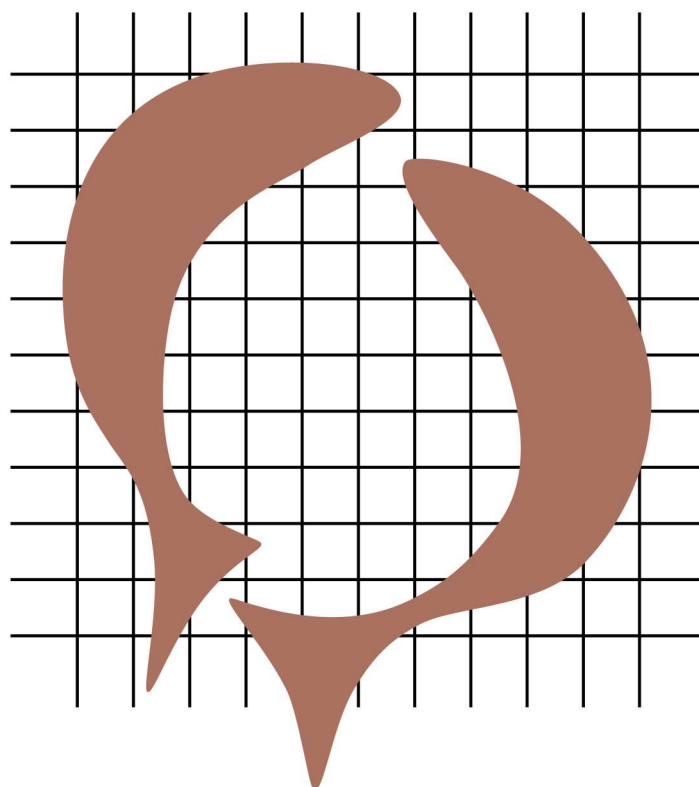


NVG NIEUWSBRIEF
achttiende jaargang no. 1, juli 2009

Nederlandse Vereniging voor
Gedragsbiologie



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DE NEDERLANDSE VERENIGING VOOR GEDRAGSBIOLOGIE

De Nederlandse Vereniging voor Gedragsbiologie (NVG) stelt zich ten doel de gedragsbiologie in Nederland te bevorderen.

Daartoe organiseert zij symposia en discussies, en geeft zij deze nieuwsbrief uit.

Bestuur

Simon Verhulst (voorzitter)
Niels Dingemanse (nieuwsbrief, website)
Marcel Eens (België)
Bart Houx (penningmeester)
Joris Koene (Dalfsen, website)
Bas Rodenburg (secretaris)
Liesbeth Sterck (internationale zaken en PhD-workshop)

Informatie

Informatie over de NVG kan gevonden worden op de website:
<http://www.gedragsbiologie.nl>

Informatie kan ook worden ingewonnen bij de voorzitter, Simon Verhulst, e-mail: s.verhulst@rug.nl.

Lidmaatschap

U kunt zich opgeven als lid bij onze secretaris Bas Rodenburg:

e-mail: bas.rodenburg@wur.nl

of via de bovengenoemde website.

De contributie bedraagt € 22,- per jaar voor studenten, promovendi (AIO/OIO) en werkzoekenden. Voor anderen € 27,- per jaar.

Kopij voor de nieuwsbrief

U kunt kopij voor de nieuwsbrief sturen aan Bas Rodenburg:

e-mail: bas.rodenburg@wur.nl

Redactioneel voorwoord

Voor U ligt NVG Nieuwsbrief nummer 1 van alweer de achttiende jaargang. Het nummer bevat aandacht voor de NVG PhD-workshop en de jaarlijkse NVG-meeting van 25 tot 27 november 2009 (houdt de data alvast vrij!), en andere nieuws-items zoals nieuwsberichten, personalia, aankondingen van congressen en samenvattingen van een viertal proefschriften. Daarnaast een stuk van Mark Bracke over wat we kunnen leren van Darwin. Reageren? Mail je bijdrage naar bovenstaand adres.

Bas Rodenburg

NVG PhD-workshop

Wednesday 25 November 2009

Location

11h00 – 17h00, conference centre “Mooirivier” in Dalfsen (formerly called “De Bron”, <http://www.mooirivier.nl>), preceding our annual NVG meeting in Dalfsen.

Why again?

