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.

Bibliography

Abouheif, E., Favé, M.-J., Ibarrarán-Viniegra, A. S., Lesoway, M. P., Rafiqi, A. M., and Rajakumar, R. (2014). Eco-evo-devo: The time has come. In *Ecological genomics*, pages 107–125.

Abrams, P. A. and Ginzburg, L. R. (2000). The nature of predation: Prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution*, 15(8):337–341.

Andraso, G. M. and Barron, J. N. (1995). Evidence for trade-off between defensive morphology and startle-response performance in the brook stickleback (*Culaea inconstans*). *Canadian Journal of Zoology*, 73(6):1147–1153.

Archambeault, S. L., Bärtschi, L. R., Merminod, A. D., and Peichel, C. L. (2020). Adaptation via pleiotropy and linkage: Association mapping reveals a complex genetic architecture within the stickleback Eda locus . *Evolution Letters*, 4(4):282–301.

Augspurger, J. M., Warburton, M., and Closs, G. P. (2017). Life-history plasticity in amphidromous and catadromous fishes: a continuum of strategies. *Reviews in Fish Biology and Fisheries*, 27(1):177–192.

Baker, J. A., Heins, D. C., King, R. W., and Foster, S. A. (2011). Rapid shifts in multiple life history traits in a population of threespine stickleback. *Journal of Evolutionary Biology*, 24(4):863–870.

Baldauf, S. A., Engqvist, L., and Weissing, F. J. (2014). Diversifying evolution of competitiveness. *Nature Communications*, 5(1):1–8.

Barber, I. and Arnott, S. A. (2000). Split-Clutch ivf : A technique to examine indirect fitness consequences of mate preferences in sticklebacks. *Behaviour*, 137(7-8):1129–1140.

Barrett, R. D. H., Rogers, S. M., and Schluter, D. (2008). Natural selection on a major armor gene in threespine stickleback. *Science*, 322(5899):255–257.

Bates, D., Mächler, M., Bolker, B., and Walker, S. (2015). Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67(1):1–48.

Bateson, M. (2016). Optimistic and pessimistic biases: a primer for behavioural ecologists. *Current opinion in behavioral sciences*, 12:115–121.

Beldade, P., Mateus, A. R. A., and Keller, R. A. (2011). Evolution and molecular mechanisms of adaptive developmental plasticity. *Molecular Ecology*, 20(7):1347–

1363.

Bell, A. M. (2005). Behavioural differences between individuals and two populations of stickleback (*Gasterosteus aculeatus*). *Journal of evolutionary biology*, 18(2):464–473.

Bell, A. M. and Sih, A. (2007). Exposure to predation generates personality in three-spined sticklebacks (*Gasterosteus aculeatus*). *Ecology Letters*, 10(9):828–834.

Bell, A. M. and Stamps, J. A. (2004). Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, 68(6):1339–1348.

Bell, M. A. and Aguirre, W. E. (2013). Contemporary evolution, allelic recycling, and adaptive radiation of the threespine stickleback. *Evolutionary Ecology Research*, 15(4):377–411.

Bell, M. A., Aguirre, W. E., and Buck, N. J. (2004). Twelve years of contemporary armor evolution in a threespine stickleback population. *Evolution*, 58(4):814–824.

Bell, M. A. and Foster, S. A. (1994). *The evolutionary biology of the threespine stickleback*. Oxford University Press.

Bell, M. A., Ortí, G., Walker, J. A., and Koenings, J. P. (1993). Evolution of pelvic reduction in threespine stickleback fish: a test of competing hypotheses. *Evolution*, 47(3):906–914.

Benjamini, Y. and Hochberg, Y. (1995). Controlling the false discovery rate: A practical and powerful approach to multiple testing. *Journal of the Royal Statistical Society B*, 57(1):289–300.

Bennett, A. F. (1987). Interindividual variability: an underutilized resource. *New directions in ecological physiology*, pages 147–169.

