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Bewick's swans in a changing world

Species responses and the need for dynamic nature conservation

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References
Author Contributions
Author Affiliations
PE&RC Training and Education Statement

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Chapter 2 RJMN, SJGV and BAN conceptualized the study. TH, ECR and BAN provided data. RJMN and SGJV built the model, analyzed the data. BAN and EJ consulted on model design. RJMN and SJGV wrote the manuscript. KAW, ECR, EJ, BAN provided comments on the manuscript.

Chapter 3 RJMN conceptualized the study. EFP, JL CM facilitated data collection in the zoo. RJMN collected and analyzed the data. BAN consulted on the initial results. RJMN wrote the manuscript. EFP, JL, CM and BAN provided comments.

Chapter 4 RJMN and TG conceptualized the study. TG designed and produced the GPS/GSM collars, and hosted the server for data retrieval. RJMN and BAN performed the field work. RJMN analyzed the data. RJMN wrote the manuscript. TG provided technical consultation. JS-B and BAN provided comments on the manuscript.

Chapter 5 RJMN and BAN conceptualized the study. RJMN and BAN performed the field work. RJMN analyzed the data. RJMN and BAN wrote the manuscript.

Box 1 RJMN and BAN conceptualized the study, and performed the field work. AK provided initial script (R code). RJMN analyzed the data. RJMN wrote the text. BAN provided comments.

Chapter 6 RJMN and BAN conceptualized the study. TH, ECR and BAN provided data. RJMN analyzed the data. BAN consulted on initial results. RJMN wrote the manuscript. KAW, TH, ECR and BAN provided comments on the manuscript.

Chapter 7 RJMN and EK conceptualized the study. JW, TH, ECR and BAN provided data. RJMN analyzed the data. EK consulted on data analysis and manuscript writing. RJMN wrote the manuscript. JW, TH and BAN provided comments.

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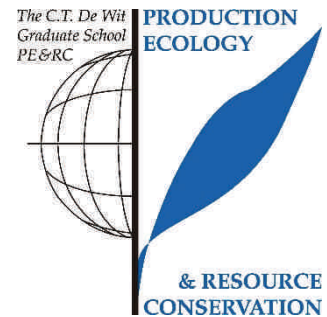
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PE&RC Training and Education Statement

PE&RC TRAINING AND EDUCATION STATEMENT

With the training and education activities listed below the PhD candidate has complied with the requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)



Review of literature (4.5 ECTS)

- Unravelling the annual cycle of an Arctic migrant in search of the cause of its decline

Post-graduate courses (6.9 ECTS)

- Integrated population modelling using BUGS and JAGS; Swiss Ornithological Institute and university of Cape Town (2015)
- Animal movement ecology; IBED, UVA (2015)
- Laboratory animal science designing procedures and projects and bird specific module; KNAW (2016)

Invited review of (unpublished) journal manuscript (7 ECTS)

- Global Change Biology: demography migratory birds (2015)
- Biological Conservation: migratory connectivity (2016)
- Global Change Biology: demography migratory birds (2016)
- Ecology and Evolution: conservation whooping cranes (2016)
- Bird Conservation International: stopover site protection (2017)
- Biology and Environment: bird monitoring Ireland (2017)

Competence strengthening / skills courses (2.8 ECTS)

- Workshop clim-win R-package; NIOO-KNAW (2016)
- An introduction to R for spatial analysis and mapping; Datacamp (2016)
- Systematic literature review; WGS (2016)

Scientific integrity / ethics in science activity (0.3 ECTS)

- Workshop on ethics in science; SENSE (2015)

PE&RC ANNUAL MEETINGS, SEMINARS AND THE PE&RC WEEKEND (1.2 ECTS)

- PE&RC Day (2016, 2017)
- PE&RC Weekend (2017)

DISCUSSION GROUPS / LOCAL SEMINARS / OTHER SCIENTIFIC MEETINGS (8.4 ECTS)