Last year’s participants experienced the NVG PhD-workshop as a lively and educative day full of discussions. Both the PhD students delivering talks and the audience felt it was a fruitful day that deserved to become a tradition.

Organisation

The NVG PhD-workshop 2009 will again be organised by Liesbeth Sterck. PhD students can sign up in September 2009, when registrations for the NVG meeting can also be made.

Goal of the NVG PhD-workshop
Facilitating discussion among PhD

students working in the field of behavioural biology, especially about their own research.

Format

Eight PhD students present (a part of) their research plans in 10 minutes. We aim at PhD students who are in the first or second year of their PhD research. Other PhD students present at the meeting, three senior researchers, and the keynote speaker will then discuss these plans (20 minutes). This year’s PhD workshop topic is “Designing experiments in behavioural research”

Keynote speaker in 2009

A keynote speaker of the annual NVG-meeting, Dr. Melissa Bateson (see meeting announcement below), will give a presentation that aims at promoting discussions among PhD students.

Liesbeth Sterck (PhD workshop)
030-2535405, e.h.m.sterck@uu.nl

Annual meeting 25-27 November 2009 in Dalfsen

Dear members,

From **25 to 27 November 2009** the annual scientific and general meeting of the NVG will again be held at the conference centre "Moorivier" (<http://www.moorivier.nl>) in Dalfsen. The meeting will officially start with a dinner on Wednesday 25 November at 18h00 followed by the Baerends keynote lecture and will run until 15h30 on Friday 27 November. As usual, the meeting will be in English. The scientific programme will comprise two evening keynote lectures by prominent international scientists, contributed oral and poster presentations, and the annual general meeting. The meeting ends with the awarding of the poster prizes by the president of the society.

The Baerends lecture will this year be given by **Hans Hofmann** from the University of Texas at Austin in the USA (<http://cichlid.biosci.utexas.edu>). Hofmann performs cutting-edge integrative research into the brain mechanisms that underlie complex social behaviour and its evolution. He mainly uses cichlid fish and combines a spectrum of approaches, including ecological studies, functional genomics, endocrinology and neuroanatomy. The title of his presentation will be "*Genes, hormones and social behaviour: An integrative approach towards decision making*".

The second keynote speaker will be **Melissa Bateson** from Newcastle University in the UK (<http://www.ncl.ac.uk/psychology/staff/profile/melissa.bateson>). She is well-known for her fundamental research on mechanisms of decision-making. More recently, she has started to use her expertise in animal decision-making to assess animal welfare. The

title of her presentation will be "*Is it possible to measure how animals feel?*". In her scientific approach she explicitly integrates different disciplines including behavioural ecology, cognitive psychology, economics and marketing. In addition, besides working with a range of animals (starlings, hummingbirds, rats) she extends her behavioural research to humans.

This year's **PhD workshop** topic is "*Designing experiments in behavioural research*". As usual the workshop, preceding the meeting, will take place on Wednesday (25 Nov.) between 11h00 and 17h00. The aim is to promote discussion between PhDs in behavioural biology in its widest sense. Especially starting PhDs are encouraged to present their research plans, which will subsequently be discussed with the attending PhDs as well as several senior scientists. This meeting will also feature a lecture by Melissa Bateson, who will be present throughout the workshop. After the summer you will be able to register using the online form available at <http://www.gedragbiologie.nl>. Please **register before 15 October 2009**. For further information see the society's website or contact:

Joris Koene (general organisation)
020-5987095, joris.koene@falw.vu.nl

Liesbeth Sterck (PhD workshop)
030-2535405, e.h.m.sterck@bio.uu.nl

Bart Houx (financial issues)
030-2534868 (2615), b.houx@uu.nl

We hope to see you all in Dalfsen!

Joris Koene

Overige nieuwsberichten

De NVG en de EU richtlijnen voor proefdiergebruik

U heeft het waarschijnlijk al gehoord: de Europese Unie is druk bezig met het ontwerpen van nieuwe richtlijnen voor proefdiergebruik die veel strenger zullen zijn dan de huidige. Op dit moment kunnen belanghebbenden, zowel vóór- als tegenstanders, input leveren op de uiteindelijke tekst. Dat wordt zeker vanuit de proefdiergebruikers flink gedaan.