Bergmüller, R. and Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology & Evolution*, 25(9):504–511.

Berner, D., Kaeuffer, R., Grandchamp, A., Raeymaekers, J. A. M., Hendry, A. P., and Ra, K. Quantitative genetic inheritance of morphological divergence in a lake – stream stickleback ecotype pair : implications for reproductive isolation. *Journal of Evolutionary Biology*, 24:1975–1983.

Bohlin, T., Pettersson, J., and Degerman, E. (2001). Population density of migratory and resident brown trout (Salmo trutta) in relation to altitude: Evidence for a migration cost. *Journal of Animal Ecology*, 70(1):112–121.

Bolhuis, J. E., Schouten, W. G., de Leeuw, J. A., Schrama, J. W., and Wiegant, V. M. (2004). Individual coping characteristics, rearing conditions and behavioural flexibility in pigs. *Behavioural Brain Research*, 152(2):351–360.

Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., Rudolf, V. H., Schreiber, S. J., Urban, M. C., and Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution*, 26(4):183–192.

Bolnick, D. I., Snowberg, L. K., Patenia, C., Stutz, W. E., Ingram, T., and Lau, O. L. (2009). Phenotype-dependent native habitat preference facilitates divergence between parapatric lake and stream stickleback. *Evolution*, 63(8):2004–2016.

Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D., and Forister, M. L. (2003). The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, 161(1):1–28.

Bonnot, N. C., Goulard, M., Hewison, A. M., Cargnelutti, B., Lourtet, B., Chaval, Y., and Morellet, N. (2018). Boldness-mediated habitat use tactics and reproductive success in a wild large herbivore. *Animal Behaviour*, 145:107–115.

Boon, A. K., Réale, D., and Boutin, S. (2008). Personality, habitat use, and their consequences for survival in north american red squirrels, *Tamiasciurus hudsonicus*.

Oikos, 117(9):1321–1328.

Botero, C. A., Weissing, F. J., Wright, J., and Rubenstein, D. R. (2015). Evolutionary tipping points in the capacity to adapt to environmental change. *Proceedings of the National Academy of Sciences*, 112(1):184–189.

Breckling, B., Middelhoff, U., and Reuter, H. (2006). Individual-based models as tools for ecological theory and application: Understanding the emergence of organisational properties in ecological systems. *Ecological modelling*, 194(1-3):102–113.

Brown, C., Jones, F., and Braithwaite, V. (2005). In situ examination of boldness-shyness traits in the tropical poeciliid, *Brachyraphis episcopi*. *Animal Behaviour*, 70(5):1003–1009.

Budaev, S. V. (1997). Alternative styles in the European wrasse, *Symphodus ocellatus*: Boldness-related schooling tendency. *Environmental Biology of Fishes*, 49(1):71–78.

Burnham, K. P. and Anderson, D. R. (2002). A practical information-theoretic approach. *Model selection and multimodel inference*, 2:70–71.

Burns, J. G., Saravanan, A., and Helen Rodd, F. (2009). Rearing environment affects the brain size of guppies: Lab-reared guppies have smaller brains than wild-caught guppies. *Ethology*, 115(2):122–133.

Calisi, R. M. and Bentley, G. E. (2009). Lab and field experiments: Are they the same animal? *Hormones and Behavior*, 56(1):1–10.

Campos-Candela, A., Palmer, M., Balle, S., Álvarez, A., and Alós, J. (2019). A mechanistic theory of personality-dependent movement behaviour based on dynamic energy budgets. *Ecology Letters*, 22(2):213–232.

Careau, V., Thomas, D., Humphries, M. M., and Réale, D. (2008). Energy metabolism and animal personality. *Oikos*, 117(5):641–653.