- Netherlands annual ecology meeting (2015-2017)
- NIOO Journal club (2015-2020)
- NIOO Theme global environmental change (2017-2019)

INTERNATIONAL SYMPOSIA, WORKSHOPS AND CONFERENCES (6.6 ECTS)

- British Ornithological union conference; oral presentation; Warwick (2017)
- International ornithological conference; poster presentation; Vancouver (2018)
- 6th International swan symposium; oral presentation; Tartu (2018)

SOCIETALLY RELEVANT EXPOSURE (1.5 ECTS)

- Pinguïn veren verraden migratieroute; Nieuws & Co, NPO Radio 1 (2017)
- Wetenschappers wereldwijd: mens verziekt aarde op grote schaal; Nieuws & Co, NPO Radio 1 (2017)
- Uitkijk over afnemende biodiversiteit; Nieuws & Co, NPO Radio 1 (2018)
- Waar zijn de kleine zwanen?; Vroege Vogels, NPO Radio 1 (2020)

- Scientific American's 60 second science (2020)

SUPERVISION OF STUDENTS (12 ECTS)

- Integrated population model Bewick's swan
- Distribution shift Bewick's swan
- Migration phenology
- Behavioural classification

Summary / Samenvatting

Summary

Many species are currently threatened with extinction due to global environmental changes. Their ability to respond to these changes will determine their fate. Our efforts to protect nature, are often fixed in both time and space. This could undermine the effectiveness of conservation efforts. Therefore, it is argued, that nature conservation may benefit from a more dynamic approach.

Within this thesis I studied individual and population level changes of a migratory bird, the Bewick's swan *Cygnus columbianus bewickii*, in a period of environmental change. The western population of Bewick's swan, wintering in North-Western Europe and breeding at the Russian Arctic tundra, was shown to be declining between 1995-2015. In search of the cause of this decline we first studied the demographic rates of the population. Previous research based on a capture-mark-resighting survival analysis did not yield concluding results. By including population counts and reproductive counts in an integrated analysis with mark-resighting data, we were able to show a decreasing trend in apparent breeding success and a simultaneous increasing trend in juvenile survival (**Chapter 2**). None of the explanatory variables (except for year) explained the decline in apparent breeding success, while both water level in autumn and temperature in summer/autumn positively affected juvenile survival. The results raised the question whether juvenile survival might be able to compensate for low breeding success.

As was confirmed by the population model (Chapter 2), the Bewick's swans showed a negative population trend between 1995 and 2015. The shape of this curve was however dependent on the range country. Further analysis of capture-mark-resighting data revealed that the population as well as swans have significantly shifted their wintering distribution eastwards (i.e. 'short-stopping'; **Chapter 6**) which can explain the drastic declines in the western part of the range (Ireland and UK) when compared to counts in the east (Germany and Poland). In addition, the swan population also shortened their stay in the wintering area (i.e. 'short-staying'; Chapter 6). These changes happened in parallel with climate warming in NW Europe.

Zooming in to the wintering area even more, the wintering area of the swans can be described as a well-connected network of sites, between which the swans traverse to fulfill their needs (**Chapter 7**). The importance of the different sites changed over time, partly in concordance with the eastward shift, but also related to the habitat of the sites. Agricultural field gained interest by the swans, whereas grasslands were used less in recent years.

Capture-mark-resighting data can yield valuable information on both the individual and, when analyzed in concordance, population level. Especially in species with high detection probabilities like the Bewick's swan. However, these detection probabilities are only reached on the wintering grounds, where observer density is high. GPS tracking provides much more detail and is independent of observer efforts and differences therein between geographic areas.

Following the rapid development in GPS tracking devices, 3D printed GPS/GSM collars were extended with an accelerometer and conductivity sensor to collect additional data during the migration of the Bewick's swans. Through thorough calibration by testing the collars on captive

individuals, 6 different behavioural classes could be identified with 91% accuracy (**Chapter 3**). Time-activity budgets during spring migration of individual swans showed considerable variation in levels of aquatic foraging, although the seasonal patterns were similar between individuals, with increased levels of aquatic foraging in Estonia and in the White Sea area (Russia).