Ook de NVG heeft hiertoe initiatieven genomen. De reden daarvoor is dat de huidige voorstellen zodanig op laboratoriumonderzoek gericht zijn, dat de belangen van observatie- en veldonderzoek ondergesneeuwd dreigen te raken. De tot nu toe voorgestelde richtlijnen zijn voor dergelijk onderzoek op z'n minst onduidelijk en kunnen bij letterlijke toepassing in potentie sommige vormen van veldonderzoek onbedoeld onmogelijk maken. De NVG heeft inmiddels op verschillende manieren uiting gegeven aan deze punten van zorg, o.a. via de European Coalition for Biomedical Research (ECBR). Bovendien heeft de NVG zich aangesloten bij een groep organisaties en verenigingen onder leiding van de Nederlandse Vereniging voor Proefdierkunde (NVP) om gezamenlijk de Nederlandse standpunten in Europa in te brengen.

Indien u interesse heeft in het *Proposal for the EU Directive on the protection of animals used for scientific*

purposes (COM(2008) 543 - C6-0391/2008 - 2008/0211(COD) dan kunt u de officiële EU informatie vinden via http://ec.europa.eu/environment/chemicals/lab_animals/proposal_en.htm.

Bart Houx
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Toekenning subsidies NWO-LNV onderzoeksprogramma Waardering van Dierenwelzijn

Op 30 juni 2009 zijn binnen NWO-LNV onderzoeksprogramma Waardering van Dierenwelzijn vier projecten gehonoreerd. Per project is 750.000 Euro beschikbaar voor drie AIO of post-doc posities.

1. **Verenipikken bij legkippen** – Bas Rodenburg (WUR), Mechiel Korte (UU), Ton Groothuis (RUG) en Jan te Napel (WUR-ASGI)
2. **Agressie bij meervallen** – Gert Flik (KUN), Ruud van den Bos (UU) en Bert Lambooy (WUR-ASG)
3. **Genetische selectie van sociale varkens** – Johan van Arendonk (WUR), Frans Brom (Rathenau Instituut), Jaap Koolhaas (RUG) en Liesbeth Bolhuis (WUR)
4. **Mobiliseren van consumenten voor diervriendelijke producten** – Volkert Beekman (VU), Rob van Tulder (EUR), Hans Hopster (VHL) en Helmut Saatkamp (WUR)

Personalia

Theunis Piersma (1958), hoogleraar dierecologie, Rijksuniversiteit Groningen en Waddenonderzoeker bij het Koninklijk Nederlands Instituut voor Zeeonderzoek (NIOZ) is door de KNAW benoemd als nieuw lid Akademie van Wetenschappen. De Koninklijke Nederlandse Akademie van Wetenschappen (KNAW) heeft 28 nieuwe leden gekozen. De in totaal ruim tweehonderd gewone leden van de Akademie zijn vooraanstaande wetenschapsbeoefenaren, werkzaam op alle terreinen van het wetenschappelijk onderzoek.

Jaap Koolhaas (1948), hoogleraar gedragsfysiologie bij de Rijksuniversiteit Groningen, is op 29 april 2009 benoemd tot Officier in de Orde van Oranje Nassau.

De winnaar van de Nederlandse Zoölogieprijs 2009 is **David Lentink** van de leerstoelgroep Experimentele Dierkunde van Wageningen Universiteit. Hij krijgt de prijs voor zijn werk aan vliegende en zwemmende dieren o.a de gierzwaluw. Hij integreert hierbij zowel de biologie als de fysica.

Hij heeft voor dit onderzoek experimenten ontworpen en gerealiseerd aan de hand van een nieuwe door hemzelf ontwikkelde, integrale stromingstheorie voor organismen die met flapperende, roterende of translerende vleugels of vinnen, vliegen of zwemmen.