Chan, Y. F., Marks, M. E., Jones, F. C., Villarreal, G., Shapiro, M. D., Brady, S. D., Southwick, A. M., Absher, D. M., Grimwood, J., Schmutz, J., Myers, R. M., Petrov, D., Jónsson, B., Schluter, D., Bell, M. A., and Kingsley, D. M. (2010). Adaptive Evolution of Pelvic Reduction in Sticklebacks by Recurrent Deletion of a Pitx1 Enhancer. *Science*, 327(5963):302–305.

Chapman, B. B., Brönmark, C., Nilsson, J. Å., and Hansson, L. A. (2011). The ecology and evolution of partial migration. *Oikos*, 120(12):1764–1775.

Closs, G. P., Hicks, A. S., and Jellyman, P. G. (2013). Life histories of closely related amphidromous and non-migratory fish species: a trade-off between egg size and fecundity. *Freshwater Biology*, 58(6):1162–1177.

Coates, W. D., Hale, R., and Morrongiello, J. R. (2019). Dispersal decisions and personality in a freshwater fish. *Animal Behaviour*, 157:209–218.

Colosimo, P. F. (2005). Widespread Parallel Evolution in Sticklebacks by Repeated Fixation of Ectodysplasin Alleles. *Science*, 307(5717):1928–1933.

Cordero-Rivera, A. (2017). Behavioral diversity (ethodiversity): a neglected level in the study of biodiversity. *Frontiers in Ecology and Evolution*, 5:7.

Costa, P. T., Terracciano, A., and McCrae, R. R. (2001). Gender differences in personality traits across cultures: Robust and surprising findings. *Journal of Personality and Social Psychology*, 81(2):322–331.

Cote, J. and Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1608):383–390.

Cote, J., Fogarty, S., Tymen, B., Sih, A., and Brodin, T. (2013). Personality-dependent dispersal cancelled under predation risk. *Proceedings of the Royal Society B: Biological Sciences*, 280(1773):20132349.

Cote, J., Fogarty, S., Weinersmith, K., Brodin, T., and Sih, A. (2010). Personality traits and dispersal tendency in the invasive mosquitofish (*Gambusia* affinis). *Proceedings of the Royal Society B: Biological Sciences*, 277(1687):1571–1579.

Cousin, X., Daouk, T., Pean, S., Lyphout, L., M, S., and M, B. (2012). Electronic individual identification of zebrafish using radio frequency identification (RFID) microtags. *Journal of Experimental Biology*, 215:2729–2734.

Couzin, I. D. and Krause, J. (2003). Self-Organization and Collective Behavior in Vertebrates. *Advances in the Study of Behavior*, 32:1–75.

Couzin, I. D., Krause, J., Franks, N. R., and Levin, S. A. Effective leadership and decision- making in animal groups on the move. *Nature*, 433:2–5.

Dall, S. R., Bell, A. M., Bolnick, D. I., and Ratnieks, F. L. (2012). An evolutionary ecology of individual differences. *Ecology Letters*, 15(10):1189–1198.

Dall, S. R. X., Houston, A. I., and McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8):734–739.

Dalziel, A. C. and Schulte, P. M. (2012). Correlates of prolonged swimming performance in F2 hybrids of migratory and non-migratory threespine stickleback | Journal of Experimental Biology. *Journal of Experimental Biology*, 215(20):3587–3596.

Dalziel, A. C., Vines, T. H., and Schulte, P. M. (2012). Reductions in prolonged swimming capacity following freshwater colonization in multiple threespine stickleback populations. *Evolution*, 66(4):1226–1239.

Day, R. L., MacDonald, T., Brown, C., Laland, K. N., and Reader, S. M. (2001). Interactions between shoal size and conformity in guppy social foraging. *Animal Behaviour*, 62(5):917–925.

Day, T. and McPhail, J. D. (1996). The effect of behavioural and morphological plasticity on foraging efficiency in the threespine stickleback (*Gasterosteus* sp.). *Oecologia*, 108:380–388.

