Animal personalities on the move

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Summary

The diversity of animal movement and its link to personality

Movement is a key factor connecting an organism with its environment. Movement can be induced by environmental conditions, and it can lead to a change in these conditions. Movement requires more than the morphological and physical abilities that are necessary for a change in location – it also requires sensory and cognitive abilities for navigation, behavioural tendencies such as novelty-seeking or boldness, and social capabilities allowing the coordination with conspecifics. As movement is an important determinant of organismal survival and reproduction (and, hence, organismal fitness), one would expect that movement and all its underlying features are jointly shaped by natural selection. But this does not imply that, in a given environment, evolution will result in a single fitness-maximising movement strategy. In fact, it is recently becoming clear that, even within a population, animals exhibit a wide array of movement types. Moreover, various other morphological, physiological, and behavioural traits are associated with movement, forming a so-called 'syndrome'. All this raises several questions: Why is there variation in movement types? What drives the evolutionary emergence and stable persistence of different movement types? Which factors determine the evolution of movement-related syndromes?

To address these questions, I studied the movement behaviour of three-spined sticklebacks in the wild, in the lab, and in a semi-natural system of connected ponds. Moreover, I conducted some theoretical studies on the evolution of movement types and behavioural syndromes.

Migration in sticklebacks - a natural experiment

In the north of the Netherlands, three-spined sticklebacks breed in inland freshwaters in spring and early summer. In autumn, the juveniles of the year migrate to the sea

where they grow to adult size during winter, before returning to the freshwater in the next spring. In the last 50 years, man-made barriers (such as pumping stations and sluices) have been extensively built in rivers to maintain water levels below sea level, with the consequence that some of the side water drainages are cut off from the main river channel. As a result, several populations of 'resident' sticklebacks are trapped in freshwater for their whole lifecycle. This leads to two types of stickleback populations in the Netherlands: one part still able to migrate to the sea ('migrant'), and a 'resident' counterpart. This unique situation can be viewed as an unintended large-scale replicate experiment, where we can compare several populations of residents and migrants, allowing us to study the implications of restricted movement. In particular, we can use the system to ask if 50 years of isolation are enough to shape a new movement type and, potentially, a new movement syndrome.

As a first step, we caught wild sticklebacks from migratory and nearby resident populations and measured several traits (including body size, lateral plates on the body and behaviours such as movement tendency, shoaling, exploration in a novel environment, response to a predator and so on). We found that migratory sticklebacks are bigger, have more armament (lateral plates) and differ from residents in virtually all behavioural traits we measured (**Chapter 2**). Specifically, migrants show a higher movement tendency and a higher tendency to be in a group (shoaling), behaviours that are both important for a migratory lifecycle. However, as the measurements were made on wild fish that have spent their lives under different environmental conditions, it is unclear whether the observed differences in morphology and behaviour reflect a response to the environment (developmental plasticity) or genetic differentiation between migrant and resident populations.

In **Chapter 3**, we address this point by conducting a 'common-garden' experiment – we made four crossings (migrant x migrant, resident x resident, migrant x resident, resident x migrant) and raised the offspring under the same environmental conditions. It turned out that some of the conspicuous differences between migrants and residents that we observed in Chapter 2 (e.g. the large size difference and the armament in migrants) did not occur in the F1 offspring. Apparently, these differences were caused by the environmental differences experienced by the wild-caught fish in Chapter 2. However, some differences reappeared, despite the fact that the F1 offspring had experienced identical rearing conditions. Most notably, movement and shoaling tendencies, crucial behaviours related to migration, were highest in migrant x migrant offspring and lowest in resident x resident offspring, indicating that 50 years of isolation were sufficient to produce substantial genetic differentiation between neighbouring resident and migrant populations.

