Dissecting yeast-dependent population differentiation and spatial segregation in Drosophila melanogaster

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English Summary

Adaptation to different environments is a major mechanism in phenotypic evolution and species diversification. Among the different environmental factors, food is a key driver of local adaptation and speciation. Numerous cases of food-mediated speciation are seen in birds and insects, but how populations exploiting different food resources differentiate and become reproductively isolated from each other remain poorly understood. The research presented in this thesis aimed at dissecting how heterogeneous food resources can drive population differentiation and assortative mating between populations, using the model organism *Drosophila melanogaster* and its essential food resource – yeast.

The chemosensory system is the most ubiquitous sensory channel in animals to detect and respond to food resources. Chemosensory divergence may thus play a crucial role in food-mediated adaptation and speciation. In **Chapter 2**, we formulated seven key questions to explore how the chemosensory system can facilitate food-mediated ecological speciation. We used examples of insect research and integrated approaches from different scientific disciplines. We started by identifying which aspects of food resources are heterogeneous in a given environment (Question 1), as this is the starting point of divergent selection. We then discussed which aspects of food exert selection on consumers (Question 2), and explored how consumers detect (Question 3), exploit (Question 4) and adapt to these resources (Question 5) to understand how local adaptation proceeds. Finally, we discussed whether successful exploitation of new food resources is genetically inherited and/or acquired during an individual's lifetime (Question 6) and reviewed the mechanisms that reduce gene flow between populations that specialize on alternative resources (Question 7). The formulated seven questions allowed us to find some knowledge gaps. Notably, different approaches are needed for different questions. There is rarely one model system in which all seven questions have been thoroughly answered. It is often not clear what kind of heterogeneity, or which aspect of a particular resource, will generate divergence in consumers. Because of the important roles gut microbes play in resource exploitation ability and mate choice of hosts, we proposed microbes in the gut as a promising direction for future research on food-mediated ecological speciation.

The successful exploitation of a food resource is a multifactorial phenotype that involves a range of traits. Thus, dietary specialization will be facilitated by the correlated evolution of these traits. In **Chapter 3,** we used *Drosophila melanogaster* and yeast to explore the scope for dietary specialization. We quantified how different *D. melanogaster* strains from around the globe respond to different yeast species, across multiple yeast-dependent life history traits including feeding, mating, egg-laying, egg development and survival. We found fly strains varied in their responses to different yeast species: some strains performed well on a specific yeast species, while other strains did not. We did not detect the trade-offs in performance on different yeast species: performance on alternative yeast species is positively correlated. Yeast-dependent trait responses were not aligned: different life-history traits were maximized on different yeast species. Our results confirmed the existing insight that *D. melanogaster* is a resource generalist: it can grow, reproduce and survive on all the yeast species we tested.

Taken together, our findings suggest that there are evolutionary constraints for these important life-history traits to adapt in concert, possibly providing a mechanistic explanation of the limited extent of dietary specialization in *D. melanogaster* strains across the globe.

Heterogeneity in food resources can facilitate assortative mating: when mating takes place on food resources, assortative mating can arise as a by-product of food choice. In **Chapter 4 & 5,** we studied the spatial coupling of food and mates, the sensory and behavioural mechanisms underlying this spatial coupling, and whether this coupling would potentially promote assortative mating. To quantify the location of foraging and sexual behaviour of individuals in a heterogeneous environment, we built a system which combined the low-cost Raspberry Pi video recording system with the fast and efficient TRex tracking software and Matlab scripts to provide an automated, fast, efficient and easy-to-use method for fly tracking in **Chapter 4**. By tracking the location of fruit flies in environments containing heterogeneous food patches, we observed that *D. melanogaster,* either alone or in pairs with the opposite sex, stayed on yeast at night, but individuals' tendencies to be on the yeast during the day depended on several variables including sex, light conditions and presence of the other sex. To further explore the spatial coupling of food and mates and the underlying mechanism mediating the dynamics of the spatial coupling of food and mates, we tracked the mating location of both virgin and mated flies under different light conditions for 24h. We found that *D. melanogaster* and several of its sibling species generally chose to mate on patches containing yeast. In *D. melanogaster* however, virgin females primarily mated away from yeast, but previously mated females re-mated on yeast. Using experimental manipulation of the chemical composition of the yeast-containing patches and mutant flies lacking sex peptide (males; SP) and sex peptide receptor (females; SPR), we established the sensory and behavioural mechanisms underlying this spatial coupling of food and mates. We found that mating location preference involved attraction to yeast-derived chemical cues (the combination of acetic acid and protein) and was modulated by the male-derived sex peptide received by females during mating. This preference for mating on yeast-containing patches was stronger at night than during the day, and increased with the passing of time since the first mating. In choice experiments with two different yeast species, we discovered that *D. melanogaster* pairs exerted preferences for mating on one yeast species over another. Together, our study suggests that some level of assortative mating may result from the preference for mating on yeast, but the strength of such assortative mating will depend on several variables including the presence of multiple yeast species and timing of (re)mating with respect to light cycle.

