Adaptation and constraints in avian reproduction: integrating ecology and endocrinology

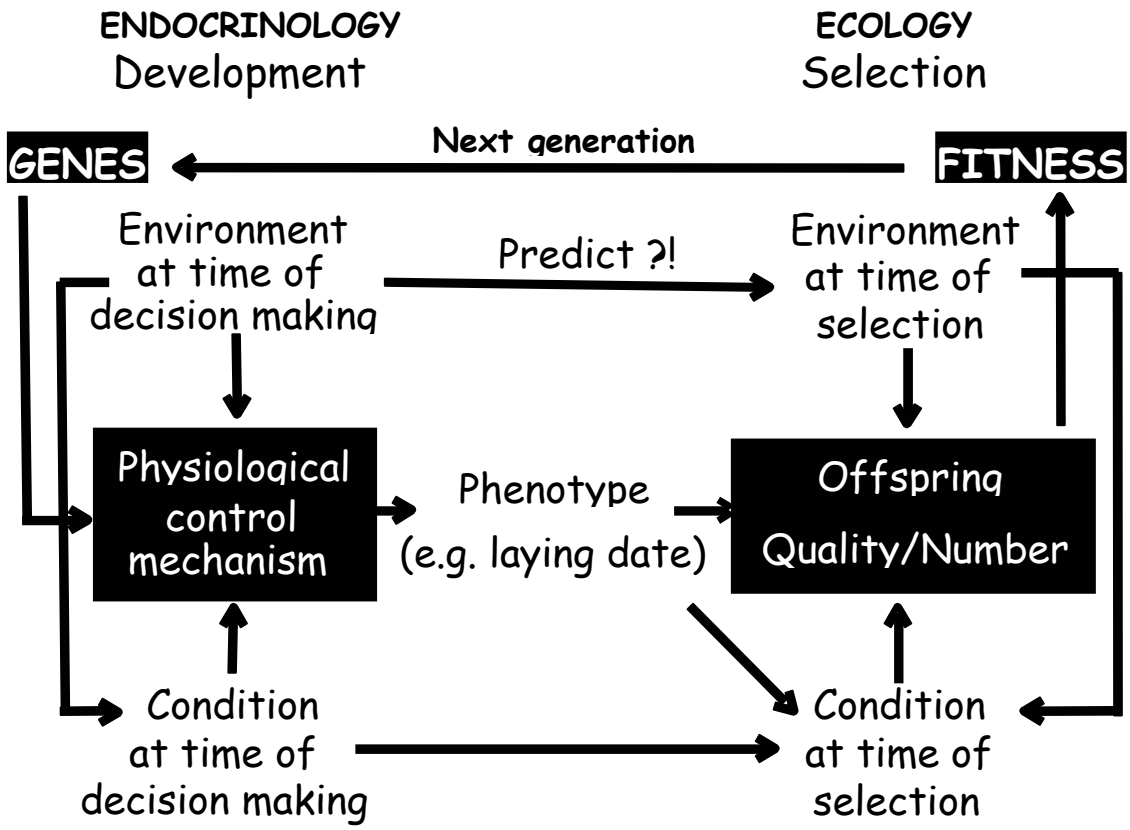
A linked ESF and NSF workshop, 5-7 September 2002 – Wageningen, The Netherlands

Scientific report

The ESF/NSF workshop aimed to bring together avian specialists with different scientific backgrounds to establish new contacts and initiate profound discussions how ecologists and endocrinologists can collaborate in future research networks. A common goal is to ameliorate simultaneously the knowledge of the proximate and ultimate determinants of ecological traits and major events of annual life cycles in free-living bird populations that face rapid environmental change.