Mesocosm system - a stepping stone between the lab and the field

Ideally, questions such as those tackled by my thesis should be studied under natural conditions. This, however, is a major challenge. Tracking individuals in the wild is often technologically demanding and for a small fish such as the stickleback, it is virtually impossible to track groups in the wild. Therefore, field studies on fish are often complemented by aquarium studies in the lab. We undertook this as the first step in Chapters 2 3. Lab studies have the advantage of offering control over confounding variables and recording high-resolution behavioural data but they hardly represent the situation in the wild in terms of the complexity of the environment. For this reason, we developed a system of connected ponds that allowed us to study the sticklebacks in considerable detail under much more natural conditions. This 'mesocosm' system was connected to a nearby freshwater ditch allowing natural water, nutrients etc. to be pumped in. We also allowed the growth of plants and algae and water flow, mimicking the ditches through which stickleback in the Netherlands usually move and which they use for breeding. We saw that sticklebacks readily used the mesocosm, moving between the ponds through the corridors and readily started breeding in spring, indicating that the mesocosm indeed mimics the natural environment for these fish and hence can be used as a stepping stone between lab and field studies. We equipped the ponds with antennas between the corridors and within the ponds such that we can remotely record when a tagged fish is detected in the vicinity of an antenna. Thus we are able to remotely track large numbers of fish, over longer duration of time while allowing a semi-natural environment.

In **Chapter 4**, we asked if groups of migrant and resident sticklebacks differ in their movement tendencies in the ponds. We did not find differences in short-scale movement (within ponds), but, as expected, migrants moved much more than residents over larger scales (between ponds), confirming that the two types have indeed diverged in their movement tendencies. In order to explore this in more detail, we also tested the fish under various ecological conditions such as different water flows and group sizes. We found that, irrespective of these conditions, migrants consistently exhibit higher larger-scale movement tendencies than residents.

Behavioural tendencies can be strongly affected by the social environment. The effect of the social environment is, however, usually difficult to quantify, due to the difficulty of tracking all individuals of a social group and of testing the same individuals in different social groups. Our mesocosm allows us to track not only focal fish but also groups of fish, in different group compositions. In **Chapter 5**, we did this by following resident and migrant individuals in different group contexts (different percentages of migrant and resident fish). To our surprise, we found that residents and migrants maintained their inherent movement tendencies across different social contexts, indicating that these movement tendencies are not affected by the social environment.

Insights from individual-based models

In addition to my empirical work, I also participated in two theoretical studies that intend to provide insights into the question of how individual differences in characteristics like competitive ability affect the movement of individuals and the distribution of individuals in space. In an **Intermezzo** and in **Chapter 6**, we ran individual-based evolutionary simulations to study movement in the context of foraging on a resource landscape. When the resource landscape is relatively stable throughout the lifetime of individuals, individual differences in competitive ability quickly disappear in the course of evolution. This changes considerably when the resource distribution is reshuffled repeatedly. Now, a broad spectrum of competitive types evolves from an initially homogeneous population. We could explain this novel mechanism for the evolutionary emergence of individual differences by the fact that strong competitors have a fitness benefit under stable environmental conditions, while weak competitors profit from environmental change. Hence, the spatiotemporal variation of the environment is key to the evolution of individual differences.

Finally, I conclude my thesis with a general discussion where I reflect on the question "Where are we now - where should we go next?" with regards to the questions and methodologies pertaining to the stickleback system and also more broadly the field of animal personality research.