Joris Koene wins German Research Award. Faculty member of the VU University - Dr. Joris Koene- has been elected the recipient of a Friedrich Wilhelm Bessel Research Award after having been nominated for this award by Prof. Dr. Nicolaas Michiels, University of Tübingen. This award is conferred in recognition of lifetime achievements in research. In addition, the awardee is invited to carry out research projects of his own choice in cooperation with specialist colleagues in Germany. The Alexander von Humboldt-stiftung hopes that thereby the international scientific cooperation will be further promoted. You will find further information on the website: <http://www.humboldt-foundation.de/web/7806.html>

Darwin, Domestication and the dumb blonde

Darwin's views on natural selection have been extremely 'fit' as judged by their numerous reproductions in scientific writings since their first publication in 1859. In the vertebrate world perhaps only the domesticated chicken has achieved a comparable prolificacy with its number of over 40 billion birds produced annually to meet current worldwide consumer demands. Despite their high fitness, domesticated animals, especially farm animals, are

not always considered to be very happy. In order to understand their feelings, behaviour and phenotype, evolutionary thinking helps to interpret these phenomena as adaptations to natural conditions. When wild species were domesticated they showed a reduced body size, lack of pigmentation, a higher reproductive rate, reduced fearfulness, reduced activity and increased social tolerance, compared to their wild ancestors. This

so-called domesticated phenotype results from adaptation to a captive environment, and these traits appear to be genetically correlated in different species, i.e. when there is artificial selection for one of these traits the other traits tend to appear in the offspring. This suggests that the domesticated phenotype could also itself be an adaptation to more natural conditions. Such conditions may arise temporarily in the wild namely when animals occupy a new ecological niche, e.g. when they colonise new land, with abundant food and few predators or other hazards. In the wild these conditions are usually only temporary as niches are usually filled up rapidly. Humans may be an exception to this rule, as we have lived under relatively affluent conditions for a very long time, first as hunter-gatherers, later as farmers domesticating plants and animals, and now mostly as city dwellers. As we gradually colonised the world we encountered whole continents with relatively abundant food and few predators. According to evolution theory the domestic phenotype could, therefore, perhaps be found in the human species. And yes, it appears she might: the dumb blonde. She lacks hair pigmentation, and together the traits of reduced fearfulness, reduced activity and enhanced social tolerance may well qualify as 'dumb' in human folk psychology. The dumb blonde also poses a problem for evolution theory:

Why would men prefer dumb blondes? There is no question that they do. Women even perform mimicry by dyeing their hair and highly educated women have considerable difficulties finding a partner. Blondes are more conspicuous for predators and this would appear to reduce their fitness value. Like the peacock's tail, however, such traits may nevertheless evolve as a sign of fitness, but in that case blondes would have to be smart and strong, not dumb. A better explanation, therefore, is that the dumb-blond phenotype signals that the individual (and its kin, human or animal) has evolved under relaxed evolutionary conditions, similar to the conditions prevailing under domestication. This, of course, could make the human dumb blonde highly attractive for men as it raises the hope that the offspring will accrue similar benefits (plenty of food; few predators, enhanced reproductive capacity). Herein, also lays an important Darwinian warning. Success of the past is no guarantee for the future. We learned from Hitler's illusion to establish a blonde Arien Third Reich; we learned from the economy, which many thought would continue to grow. Similarly, many involved in livestock breeding still believe selection for increased production-efficiency can go on forever. It can't. There is a limit to unidirectional growth in all biological systems. That much should be clear from Darwin's legacy.

To the memory of Charles Darwin with whom I happen to share an interest in evolution, domestication and emotion.

Dr. Marc Bracke
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Congressen en andere bijeenkomsten

- **ISAE – 2009**, 43th Congress of the International Society for Applied Ethology, 6-10 July, 2009, Cairns, Australia (<http://www.isae2009.com>).
- **15th European Meeting for PhD Students in Evolutionary Biology**, 14-19t August 2009, Schoorl, The Netherlands (<http://www.empseb2009.nl>)
- **IEC – 2009**, XXXI International Ethological Conference, 19-24 August, 2009, Rennes, France (<http://iec2009.univ-rennes1.fr>).
- **Workshop Context, Causes and Consequences of Conflict**, Leiden, The Netherlands, 31 August – 4 September 2009 (<http://www.lorentzcenter.nl/lc/web/2009/343/info.php3?wsid=343>)
- **Summer Conference of the ASAB** "The Descent of Man and Selection in Relation to Sex" 2 to 4 September 2009, St. John's College, University of Oxford, UK, (<http://www.zoo.ox.ac.uk/events/asab09/>)
- **16th Benelux Congress of Zoology**, 28 to 30 October 2009 Wageningen, The Netherlands (<http://www.beneluxcongress.com>)
- **Annual meeting of the Netherlands Society for Behavioural Biology**, 25 to 27 November 2009 Dalfsen (The Netherlands) (<http://www.gedragsbiologie.nl>)
- **ISAE – 2010**, 44th Congress of the International Society for Applied Ethology, 4-7 August, 2010, Uppsala, Sweden, (<http://www.isaesweden2010.se/>)