Ecologists and endocrinologists often investigate the same biological phenomena, but approach these using different scientific key-questions and methodologies. This has been illustrated in detail during the first two talks of the workshop (20:00–22:00, 5 September), one presented by an ecologist (K. Lessells), the other presented by an environmental endocrinologist (J. Wingfield). Ecologists want to know how ecological traits (e.g. reproductive traits) are shaped by natural selection, but often ignore the underlying physiological mechanisms responsible for the ontogeny of optimal phenotypes. In addition, evolutionary responses to selection pressures are only possible if phenotypic variation has a genetic basis. Endocrinologists investigate phenotype development that results from interactions between genes, environmental factors (resources, cues, stimuli) and the physiological response mechanism (endocrine, neuro-endocrine system). Hormones do not only determine phenotypic expression and plasticity, but also regulate the developmental phase, the mature capability phase, and termination phase of life-cycle events and the transitions between these events. Endocrinologists are aware that physiological response mechanisms can be studied in an evolutionary context, but often do not take selection processes and fitness consequences into account. Integrated multi-disciplinary research becomes indispensable, given the general consensus among the workshop participants that selection shapes physiological response mechanisms across generations, and that

developmental processes determine optimal responses to selection pressures within generations (summarised in Figure 1).



Integration of ecological and endocrinological approaches is indeed possible. Two examples of successful integrated multi-disciplinary projects have been presented during the morning session of the second day (09:00–10:00, 6 September). E. Ketterson and her group applied "phenotypic engineering" to artificially create "sub-optimal" phenotypes. Free-ranging males were treated with testosterone implants to quantify numerous potential implications for expression of morphology, physiology, behaviour, and fitness. These investigations also examined social consequences for offspring and mates. Ketterson argued that the evolution of male testosterone may be slowed down by constraints acting at the proximate organisational (impact of T on many target tissues) or ultimate social (selection on females) level. T. Groothuis' integrated study aimed to identify constraints, fitness costs and benefits of hormone transfer from the mother to the egg using both comparative and experimental analyses. Potential short-term and long-term consequences of land use changes for maternal/paternal determined offspring development have been discussed in this context.

During the next session, which took up the rest of the second working day (11:00-21:50, 6 September), all participants presented briefly their research activities to provide a more detailed overview of the state-of-art in avian ecology and endocrinology. Each speaker handled one or more aspects of the multi-factor network presented in Figure 1. This session described research on over 10 endocrine or neuro-endocrine chemicals (e.g. testosterone, prolactin, androstenedione, LH, GnRH peptide, GnRH mRNA, aromatase, corticosteroids, leptin, triiodithyronine), discussed more than 20 biological phenomena (e.g. timing of breeding, reproductive effort, egg quality, conflicts between sexes, offspring and generations, sex ratios, growth patterns, copulation behaviour, incubation behaviour, maternal effects, nestling competition, chick begging behaviour, dispersal, territoriality, BMR, mating systems), citing more than 30 avian model systems (e.g. passerines, seabirds, tropical birds, birds of prey, non-domesticated and domesticated species). Studies described links between environmental factors (photoperiod, climate, resources, social stimuli, environmental perturbations), physiological responses of the neuro-endocrine (e.g. aromatase, brain estrogens, ZENK) and endocrine system (adrenocortical responses), behavioural responses (e.g. aggression, sexual behaviour, onset or effort of reproduction, parental care, moult, movements), fitness components (e.g. offspring quality, survival), population parameters (e.g. breeding density), and/or different aspects of natural selection (e.g. selection differentials and gradients). Some researchers investigated the genetic basis of life-history trait variation using approaches developed in quantitative genetics. Studies mentioned constraints (e.g. resource allocation trade-offs), costs and/or benefits at the level of the physiological response mechanism, the phenotype, and the selection mechanism. Work has been done at different spatial (e.g. within vs. between individuals, within vs. between populations, within vs. between species) and temporal scales (short-term vs. long-term), also showing that factors that explain between-species variation are not necessarily those factors that explain within-species variation. The session clearly revealed that different investigators often study the same phenotypic traits, and sometimes use the same biological model systems (e.g. European starlings, great tits, zebra finches), but do not necessarily address the same specific scientific questions, and consequently do not apply the same methodologies. Some focus on laboratory work with domesticated species, looking often at the impact of experimental alterations of the environment (e.g. photoperiod, temperature) or circulating hormone levels (e.g. implants) on phenotypic expression, such as aggressive or sexual behavior. Others looked at implications of life-history trait (e.g. brood size) manipulations for reproduction and fitness components