Dean, L. L., Dunstan, H. R., Reddish, A., and Maccoll, A. D. C. (2021). Courtship behavior, nesting microhabitat , and assortative mating in sympatric stickleback species pairs. *Ecology and Evolution*, pages 1741–1755.

DeAngelis, D. L. and Mooij, W. M. (2005). Individual-based modeling of ecological and evolutionary processes. *Annual Review of Ecology, Evolution, and Systematics*, 36:147–168.

Dhellemmes, F., Finger, J. S., Laskowski, K. L., Guttridge, T. L., and Krause, J. (2020). Comparing behavioural syndromes across time and ecological conditions in a free-ranging predator. *Animal Behaviour*, 162:23–33.

Di-Poi, C., Lacasse, J., Rogers, S. M., and Aubin-Horth, N. (2014). Extensive Behavioural Divergence following Colonisation of the Freshwater Environment in Threespine Sticklebacks. *PLoS ONE*, 9(6):e98980.

Dingemanse, N. J. and Araya-Ajoy, Y. G. (2015). Interacting personalities: Behavioural ecology meets quantitative genetics. *Trends in Ecology and Evolution*, 30(2):88–97.

Dingemanse, N. J., Barber, I., and Dochtermann, N. A. (2020). Non-consumptive effects of predation: does perceived risk strengthen the genetic integration of behaviour and morphology in stickleback? *Ecology Letters*, 23(1):107–118.

Dingemanse, N. J., Both, C., Drent, P. J., Van Oers, K., and Van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, 64(6):929–938.

Dingemanse, N. J., der Plas, F., Wright, J., Réale, D., Schrama, M., Roff, D. A., der Zee, E., and Barber, I. (2009). Individual experience and evolutionary history of predation affect expression of heritable variation in fish personality and morphology. *Proceedings of the Royal Society B: Biological Sciences*, 276(1660):1285–1293.

Dingemanse, N. J., Kazem, A. J. N., Réale, D., and Wright, J. (2010). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology and Evolution*, 25(2):81–89.

Dingemanse, N. J. and Wolf, M. (2010). Recent models for adaptive personality differences: A review. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560):3947–3958.

Dingemanse, N. J., Wright, J., Kazem, A. J. N., Thomas, D. K., Hickling, R., and Dawnay, N. (2007). Behavioural syndromes differ predictably between 12 populations of three-spined stickleback. *Journal of Animal Ecology*, 76(6):1128–1138.

Dingle, H. (2006). Animal migration: is there a common migratory syndrome? *Journal of Ornithology*, 147(2):212–220.

DiNuzzo, E. R. and Griffen, B. D. (2020). The effects of animal personality on the ideal free distribution. *Proceedings. Biological sciences*, 287(1934):20201095.

Dochtermann, N. A. and Dingemanse, N. J. (2013). Behavioral syndromes as evolutionary constraints. *Behavioral Ecology*, 24(4):806–811.

Dochtermann, N. A., Schwab, T., Anderson Berdal, M., Dalos, J., and Royauté, R. (2019). The Heritability of Behavior: A Meta-analysis. *Journal of Heredity*, 110(4):403–410.

Dodson, J. J., Aubin-Horth, N., Thériault, V., and Páez, D. J. (2013). The evolutionary ecology of alternative migratory tactics in salmonid fishes. *Biological Reviews*, 88(3):602–625.

Duckworth, R. A. (2006). Behavioral correlations across breeding contexts provide a mechanism for a cost of aggression. *Behavioral Ecology*, 17(6):1011–1019.

Duckworth, R. A. and Badyaev, A. V. (2007). Coupling of dispersal and aggression facilitates the rapid range expansion of a passerine bird. *Proceedings of the National Academy of Sciences*, 104(38):15017–15022.

Duckworth, R. A., Belloni, V., and Anderson, S. R. (2015). Cycles of species replacement emerge from locally induced maternal effects on offspring behavior in a passerine bird. *Science*, 347(6224):875–877.