Het Proefschrift

Guido Bosch

Can diet composition affect behaviour in dogs? Food for thought

Wageningen University, 18 March 2009
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The consumption of food goes beyond the basic provision of energy and essential nutrients for the maintenance of physical health. Studies in rats, pigs, and human subjects have shown that behaviour and mood can be influenced by specific nutrients consumed. The research described in this thesis aimed to evaluate the impact of dietary composition on two physiological systems involved in the regulation of canine behaviour. Studies in pigs has shown that physical activity of pigs can be influenced by dietary fibre type, likely through sustaining satiety after a meal. It appears that the fermentable fibres can stimulate several mechanisms involved in sustaining satiety including the stimulation of the secretion of satiety-related metabolites by the gastrointestinal tract. Furthermore, hunger has been found to influence anxiety in rats. Studies were conducted to evaluate the potential impact of dietary fibre types for effects on satiety and behaviour in dogs. Two diets were formulated differing in fibre fermentability (low vs. high-fermentable) and fed to kennelled beagle dogs. The secretion of satiety-related metabolites (PYY, GLP-1, and ghrelin) was found not to differ between treatment groups. Feeding dogs a high-fermentable fibre diet did result in a lower motivation to eat 6 hours after their morning meal and these dogs showed a lower activity in their home-kennel compared to dogs fed a low-fermentable fibre diet. Treatment groups did not differ in their responses to short-lasting challenges in a test arena conducted 5 to 7 hours

after their morning meal. The second dietary strategy investigated was the use of the essential amino acid tryptophan, the precursor of the neurotransmitter serotonin in the brain. It has been shown that dietary tryptophan supplementation reduces anxiety in rats and increases resilience in dealing with stress in pigs. To investigate if similar effects would occur in dogs, a study was designed and conducted in mildly anxious privately-owned dogs fed diets differing in tryptophan content. Dogs were fed the study diet for 8 weeks using a randomised double-blinded, placebo-controlled design. Intake of the tryptophan supplemented diet increased plasma tryptophan concentrations and its ratio with large neutral amino acids compared to the control diet but the data reported by owners did not show a significant change in the behavioural of the dogs over time that could be attributed to the specific dietary treatment. More controlled behavioural tests conducted on a subset of dogs in both dietary treatment groups failed to show a significant difference of supplementation of the diet with tryptophan. In conclusion, the present work has shown that dietary fibre type can have an impact on canine behaviour through feeding motivation. The measured satiety-related metabolites were not affected by dietary fibre type indicating that other mechanisms were involved in sustaining satiety. Dietary supplementation of tryptophan had no effect on the behaviour of privately-owned dogs.

Het Proefschrift

Ralf Mullers

The commuting parent. Energetic constraints in a long distance forager, the Cape gannet.

University of Groningen, 4 May 2009
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Cape gannets (*Morus capensis*) breeding at the west coast of Namibia and South Africa, decreased in numbers of breeding pairs over the last few decades. In Namibia this decline was associated with extensive over-fishing of their pelagic fish prey sardines (*Sardinops sagax*) and anchovies (*Engraulis encrasicolus*), whereas in South Africa these prey species showed a south-eastward distribution shift away from the gannet breeding colonies. The aim of my PhD-project was to study the behavioural mechanisms that underlie these population changes.

In South Africa the distribution shift of the pelagic prey had two main consequences; either the parents looked for alternative prey or they made longer foraging trips, possibly to search for sardines and anchovies. At Malgas Island the only alternative at the beginning of the breeding season seemed to be fishery discards.

Although these are easy to obtain, they are of very poor quality (low energy and lipid content). The growth of gannets chicks was associated with the proportion of anchovies and sardines in the diet and fishery discards were not a suitable alternative. In periods of food shortage parents also made longer foraging trips and left their young alone when they were still too young. These chicks then became vulnerable for predation; eggs and young chicks were taken by kelp gulls (*Larus dominicanus*), older chicks (between 4 – 8 weeks) by great white pelicans (*Pelecanus onocrotalus*) and fledglings by the thousands by Cape fur seals (*Arctocephalus pusillus pusillus*). I calculated that at Malgas only 0.17 chicks were reared by gannet couples, where 0.32 chicks would be needed to keep the colony stable.