using long-term studies of free-ranging species. Investigations that combined long-term and laboratory studies in non-domesticated avian species are rare. The session of the 32 talks provided an essential overview of the two research fields and gave us a unique opportunity to see where the fields complement each other and where ecologists and endocrinologists need to collaborate to get to a full understanding on how bird populations cope with changing environments.

During the last working day (09:00-12:00, 14:00-15:30, 7 September) discussion between endocrinologists and ecologists were organised. Using Figure 1 as a starting point, following key-question was presented to stimulate discussion: "How is an event of the annual cycle influenced by alterations of the environment based on what we know about its endocrine basis, with predictions for both phenotypic expression and plasticity (proximate level) and selection and evolution (ultimate level)?" Groups of 5-8 members were formed to discuss the themes (1) pair formation and territoriality (Ball, Balthazart, Sheldon, Ketterson, Silverin, Sandell) (2) timing of reproduction (Wingfield, Hau, Schoech, Lambrechts, Visser), (3) clutch size and parental care (Thompson, Dunn, Martin, Monaghan, Eens, Chastel, Boswell, Badyeav), (4) egg characteristics (size/quality) (Groothuis, Williams, Adkins-Regan, Lessells, Schwabl, Reed), and (5) moult, migration and over-wintering (Breuner, Le Maho, Jenni, Dufty, Helm, Dawson). Each group provided a summary of what is know, and what should be known on the subject, and a list of aspects to be addressed in future research programs. The theoretical advancement in the fields of ecology and endocrinology apparently differs between research themes. For instance, the neuro-endocrine basis of pair formation is well known, but seems to be understudied for other aspects of the annual life cycle. Another example is clutch size examined extensively in experimental and comparative ecological research, but of which the physiological basis is poorly understood. The final general conclusion of these discussions is that current ecological and endocrinological knowledge remains insufficient for the construction of powerful predictions related to causes and consequences of environmental change on the functioning of bird populations. This last point has also been made in the next session.

The following session has been devoted to research themes deserving much more attention in future research programs (15:30-16:30, 7 September). Birds, as many other free-living organisms, are affected by processes related to global changes. Global changes are defined "as those that (1) alter the atmosphere and oceans and hence are experienced globally (e.g.

climate change), and (2) those that occur in discrete sites but are so widespread as to constitute a global change" (e.g. changes in land use). M. Lambrechts' overview of impacts of pollution, climate change and land use changes on birds point out that future research should put extensive effort into the identification of the physiological response mechanisms that shape phenotypes in response to global change. Research should also be devoted to determine the capacity of free-ranging bird populations to adapt to global change processes. In addition, each modern avian scientist would very much like to know the genes that are involved in phenotypic expression and plasticity, which, unfortunately, is not yet possible. T. Boswell's final talk summarised the recent progress made in the application of knowledge of DNA sequences in avian species focusing on research in Galliformes, and the potential use of genomic research for free-ranging bird species.

The final discussion of the workshop (17:00-18:30, 7 September) was devoted to the request of the need to construct a network stimulating exchange of knowledge among ecologists and endocrinologists. All workshop participants agreed that both research domains would certainly benefit from such an initiative. Remarks have been made that such a network should also include other aspects of ecophysiology, especially those aspects that are related to the quantification of nutrition, body condition, metabolic rate, and energy budgets (see Figure 1). Subjects have been proposed for the organisation of other workshops related to priority themes, such as (1) Development, (2) Tradeoffs/Constraints, (3) Modulation of stress in response to environmental change, (4) Maternal effects, (5) Individual variation and (6) Techniques, and for the creation of a Web-site devoted to studies integrating ecological and endocrinological research.