As a solution to the technical challenges that came with GPS/GSM tracking of a species that is outside phone reception for part of the year, a lossy data reduction method was developed to be able to collect accelerometer with small intervals (**Chapter 4**). The use of the 'summary statistics' rather than the raw accelerometer data increased the monitoring frequency (limited by the energy and storage capacity of the device) by a factor six, without compromising the ability to remotely detect behaviour in the downloaded data.

Between 2007 and 2019, 81 individual spring migration tracks and 68 individual autumn migration tracks were collected (**Box 1**). Although variation was small, swans were shown to time their migration in response to year-to-year variation in environmental conditions. At the same time, an analysis of multiple year tracks from the same individuals convincingly showed that both migration speed and their relative route (expressed as sinuosity) were highly consistent within individuals between years. Furthermore, we found that, although juveniles accompany their parents on their first autumn and spring migrations, they start developing their own migratory tradition in subsequent years. This finding has implications for how we perceive the development of migratory behaviour in species with extended parental care.

Reflecting on the status of the Bewick's swan population as 'Threatened' on the European Red List of Birds, we assessed whether current protective measures in NW Europe (mainly the Natura 2000 network) are sufficient to secure key habitats for this population. As these key sites have shifted over time (**Chapter 7**) it was found that, especially in recent years, some important sites were not protected. Considering the short-stopping process observed in this population (Chapter 6), it is to be expected that the mismatch between the important sites for the swans and the Natura 2000 protected areas with conservation objectives for this species will increase.

A similar analysis during the spring migration season showed ambiguous results. The stopover sites that were known to be important for the swans, were still used in recent years (**Chapter 5**). In the southern part of the migratory route, where circumstances regarding macrophyte coverage and condition are relatively well known, the swans predominantly foraged within the boundaries of protected areas. However, in the northern part, less protected areas are in place and Bewick's swans were found to frequently use areas that are not protected. The increasing pressure of human development in combination with lucrative oil and gas exploitation in the area poses a significant threat to the existence of vital stopover areas for the swans and other migratory waterfowl in this flyway (Chapter 5).

Taking in the results of this thesis, it can be concluded that the western population of Bewick's swans has shown considerable changes over the study period of ~ 50 years. These changes can in part explain the population decline and have shown that the observed Bewick's swan population trend is liable to the geographic scale and the timing of monitoring. Conjointly however, the increasing mismatch between swan site use with Natura 2000 protected areas and the foreseen threats to some vital stopover sites on this species flyway, make the

population vulnerable to declines. To effectively protect species such as the Bewick's swan that show changes over time in their site use and timing, a dynamic form of nature conservation is proposed in which ecological knowledge drives decisions made on the local level.

Samenvatting

Veel soorten worden momenteel met uitsterven bedreigd als gevolg van wereldwijde veranderingen in bijvoorbeeld landgebruik en het klimaat. Hun vermogen om op deze veranderingen te reageren zal hun lot bepalen. Onze inspanningen om de natuur te beschermen, liggen vaak vast in tijd en ruimte. Dit kan de effectiviteit van de inspanningen voor natuurbehoud ondermijnen. Daarom wordt gesteld, dat natuurbehoud kan profiteren van een meer dynamische aanpak.

Binnen dit proefschrift heb ik de individuele en populatieveranderingen van een trekvogel, de kleine zwaan *Cygnus columbianus bewickii*, bestudeerd in een periode van veranderingen in klimaat en landgebruik. De westelijke populatie van de Bewick's zwaan, die overwintert in NW Europa en broedt op de Russische Arctische toendra, toonde een dalende populatietrend tussen 1995 en 2015. Op zoek naar de oorzaak van deze daling hebben we eerst de demografie van de populatie bestudeerd. Eerder onderzoek op basis van terugmeldingen van individueel gemerkte individuen leverde geen sluitende resultaten op. Door het combineren van populatietellingen en reproductieve tellingen in een geïntegreerde analyse met de terugmeldingen, konden we een dalende trend in schijnbaar broedsucces en een gelijktijdige stijgende trend in juveniele overleving aantonen (**hoofdstuk 2**). Geen van de verklarende variabelen (behalve het jaartal) verklaarde de afname van het schijnbare broedsucces, terwijl zowel het waterpeil in de herfst als de temperatuur in de zomer/herfst de overleving van de jongen positief beïnvloedde. De resultaten roepen de vraag op of juveniele overleving een laag broedsucces zou kunnen compenseren.