At Ichaboe Island (Namibia), parents made longer trips than gannets from Malgas, but their chicks grew faster and

were heavier at fledging for three consecutive years. I did not find any indication that processes during the breeding season were associated with population dynamics. Possibly processes outside the breeding season determine population changes for this colony. However, the Benguela is a dynamic system and possibly we did our project under favourable conditions for this colony.

In accordance with life-history theory, we found that Cape gannet parents, as a long-lived species, did not risk their own survival for that of their young. In a handicapping study we showed that unmanipulated parents were able to compensate for the reduced parental care of their partner; when their chicks were young (< 30 days old) they increased nest attendance and when chicks were older they increased trip frequency. However, they did not risk their own body condition. For example, chicks that died during the experiment had parents with a lower body condition at the beginning of the experiment. This was confirmed in a year when food availability decreased and parents

stayed away longer. Chick growth and survival was associated with parental behaviour, but not with parental body condition. Parents first secured their own body condition, before the condition of their young.

Descriptive research, like this PhD project, often has some interesting surprises in the dataset. The Cape gannet is a monomorphic species, and we determined the sexes through DNA-analyses in retrospect. We found that the sexes differed quite substantially in behaviour; females stay away longer (4.8 h) and covered more distance (70 km) during their foraging trips than males (data obtained from GPS-loggers). Until now we could not determine the evolutionary significance of this difference. Males and females brought back the same sort and amount of food and, seemed to be foraging at the same feeding sites. A more detailed analysis on their diving behaviour might reveal why females need more time during their foraging trips.

Het Proefschrift

Marion Nicolaus

Reproductive rates under competition

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Life-history theory predicts that individuals behave optimal and hence the reproductive decisions they take should maximize fitness. Optimal reproductive investment involves trading-off both the number versus the quality of offspring produced and the current versus the future reproduction of the parent. In this thesis an experimental approach was used to establish causal effects of altered social environment on habitat choice and reproductive trade-offs of great tits

(*Parus major*). Local social environments (nestling density and sex ratio) were manipulated for three years via simultaneous brood size and brood sex ratio manipulations of 12 woodlots (plots) in the Lauwersmeer area. I will summarize some of the main findings:

Social effects on dispersal and habitat selection

Dispersal and habitat selection can be influenced by social effects through opposite mechanisms (1) High density

male biased plots may be unattractive for settlement if they elicit high level of competition (2) High density male biased plots may be attractive for settlement if they signal high quality habitat. In this thesis I investigated which mechanisms explained juvenile redistribution in the area the next year. Natural plot density had a strong negative effect on yearling habitat selection. Birds were more likely to emigrate from high density plots and less likely to settle in these plots, especially males. In high density plots, juveniles had also a reduced recruitment chance. Avoiding settling in high density plots may have been a mean to avoid negative effect of competition among juveniles and adults. Interestingly, habitat choice was also affected by the plot sex ratio manipulation. Juveniles settled preferentially in plots that were male biased the previous year. High juvenile plot densities resulting from male philopatric behavior may have signaled good quality habitat to prospecting young in the summer and consequently may have appeared attractive for settlement. Juvenile emigration and settlement decisions were thus the outcome of a balance between positive (use of social information as cue for habitat quality) and negative (competition avoidance) effects of social environment.

Fitness consequences of competition

Once birds settled, the fitness costs associated with large broods were expected to be higher in high competitive environments (high density and/or male biased plots). The effect of altered social environment on the fitness costs and benefits of brood size were thus quantified. I found no effects of the experiment (brood size and plot manipulations) on the number of recruits per nest. The increased productivity of enlarged broods may have been counter-balanced by a reduced recruitment probability of those young that were in poorer body condition. This may have resulted in an apparent lack of experimental effects of brood size variation on the number of recruits per brood. Importantly, brood size manipulation did entail reproductive costs. These costs expressed in terms of reduced probability of producing a second brood and adult local survival probability depended on the proportion of males in the plot, i.e. on the level of local competition. In high competitive environments, parents with enlarged brood size paid a higher cost of reproduction because they may have become of lower phenotypic quality and may then have been outcompeted by birds in better shape. The pattern was opposite in female biased plots. These results imply that optimal clutch sizes depend on local social environments and that social effects can play an important role in micro-evolutionary processes determining clutch size.