To conclude, there was consensus among the participants that the workshop had been very successful in bringing together scientists from the two fields, and in identifying where ecologists and endocrinologists complement each other. There is a very clear and urgent need to establish contacts between researchers from both fields and the meeting was very much in favour of applying for a network on avian ecology and endocrinology. It was therefore decided to apply both with the ESF and the NSF for such a network, to be launched in 2003.

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Final Programme

Day 0 (Thursday)

17:00 Arrival & Bar open
18:30 Dinner

20:00 Opening

Visions from an ecological and endocrinological point of view: where are the differences
20:10 Kate Lessells – Ecology (30 min talk – 15 min. discussion)

20:55 John Wingfield – Endocrinology (30 min talk – 15 min. discussion)

21:40 Bar & hand in all Powerpoint files for the 9 minutes talks of day 1

Day 1 (Friday)

Examples showing successful integration of ecology and endocrinology
09:00 Ellen Ketterson (20 min. talk – 10 min. discussion)

09:30 Ton Groothuis (20 min. talk – 10 min. discussion)

10:00 General Discussion

Rest of day 1: Current research programmes (31 talks of 9 minutes)

11:00 Introduction to rest of day 1

11:10 8 short talks (7 min. talk plus 2 min. discussion)

Liz Adkins-Regan
Greg Ball
Creagh Breuner
Al Dufty
Michaela Hau
Steve Schoech
Hubert Schwabl
Tony Williams

12:30 Lunch

14:00 6 short talks (7 min. talk plus 2 min. discussion)

John Wingfield
Jacques Balthazart
Olivier Chastel
Alistair Dawson
Barbara Helm
Yvon Le Maho

15:00 Break

15:30 9 short talks (7 min. talk plus 2 min. discussion)

Tim Boswell
Bengt Silverin
Alexander Badyaev
Peter Dunn
Ellen Ketterson
Tom Martin
Wendy Reed
Charles Thompson
Marcel Eens

17:00 Break

17:30 6 short talks (7 min. talk plus 2 min. discussion)

Ton Groothuis
Susi Jenni
Kate Lessells
Pat Monaghan
Maria Sandell
Ben Sheldon

18:30 Dinner

20:00 2 short talks (7 min. talk plus 2 min. discussion)

Marcel Lambrechts
Marcel Visser

20:20 General discussion & introduction to day 2

20:45 Bar

Day 2 (Saturday)

Discussion of 6 themes to be developed with working groups
9:00 Introduction

9:15 Discussion in small working groups, focussing on the events of the annual cycle and asking how each might be affected by environmental change (temperature, diseases, predators, etc.) based on what we know or need to know about its endocrine basis, with predictions for both the near-term (phenotypic plasticity) and far-term (selection and evolution). Themes are:
1. Pair formation/territoriality
2. Timing of reproduction
3. Clutch size
4. Egg characteristics (size/quality)
5. Parental care
6. Moult
7. Migration/overwintering

10:30 Break

11:00 Presentation of group reports
10 min per group

12:00 General Discussion

12:30 Lunch

14:00 Marcel Lambrechts: Global change: Constraints to adaptation (20 talk min., 10 min. discussion)

14:30 Tim Boswell: Towards genomics (20 min. talk, 10 min. discussion)

15:00 Break

15:30 Towards an ESF/NSF network on *Adaptation and constraints in avian reproduction: integrating ecology and endocrinology*

18:00 Pause

18:30 Dinner

Day 3 (Sunday)

09.00 Excursion to Hoge Veluwe (incl. Kröller-Müller museum)

ESF/NSF workshop: Adaptation and constraints in avian reproduction: integrating ecology and endocrinology

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