Nederlandse samenvatting

Het verband tussen bewegingsstrategieën en persoonlijkheid

Beweging (de verplaatsing van individuele dieren naar een andere locatie) is een sleutelfactor die een organisme met zijn omgeving verbindt. Beweging kan worden uitgelokt door omgevingsomstandigheden, en kan leiden tot een verandering van deze omstandigheden. Beweging vereist meer dan de morfologische en fysieke vaardigheden die nodig zijn voor een verandering van plaats - zij vereist ook zintuiglijke en cognitieve vaardigheden voor navigatie, gedragsneigingen zoals het zoeken naar nieuwigheden of stoutmoedigheid, en sociale capaciteiten die de coördinatie met soortgenoten mogelijk maken. Aangezien beweging in belangrijke mate bepalend is voor overleving en voortplanting (en dus voor het reproductieve succes van het organisme), zou men verwachten dat beweging en alle onderliggende kenmerken daarvan gezamenlijk door natuurlijke selectie worden bepaald. Maar dit impliceert niet dat, in een gegeven omgeving, evolutie zal resulteren in één enkele optimale bewegingsstrategie. De laatste tijd is duidelijk geworden dat dieren, zelfs binnen een populatie, een breed scala aan bewegingstypes vertonen. Bovendien worden verschillende andere morfologische, fysiologische en gedragskenmerken geassocieerd met beweging, waardoor een zogenaamd "syndroom" ontstaat. Dit alles roept verschillende vragen op: Waarom is er variatie in bewegingstypes? Wat is de drijvende kracht achter het evolutionaire ontstaan en de stabiele persistentie van verschillende bewegingstypes? Welke factoren bepalen de evolutie van bewegingsgerelateerde syndromen?

Om deze vragen te beantwoorden, bestudeerde ik het bewegingsgedrag van driedoornige stekelbaarsjes in het wild, in het lab, en in een semi-natuurlijk systeem van verbonden vijvers. Bovendien voerde ik enkele theoretische studies uit over de evolutie van bewegingstypes en gedragssyndromen.

Migratie bij stekelbaarsjes - een natuurlijk experiment

In het noorden van Nederland broeden driedoornige stekelbaarsjes in het voorjaar en de vroege zomer in zoete binnenwateren. In de herfst migreren de jonge stekelbaarsjes naar zee, waar ze in de winter uitgroeien tot volwassen exemplaren, alvorens in het volgende voorjaar terug te keren naar het zoete water. In de afgelopen 50 jaar zijn in de rivieren op grote schaal kunstmatige barrières (zoals gemalen en sluizen) gebouwd om het waterpeil onder de zeespiegel te houden, met als gevolg dat sommige zijwaterafvoeren van de hoofdgeul van de rivier zijn afgesneden. Het gevolg is dat verschillende populaties 'residente' stekelbaarsjes gedurende hun hele levenscyclus in zoet water gevangen zitten. Dit leidt tot twee soorten stekelbaarspopulaties in Nederland: een deel dat nog kan migreren naar zee ('migranten'), en een 'residente' tegenhanger. Deze unieke situatie kan worden gezien als een onbedoeld grootschalig replicatie-experiment, waarbij we verschillende populaties van residenten en migranten met elkaar kunnen vergelijken, zodat we de implicaties van beperkte verplaatsing kunnen bestuderen. In het bijzonder kunnen we het systeem gebruiken om ons af te vragen of 50 jaar isolatie voldoende is om een nieuw bewegingstype en, mogelijk, een nieuw bewegingssyndroom te vormen.

Als eerste stap vingen we wilde stekelbaarsjes van migrerende en naburige residente populaties en maten we verschillende eigenschappen (waaronder lichaamsgrootte, beschermende platen op het lichaam en gedragingen zoals bewegingsneiging, scholingsdrang, exploratie in een nieuwe omgeving, reactie op een predator, enzovoort). We ontdekten dat migrerende stekelbaarzen groter zijn, meer beschermende platen hebben en verschillen van residenten in vrijwel alle gedragskenmerken die we hebben gemeten (**hoofdstuk 2**). Meer specifiek, migrerende stekelbaarsjes vertonen een grotere bewegingsneiging en een grotere neiging om in een groep te zitten (scholingsdrang), gedragingen die beide belangrijk zijn voor een migrerende levenscyclus. Aangezien de metingen werden verricht bij wilde vissen die hun leven onder verschillende milieuomstandigheden hebben doorgebracht, is het echter onduidelijk of de waargenomen verschillen in morfologie en gedrag een reactie op het milieu (ontwikkelingsplasticiteit) of een genetische differentiatie tussen migrerende en residente populaties weerspiegelen.