Het Proefschrift

Katleen Huyghe

Sexual selection and the functional ecology of lizards

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In this thesis, I investigate how secondary sexual traits interrelate and how they contribute to the reproductive

success of lizards. Sexual dimorphism may arise through selection to reduce resource competition and in this way

enhance niche partitioning between the sexes. Alternatively or additionally, dimorphic traits may reflect the outcome of the conflict between the sexes and are favoured by sexual selection. Especially in polygynous species, where males compete with other males for resources (for example territories) and, ultimately, access to females, sexual selection acts on male traits, such as morphology, physiological performance, immunity, and behaviour. I examined how and to what extent these male characters interact and contribute to male dominance (intrasexual competition) and female choice (intersexual competition) in two lacertid lizard species (*Gallotia galloti* & *Podarcis melisellensis*).

Both species are polygynous and sexually dimorphic, and therefore seemed excellent model species for the study of sexual selection. Moreover, *P. melisellensis* males occur in three distinct morphs: they have a bright white, orange or yellow ventral coloration. This provides an opportunity to test hypotheses regarding the origin and maintenance of such a polymorphism in a population. The co-existence of males of the different morphs suggests that there may be more than one solution to the challenges imposed by the social (sexual) environment. The success of a morph could be considered as the balanced result of its strengths and weaknesses, and morphs may represent alternative tactics, subject to sexual selection.

Sexual selection acts on performance traits, such as sprint speed, endurance and bite capacity, which may be important in male dominance disputes and/or female choice events. In both species, I found that the ability of a male to generate bite force, and not locomotor capacity, affects the probability of winning a fight. In contrast, bite force is not implicated in female choice; female *P. melisellensis* choose males that have a better condition, not males that can bite harder.

Down the performance gradient, particularly head size and shape, and muscle mass are important underlying factors that affect performance. Not surprisingly, males with relatively larger heads bite harder. Likewise, jaw muscle mass correlates positively with bite force capacity. In *P. melisellensis*, orange males have relatively bigger heads, they have relatively heavier jaw muscles, and they bite relatively harder, than white and yellow males. However, differences in jaw muscle mass and head size do not fully explain the variation in bite force among morphs. Also, geometric morphometric analyses showed only minor differences in head shape. It is unclear which trait(s) contribute further to the orange morph's increased bite capacity.

Besides the morphological traits, behavioral traits may also influence the outcome of performance trials. Androgens, such as testosterone and corticosterone could affect morphology (muscle mass) and behaviour (the willingness to perform). I found that testosterone levels correlate positively with muscle mass and bite performance in natural (unmanipulated) conditions, and that the administration of extra testosterone results in heavier muscles, but not in better bite performance. There seems to be a role for testosterone in determining morphology and performance, but it does not explain the differences between *P. melisellensis* morphs, and increasing testosterone levels do not ameliorate performance. As no differences in hormone concentrations were found between the morphs, the mechanisms of origin and maintenance of this polymorphism are not androgen based. The immunocompetence handicap hypothesis describes a possible trade-off between the development of sexual signals, through testosterone, and immunocompetence. Contrary to the predictions of this hypothesis, testosterone, immune response and parasite load did not interrelate in *P. melisellensis*. Also, the three morphs did not differ in immune response or parasite load, rejecting the handicap

hypothesis as a possible mechanism in maintaining the polymorphism. When colour polymorphisms are associated with differences in morphology, performance, and behaviour, and when this divergence in life-history traits is genetically influenced, assortative mating may result in reproductive isolation between the morphs. Genetic divergence, therefore, provides an excellent opportunity to study the early stages of adaptive diversification, and possibly eventually sympatric speciation driven by sexual conflict. In a population genetics study of the divergence of

neutral microsatellite markers, I found signs of subtle genetic divergence between the alternate morphs.

In conclusion, this study shows that the adaptation paradigm by S.J. Arnold is useful in studies of sexual selection, as the relations between traits of different organismal levels are complex and, therefore, should not be studied in isolation. The ecomorphological approach is also useful in studying the evolutionary mechanisms of polymorphism. However, it is difficult to take into account all links that might determine survival and mating success.