Dyer, J. R. G., Croft, D. P., Morrell, L. J., and Krause, J. (2009). Shoal composition determines foraging success in the guppy. *Behavioral Ecology*, 20(1):165–171.

Edelaar, P., Jovani, R., and Gomez-Mestre, I. (2017). Should I change or should I go? Phenotypic plasticity and matching habitat choice in the adaptation to environmental heterogeneity. *American Naturalist*, 190(4):506–520.

Edelaar, P., Siepielski, A. M., and Clobert, J. (2008). Matching habitat choice causes directed gene flow: A neglected dimension in evolution and ecology. *Evolution*, 62(10):2462–2472.

Ehlinger, T. J. (1990). Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. *Ecology*, 71(3):886–896.

Eriksson, B. K., Yanos, C., Bourlat, S. J., Donadi, S., Fontaine, M. C., Hansen, J. P., Jakubavičiūtė, E., Kiragosyan, K., Maan, M. E., Merilä, J., Austin, Å. N., Olsson, J., Reiss, K., Sundblad, G., Bergström, U., and Eklöf, J. S. (2021). Habitat segregation of plate phenotypes in a rapidly expanding population of three-spined stickleback. *Ecosphere*, 12(6):e03561.

Fahrig, L. (2003). Effects of Habitat Fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics*, 34:487–515.

Fischer, S., Bohn, L., Oberhummer, E., Nyman, C., and Taborsky, B. (2017). Divergence of developmental trajectories is triggered interactively by early social and ecological experience in a cooperative breeder. *Proceedings of the National Academy of Sciences*, 114(44):E9300—-E9307.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N., and Snyder, P. K. (2005). Global consequences of land use. *Science*, 309(5734):570–574.

Foster, W. and Treherne, J. (1981). Evidence for the dilution effect in the selfish herd from fish predation on a marine insect. *Nature*, 293(5832):466–467.

Franssen, N. R., Harris, J., Clark, S. R., Schaefer, A. F., and Stewart, L. K. (2013). Shared and unique morphological responses of stream fishes to anthropogenic habitat alteration. *Proceedings of the Royal Society B: Biological Sciences*, 280(1752):20122715.

Fretwell, S. D. (1969). On territorial behavior and other factors influencing habitat distribution in birds. *Acta biotheoretica*, 19(1):45–52.

Friard, O. and Gamba, M. (2016). BORIS: a free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution*, 7(11):1325–1330.

Frommen, J. G., Herder, F., Engqvist, L., Mehlis, M., Bakker, T., Schwarzer, J., and Thünken, T. (2011). Costly plastic morphological responses to predator specific odour cues in three-spined sticklebacks (*Gasterosteus aculeatus*). *Evolutionary Ecology*, 25(3):641–656.

Fullerton, A. H., Burnett, K. M., Steel, E. A., Flitcroft, R. L., Pess, G. R., Feist, B. E., Torgersen, C. E., Miller, D. J., and Sanderson, B. L. (2010). Hydrological connectivity for riverine fish: Measurement challenges and research opportunities. *Freshwater Biology*, 55(11):2215–2237.

Garcia-Elfring, A., Paccard, A., Thurman, T. J., Wasserman, B. A., Palkovacs, E. P., Hendry, A. P., and Barrett, R. D. (2021). Using seasonal genomic changes to understand historical adaptation to new environments: Parallel selection on stickleback in highly-variable estuaries. *Molecular Ecology*, 30(9):2054–2064.

Geritz, S. A., Kisdi, É., Meszéna, G., and Metz, J. A. (1998). Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evolutionary Ecology*, 12(1):35–57.

Ghalambor, C. K., McKay, J. K., Carroll, S. P., and Reznick, D. N. (2007). Adaptive versus non-adaptive phenotypic plasticity and the potential for contemporary adaptation in new environments. *Functional Ecology*, 21(3):394–407.