Overall, this thesis dissects the mechanisms underlying food-mediated population differentiation and assortative mating. On one hand, we find that the inconsistency of responses between life-history traits forms a possible limitation to dietary specialization and population differentiation. On the other hand, we discover that food preference may directly lead to assortative mating through its spatial coupling with mates. Our findings highlight the importance of analyzing multiple life-history traits involved in food exploitation to explore the scope of food-mediated population differentiation and examining several variables including mating status, the presence of multiple food resources and timing of (re)mating with respect to light cycle to assess the potential strength of assortative mating that may result from the preference for mating on food resources.

Nederlandse Samenvatting

Translation by Gerrit Potkamp

Adaptatie aan verschillende omgevingen is een belangrijk mechanisme in fenotypische evolutie en diversificatie van soorten. Voedsel is, te midden van verschillende omgevingsfactoren, een belangrijke aanjager van lokale adaptie en soortvorming. In vogels en insecten zijn tal van voorbeelden van voedsel-gemedieerde soortvorming aan te wijzen. Hoe populaties die verschillende voedselbronnen exploiteren differentiëren en reproductief geïsoleerd raken is echter niet goed begrepen. Het onderzoek gepresenteerd in dit proefschrift richtte zich op het ontleden hoe heterogene voedselbronnen populatiedifferentiatie en assortatieve paring tussen populaties kunnen aandrijven, door gebruik te maken van het modelorganisme *Drosophila melanogaster* en zijn essentiële voedselbron – gist.

Het chemosensorisch systeem is bij dieren het belangrijkste zintuiglijk kanaal in het detecteren van en reageren op voedselbronnen. Chemosensorische divergentie zou daarom een cruciale rol kunnen spelen in voedsel-gemedieerde adaptie en soortvorming. In **Hoofdstuk 2** formuleerden we zeven sleutelvragen om te ontdekken hoe het chemosensorisch systeem voedsel-gemedieerde ecologische soortvorming kan mediëren. We begonnen met het identificeren welke aspecten van voedselbronnen heterogeen zijn in een bepaalde omgeving (Vraag 1), omdat dit het startpunt van divergente selectie is. Daarna bespraken we welke aspecten van voedsel selectie uitoefenen op consumenten (Vraag 2), en verkenden hoe consumenten deze bronnen detecteren (Vraag 3), exploiteren (Vraag 4) en zich er aan adapteren (Vraag 5) om te begrijpen hoe lokale adaptie te werk gaat. Tenslotte bespraken we of succesvolle exploitatie van nieuwe voedselbronnen genetisch is geërfd en/of verworven is gedurende het leven van een individu (Vraag 6) en bekeken we de mechanismen die genenoverdracht tussen populaties die zich op verschillende bronnen specialiseren reduceren (Vraag 7). De zeven geformuleerde vragen liet ons enkele gaten in onze kennis zien. In het bijzonder, verschillende benaderingen zijn nodig voor het beantwoorden van de verschillende vragen. Alle zeven vragen zijn maar zelden volledig beantwoord in een enkel modelsysteem. Het is vaak niet duidelijk wat voor soort heterogeniteit, of welk aspect van een bepaalde bron, divergentie in consumenten zal genereren. Vanwege de belangrijke rol die darmmicroben spelen in het vermogen bronnen te exploiteren en de partnerkeuze van gastheren wezen we deze microben in het darmstelsel aan als een veelbelovende richting voor toekomstig onderzoek naar voedsel-gemedieerde ecologische soortvorming.

De succesvolle exploitatie van een voedselbron is een fenotype met meerder facetten waar een scala aan eigenschappen bij betrokken is. Dieetspecialisatie zal daarom worden gefaciliteerd door de gecorreleerde evolutie van deze eigenschappen. In **Hoofdstuk 3** gebruikten we *Drosophila melanogaster* en gist om het domein van dieetspecialisatie te verkennen. We kwantificeerden hoe verschillende *D. melanogaster*-stammen van over de hele wereld reageren op verschillende gistsoorten, over meerdere gist-afhankelijke levensgeschiedenis-eigenschappen waaronder voeden, paren, het leggen van eitjes, de ontwikkeling van eitjes en overleving. We vonden dat vliegenstammen varieerden in hun respons op verschillende gist soorten: sommige stammen presteerden goed verschillende gistsoorten, andere stammen niet. We detecteerden geen compromis in prestatie op verschillende gistsoorten: de prestatie op alternatieve gistsoorten is positief gecorreleerd. Gist-afhankelijke reacties waren niet afgestemd: verschillende levensgeschiedenis-eigenschappen waren gemaximaliseerd op verschillende gistsoorten. Onze resultaten bevestigden het bestaande idee dat *D. melanogaster* een generalist is: hij kan groeien, reproduceren en overleven op alle geteste gistsoorten. Onze bevindingen suggereren bij elkaar genomen dat er evolutionaire beperkingen voor deze belangrijke levensgeschiedenis-eigenschappen om zich gezamenlijk aan te passen bestaan, wat mogelijk een mechanistische verklaring biedt van de beperkte dieetspecialisatie van *D. melanogaster*-stammen verspreid over de wereld.