In **hoofdstuk 3** gaan we op dit punt in door een 'common-garden' experiment uit te voeren - we maakten alle kruisingen tussen migranten en residenten en brachten de nakomelingen groot onder dezelfde milieuomstandigheden. Het bleek dat sommige van de opvallende verschillen tussen migranten en residenten die we in hoofdstuk 2 hadden waargenomen (bijv. het verschil in grootte) niet voorkwamen bij de F1-nakomelingen. Blijkbaar werden deze verschillen veroorzaakt door de milieuverschillen die de in het wild gevangen vissen in hoofdstuk 2 ondervonden. Sommige verschillen kwamen echter terug, ondanks het feit dat de F1 nakomelingen identieke opkweekomstandigheden hadden ondergaan. Met name de bewegings- en scholingsdrang , cruciale gedragingen die verband houden met migratie, waren het grootst bij nakomelingen van migranten x migranten en het kleinst bij nakomelingen van residenten x residenten, wat erop wijst dat 50 jaar isolatie voldoende was om een aanzienlijke genetische differentiatie teweeg te brengen.

Een semi-natuurlijk systeem (mesokosmos systeem) als springplank tussen het lab en het veld

Idealiter zouden vragen zoals die in mijn proefschrift onder natuurlijke omstandigheden moeten worden bestudeerd. Dit is echter een grote uitdaging. Het volgen van individuen in het wild is vaak technologisch veeleisend en voor een kleine vis als de stekelbaars is het vrijwel onmogelijk om groepen in het wild te volgen. Daarom worden veldstudies op vissen vaak aangevuld met aquariumstudies in het lab. In de hoofdstukken 2 en 3 hebben wij dit als eerste stap gedaan. Laboratoriumstudies hebben het voordeel dat ze controle bieden over verstorende variabelen en dat ze gedragsgegevens met een hoge resolutie registreren. Echter zijn ze nauwelijks representatief voor de situatie in het wild, gezien de complexiteit van het milieu. Daarom hebben wij een systeem van met elkaar verbonden vijvers ontwikkeld, dat ons in staat stelde de stekelbaarsjes in veel meer detail te bestuderen onder veel natuurlijker omstandigheden. Dit 'mesokosmos'-systeem was verbonden met een nabijgelegen zoetwatersloot, waardoor natuurlijk water, voedingsstoffen etc. konden worden binnengepompt. We lieten ook planten en algen groeien en water stromen, waarmee we de sloten nabootsten waar stekelbaarsjes in Nederland gewoonlijk doorheen trekken en die ze gebruiken om zich voort te planten. We zagen dat stekelbaarsjes de mesokosmos gemakkelijk gebruikten, zich via de gangen tussen de vijvers verplaatsten en in het voorjaar gemakkelijk begonnen met broeden, wat erop wijst dat de mesokosmos inderdaad de natuurlijke omgeving voor deze vissen nabootst en dus gebruikt kan worden als opstapje tussen lab- en veldstudies. We hebben de vijvers uitgerust met antennes in de tussengangen en in de vijvers, zodat we op afstand kunnen registreren wanneer een vis met een RFID chip in de nabijheid van een antenne wordt waargenomen. Op die manier kunnen we grote aantallen vissen op afstand volgen, over langere perioden, en in een semi-natuurlijke omgeving.

In **hoofdstuk 4** vroegen we of groepen migrerende en residente stekelbaarsjes verschillen in hun verplaatsingstendensen in de vijvers. We vonden geen verschillen in verplaatsingen over korte afstanden (binnen vijvers), maar, zoals verwacht, verplaatsten migranten zich veel meer dan bewoners over grotere afstanden (tussen vijvers), wat bevestigt dat de twee soorten inderdaad van elkaar verschillen in hun verplaatsingstendensen. Om dit nader te onderzoeken, testten we de vissen ook onder verschillende ecologische omstandigheden, zoals verschillende waterstromen en groepsgroottes. We ontdekten dat, ongeacht deze omstandigheden, migranten consistent een grotere neiging tot bewegen vertonen dan bewoners.

