur*', edited by J.M. Tinbergen, J.P. Bakker and T. Piersma). This compilation was in Dutch, with the aim to reach a wider audience in The Netherlands, in line with his activities to bridge the gap between amateur and professional ornithologists in the NOU. Because the book was a success, Drent himself took up the task to translate the book in English and new PhD students added chapters resulting in the book '*Seeking natures limits, ecologists in the field*' (2005), a good source for those who want to read more about Drent's work.

All this time Drent remained a modest man, inviting foreign visitors and students to his home where he and his wife provided a warm welcome and a perfect ambiance to discuss work and other matters that were of interest. Drent read a lot and he was a great admirer of Goethe. He loved to visit museums and could tell fascinating stories about the paintings he saw. He was always creating interest for his visitors about different facets of life. He liked to collaborate with other people including many students but also with colleagues especially from abroad who were working on similar problems. He profited from them, they profited from him. His visits to other universities were equally productive. I remember when he took me to Oxford, much of the time was taken up with intense discussions with Robin McCleery and Richard Sibley about the gull work on Walney Island.

As a teacher Rudi Drent was unexcelled through his unbound knowledge combined with his friendliness, his commitment and his wit. He was a great story builder, convincing students of a way of thinking. His lectures and talks were unprecedented because he combined a clear overall line with concise wording, clear graphics and enjoyable artwork. Drent never created barriers; everyone could walk into his office and everyone got his attention. He took his students in the field, helped them to build their observation towers on the salt marsh, but most importantly showed them how to collect and interpret data. He was an excellent observer, he loved the struggle with raw data and was an absolute master in detecting a clear line in a perhaps not so clear dataset, always being positive and stimulating in his critique. He educated many generations of students, and until his last days, he loved to discuss work or manuscripts with his own scientific offspring.

Thinking back about the importance of Rudi Drent to Ornithology: Rudi's influence was enormous, perhaps even more through personal contacts than on the basis of his papers. He had the gift of inspiring people all over the world via sparkling lectures and his open and personal approach. These unique qualities made that many of us have joined the field. In June 2008, his last (65th) PhD student, Götz Eichhorn, finished his thesis. His legacy will live in all those whom he inspired.

Joost M. Tinbergen
chairman Netherlands Ornithologists' Union

A bibliography of Drent's work can be found at www.nou.nu.

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ARDEA

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