Heterogeniteit in voedselbronnen kan assortatieve paring faciliteren: wanneer paring plaatsvindt op voedselbronnen kan assortative paring ontstaan als een bijproduct van voedselkeuze. In **Hoofdstuk 4 & 5** bestudeerden we de ruimtelijke koppeling tussen voedsel en partners, de onderliggende sensorische en gedragsmatige mechanismen hiervan, en of deze koppeling assortatieve paring zou kunnen bevorderen. Om de locatie van foerageren en seksueel gedrag van individuen in een heterogene omgeving te kwantificeren hebben we in **Hoofdstuk 4** een systeem gebouwd dat een geautomatiseerde, snelle, efficiënte en gebruiksvriendelijke methode voor het volgen van vliegen biedt door het goedkope Raspberry Pi video-opnamesysteem te combineren met de snelle en efficiënte TRex tracking software en Matlab scripts. Door de locatie van fruitvliegen in omgevingen met heterogene voedselplekken te volgen observeerden we dat *D. melanogaster,* ofwel alleen of in paren met het andere geslacht, ’s nachts op gist verbleef, maar dat de neiging van individuen zich overdag op gist te begeven afhankelijk was van verschillende variabelen, waaronder geslacht, de lichtcondities en de aanwezigheid van het andere geslacht. Om de ruimtelijke koppeling tussen voedsel en partners en de onderliggende mechanismen die de dynamiek van deze koppeling mediëren verder te onderzoeken volgden we de locatie van zowel maagdelijke als gepaarde vliegen in verschillende lichtcondities gedurende 24 uur. We vonden dat *D. melanogaster* en verschillende van zijn zustersoorten er in het algemeen voor kiezen te paren op plekken waar gist aanwezig is. In *D. melanogaster* echter paarden maagdelijke vrouwtjes voornamelijk weg van gist, terwijl eerder gepaarde vrouwtjes op gist opnieuw paarden. Door gebruik te maken van experimentele manipulatie van de chemische compositie van de plekken die gist bevatten en gemuteerde vliegen zonder geslachtspeptide (mannetjes; SP) en de receptor voor geslachtspeptide (vrouwtjes; SPR) stelden we de sensorische en gedragsmatige mechanismen die ten grondslag liggen aan de ruimtelijke koppeling van voedsel en partners vast. We vonden dat de voorkeur voor de paringslocatie te maken had met de aantrekkingskracht van chemische, van gist afgeleide, signalen (de combinatie van azijnzuur en eiwit) en werd gemoduleerd door de mannelijke geslachtspeptide die door vrouwtjes tijdens de paring wordt ontvangen. De voorkeur om te paren op plekken met gist was ’s nachts sterker dan overdag, en nam toe met de tijd na de eerste paring. In keuze-experimenten met twee verschillende soorten gist ontdekten we dat *D. melanogaster*-paren voorkeur hadden om te paren op één gistsoort in plaats van op de andere soort. Samengevoegd suggereert onze studie dat een bepaald niveau van assortatieve paring het gevolg kan zijn van de voorkeur te paren op gist, maar dat de sterkte van deze assortatieve paring afhankelijk zal zijn van verschillende variabelen, waaronder de aanwezigheid van verschillende gistsoorten en de timing van (opnieuw) paren ten opzichte van de lichtcyclus.

Samenvattend ontleedt dit proefschrift de mechanismen die ten grondslag liggen aan voedsel-gemedieerde populatiedifferentiatie en assortatieve paring. Aan de ene kant vinden we dat de inconsistentie van reacties tussen levensgeschiedenis-eigenschappen een mogelijke beperking van dieetspecialisatie en populatiedifferentiatie vormen. Aan de andere kant ontdekken we dat voedselvoorkeur direct tot assortatieve paring zou kunnen leiden door de ruimtelijke koppeling met partners. Onze bevindingen benadrukken het belang meerdere levensgeschiedenis-eigenschappen die betrokken zijn met de exploitatie van voedsel te bestuderen om het domein van voedsel-gemedieerde populatiedifferentiatie te ontdekken, en meerdere variabelen te onderzoeken, waaronder paringsstatus, de aanwezigheid van meerder voedselbronnen en de timing van (opnieuw) paren ten opzichte van de lichtcyclus, om de potentiële sterkte van assortatieve paring die het gevolg kan zijn van de voorkeur te paren op voedsel vast te stellen.

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Manuscripts

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