Zoals bevestigd door het populatiemodel (hoofdstuk 2), vertoonden de kleine zwanen tussen 1995 en 2015 een negatieve populatietrend. Opvallend was echter dat de vorm van deze curve verschilde, afhankelijk van het land waar geteld werd. Een analyse van de terugmelding toonde aan dat de populatie, maar ook individuele zwanen, hun overwinteringsgebied aanzienlijk naar het oosten hebben verschoven (d.w.z. '*short-stopping*'; **hoofdstuk 6**), wat de drastische dalingen in het westelijke deel van het verspreidingsgebied (Ierland en het Verenigd Koninkrijk) kan verklaren in vergelijking met de tellingen meer in het oosten (Duitsland en Polen). Daarnaast heeft de populatie van de kleine zwaan ook zijn verblijf in het overwinteringsgebied verkort (d.w.z. '*short-staying*'; hoofdstuk 6). Deze veranderingen vonden plaats parallel aan de opwarming van het klimaat in NW Europa.

Door nog meer in te zoomen op het overwinteringsgebied werd duidelijk dat dit kan worden omschreven als een goed verbonden netwerk van gebieden, waartussen de zwanen zich verplaatsen om in hun behoeften te voorzien (**hoofdstuk 7**). Het belang van de verschillende gebieden veranderde in de loop van de tijd, deels in overeenstemming met de verschuiving naar het oosten, maar ook in verband met de habitat van de gebieden. Velden met landbouwgewassen werden meer gebruikt in recente jaren, en grasland werd juist minder belangrijk.

Terugmeldingen kunnen waardevolle informatie opleveren over zowel het individu als het populatieniveau, vooral bij soorten met zo'n hoge detectiekansen als de kleine zwaan. Deze detectiekansen worden echter alleen gehaald in de overwinteringsgebieden, waar de dichtheid van de waarnemers hoog is. GPS-tracking geeft veel meer details en is onafhankelijk van de inspanningen van de waarnemers en de verschillen tussen de geografische gebieden.

In navolging van de snelle ontwikkeling van GPS-trackingapparaten werden 3D geprinte GPS/GSM-halsbanden uitgebreid met een versnellingsmeter en een watersensor om extra gegevens te verzamelen tijdens de migratie van de kleine zwanen. Door grondige kalibratie door het testen van de halsbanden op kleine zwanen in gevangenschap konden 6 verschillende gedrags-categorieën met 91% nauwkeurigheid worden geïdentificeerd (**hoofdstuk 3**). De activiteitsbudgetten tijdens de voorjaarsmigratie van de individuele zwanen lieten een aanzienlijke individuele variatie zien in de mate van aquatisch foerageren, hoewel de patronen over het seizoen tussen de individuen vergelijkbaar waren, met verhoogde niveaus van aquatisch foerageren in Estland en in het Witte Zee-gebied in Rusland.

Als een oplossing voor de technische uitdagingen die gepaard gingen met GPS/GSM-tracking van een soort die een deel van het jaar buiten de telefoonontvangst leeft, werd een methode ontwikkeld om met hoge frequentie versnellingsmeter gegevens te kunnen verzamelen (**hoofdstuk 4**). Door het gebruik van de 'samenvattende statistieken' in plaats van de ruwe versnellingsmeter gegevens werd de meet-frequentie (beperkt door de energie en de opslagcapaciteit van het apparaat) met een factor 6 verhoogd, zonder afbreuk te doen aan het vermogen om het gedrag in de gedownloadede gegevens te detecteren.