Gedragstendensen kunnen sterk worden beïnvloed door de sociale omgeving. Het effect van de sociale omgeving is echter meestal moeilijk te kwantificeren, omdat het moeilijk is alle individuen van een sociale groep te volgen en dezelfde individuen in verschillende sociale groepen te testen. Ons mesokosmos stelt ons in staat niet alleen individuele vissen te volgen, maar ook groepen vissen, in verschillende groepssamenstellingen. In **hoofdstuk 5** hebben we dit gedaan door residente en migrerende individuen te volgen in verschillende groepscontexten (verschillende percentages migrerende en residente vissen). Tot onze verrassing vonden we dat residenten en migranten hun inherente bewegingstendensen behielden in verschillende sociale contexten, wat erop wijst dat deze bewegingstendensen niet beïnvloed worden door de sociale omgeving.

Inzichten uit op het individu gebaseerde simulaties

Naast mijn empirische werk heb ik ook meegewerkt aan twee theoretische studies die inzicht moeten verschaffen in de vraag hoe individuele verschillen in kenmerken zoals competitief vermogen de beweging van individuen en de verdeling van individuen in de ruimte beïnvloeden. In een **Intermezzo** en in **hoofdstuk 6** bespreken we de uitkomst van evolutionaire, op individu gebaseerde, simulaties. In deze modellen worden individuen gesimuleerd, om beweging te bestuderen in de context van foerageergedrag. Wanneer de verdeling van het voedsel relatief stabiel is gedurende het leven van individuen, leidt evolutie tot één competitiestrategie. Dit verandert aanzienlijk wanneer de voedselverdeling herhaaldelijk verandert. In dat geval evolueert een breed spectrum aan competitiestrategieën. Met andere woorden, onder fluctuerende omstandigheden ontstaan verschillende 'persoonlijkheden'. We konden dit nieuwe mechanisme voor het ontstaan van individuele verschillen verklaren door het feit dat competitief sterke individuen een voordeel hebben onder stabiele milieuomstandigheden, terwijl competitief zwakke individuen profiteren van milieuveranderingen.

Tenslotte sluit ik mijn proefschrift af met een algemene discussie waarin ik reflecteer op de vraag "Waar staan we nu en waar moeten we naartoe?" wat betreft de vragen en methodologieën die betrekking hebben op het stekelbaarssysteem en ook meer in het algemeen op het gebied van persoonlijkheidsonderzoek bij dieren.

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About the author

Aparajitha (Apu) Ramesh, was born in Chennai, India on July 25, 1993. In 2011, Apu started an integrated bachelor's and master's studies in Biology at the Indian Institute of Science Education and Research, Thiruvananthapuram (IISER-TVM). In 2017, she was awarded an Adaptive Life scholarship from the University of Groningen to pursue her PhD in the groups of Franjo Weissing (Theoretical Research in Evolutionary Life Sciences), Marion Nicolaus (Conservation Ecology) and Ton Groothuis (Evolutionary Genetics, Development and Behaviour). She has broad research interests, including individual differences in behaviour, animal movement and migration, and competition. Her eventual career goal is an academic position studying the evolution of animal behaviour, using a combination of theoretical and empirical approaches, operating at the nexus of different disciplines with a strong affinity to teaching.

Publications

1. Netz, C., **Ramesh, A.**, Gismann, J., Gupte, P. R., & Weissing, F. J. (2022). Details matter when modelling the effects of animal personality on the spatial distribution of foragers. Proceedings of the Royal Society B, 289(1970), 20210903.

2. **Ramesh, A.**, Groothuis, T. G., Weissing, F. J., & Nicolaus, M. (2022). Habitat fragmentation induces rapid divergence of migratory and isolated sticklebacks.

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3. **Ramesh, A.**, Domingues, M. M., Stamhuis, E. J., Groothuis, T. G. G., Weissing, F. J., & Nicolaus, M. (2021). Does genetic differentiation underlie behavioral divergence in response to migration barriers in sticklebacks? A common garden experiment. Behavioral Ecology and Sociobiology, 75(12), 1-12.

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