Tussen 2007 en 2019 werden 81 individuele voorjaarsmigraties en 68 individuele herfstmigraties verzameld (**Box 1**). Hoewel de variatie klein was, werd duidelijk dat de zwanen tot op zekere hoogte reageerden op de jaar-op-jaar-variatie in de omgevingsvariabelen. Tegelijkertijd toonde een analyse van individuen die meerdere jaren gevolgd waren overtuigend aan dat zowel de migratiesnelheid als hun relatieve route (uitgedrukt als 'bochtigheid') binnen de individuen tussen de jaren zeer consistent waren. Verder vonden we dat, hoewel jonge vogels hun ouders vergezellen op hun eerste herfst- en voorjaarsmigratie, ze hun eigen migratietraditie beginnen te ontwikkelen in hun zelfstandige jaren. Deze bevinding heeft implicaties voor de manier waarop we de ontwikkeling van het migratiegedrag bij soorten met uitgebreide ouderlijke zorg bekijken.

In het licht van de bedreigde status van de kleine zwanen populatie in NW Europa op de Europese Rode Lijst van Vogels is beoordeeld of de huidige beschermingsmaatregelen in NW Europa (voornamelijk het Natura 2000-netwerk) voldoende zijn om belangrijke gebieden voor deze populatie veilig te stellen. Aangezien deze belangrijke gebieden voor de kleine zwaan in de loop van de tijd zijn verschoven (**hoofdstuk 7**), werd vastgesteld dat sommige belangrijke gebieden in de recente jaren niet beschermd waren. Met het oog op het '*short-stopping*' proces dat bij deze populatie is waargenomen, valt te verwachten dat de *mismatch* tussen de belangrijke gebieden voor de zwanen en de beschermde Natura 2000-gebieden met een instandhoudings-doelstelling voor deze soort zal toenemen.

Een gelijksoortige analyse tijdens het voorjaarsmigratie seizoen liet verschillende resultaten zien. De pleisterplaatsen waarvan bekend was dat ze belangrijk waren voor de zwanen, werden in recente jaren nog steeds gebruikt (**hoofdstuk 5**). In het zuidelijke deel van de trekroute, waar de aanwezigheid en de conditie van de macrofyten relatief goed bekend zijn, foerageren de zwanen voornamelijk binnen de grenzen van de beschermde gebieden. In het noordelijke deel zijn er echter minder beschermde gebieden en de zwanen bleken vaak gebruik te maken van gebieden die niet beschermd zijn. De toenemende druk van de menselijke ontwikkeling in combinatie met de lucratieve olie- en gaswinning in het gebied is een onbekende en potentieel significante bedreiging voor het bestaan van vitale pleisterplaatsen voor de zwanen en andere trekkende watervogels in deze migratie flyway (**hoofdstuk 5**).

Op basis van de resultaten van dit proefschrift kan worden geconcludeerd dat de westelijke populatie van de kleine zwanen in de loop van de studieperiode van ~ 50 jaar aanzienlijke veranderingen heeft laten zien. Deze veranderingen kunnen voor een deel de afname van de populatie verklaren en hebben aangetoond dat de waargenomen populatiegrootte onderhevig is aan de geografische schaal en de timing van de telling. Tegelijkertijd maakt de toenemende *mismatch* tussen het gebruik van de gebieden door de zwanen en de beschermde Natura 2000-gebieden met een instandhoudingsdoelstelling voor de kleine zwaan, in combinatie met de voorziene bedreigingen voor enkele vitale pleisterplaatsen tijdens de voorjaarsmigratie, deze populatie kwetsbaar voor achteruitgang. Om deze en andere soorten die in de loop van de tijd veranderingen in het verspreiding en fenologie laten zien effectief te beschermen, wordt een dynamische vorm van natuurbehoud voorgesteld, waarbij ecologische kennis de basis vormt voor beslissingen die op lokaal niveau worden genomen.

Thank you