Giesing, E. R., Suski, C. D., Warner, R. E., and Bell, A. M. (2010). Female sticklebacks transfer information via eggs: effects of maternal experience with predators on offspring. *Proceedings of the Royal Society of London B: Biological Sciences*, 278(1712):rspb20101819.

Gillespie, D. T. (1976). A general method for numerically simulating coupled chemical reactions. *Journal of Computational Physics*, 22(1999):403–434.

Gosling, S. D. (2001). From mice to men: what can we learn about personality from animal research? *Psychological Bulletin*, 127(1):45.

Gosling, S. D. and John, O. P. (1999). Personality dimensions in nonhuman animals: A cross-species review. *Current Directions in Psychological Science*, 8(3):69–75.

Greenwood, A. K., Mills, M. G., Wark, A. R., Archambeault, S. L., and Peichel, C. L. (2016). Evolution of schooling behavior in threespine sticklebacks is shaped by the Eda gene. *Genetics*, 203(2):677–681.

Groenewoud, F., Frommen, J. G., Josi, D., Tanaka, H., Jungwirth, A., and Taborsky, M. (2016). Predation risk drives social complexity in cooperative breeders. *Proceedings of the National Academy of Sciences of the United States of America*, 113(15):4104–4109.

Groothuis, T. G. and Trillmich, F. (2011). Unfolding personalities: The importance of studying ontogeny. *Developmental Psychobiology*, 53(6):641–655.

Gross, M. R., Coleman, R. M., and McDowall, R. M. (1988). Aquatic productivity and the evolution of diadromous fish migration. *Science*, 239(4846):1291–1293.

Guayasamin, O. L., Couzin, I. D., and Miller, N. Y. (2017). Behavioural plasticity across social contexts is regulated by the directionality of inter-individual differences. *Behavioural Processes*, 141:196–204.

Haldane, J. B. S. (1949). Suggestions as to quantitative measurement of rates of evolution. *Evolution*, pages 51–56.

Hanson, D., Moore, J., Taylor, E. B., Barrett, R. D. H., and Hendry, A. P. (2016). Assessing reproductive isolation using a contact zone between parapatric lake-stream stickleback ecotypes. *Journal of Evolutionary Biology*, 29:2491–2501.

Harper, D. (1982). Competitive foraging in mallards: Ideal free ducks. *Animal Behaviour*, 30(2):575–584.

Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, 2:e616.

Heckwolf, M. J., Meyer, B. S., Döring, T., Eizaguirre, C., and Reusch, T. B. (2018). Transgenerational plasticity and selection shape the adaptive potential of sticklebacks to salinity change. *Evolutionary Applications*, 11(10):1873–1885.

Hedrick, P. W. (2006). Genetic polymorphism in heterogeneous environments: The age of genomics. *Annual Review of Ecology, Evolution, and Systematics*, 37:67–93.

Hedrick, P. W., Ginevan, M. E., and Ewing, E. P. (1976). Genetic Polymorphism in Heterogeneous Environments. *Annual Review of Ecology and Systematics*, 7(1):1–32.

Hellmann, J. K., Carlson, E. R., and Bell, A. M. (2021). The interplay between sperm-mediated and care-mediated paternal effects in threespine sticklebacks. *Animal Behaviour*, 179:267–277.

Hendry, A. P., Farrugia, T. J., and Kinnison, M. T. (2008). Human influences on rates of phenotypic change in wild animal populations. *Molecular Ecology*, 17(1):20–29.

Herczeg, G., Ab Ghani, N. I., and Merilä, J. (2013). Evolution of stickleback feeding behaviour: Genetics of population divergence at different ontogenetic stages. *Journal of Evolutionary Biology*, 26(5):955–962.

Hirsch, P. E., Thorlacius, M., Brodin, T., and Burkhardt-Holm, P. (2017). An approach to incorporate individual personality in modeling fish dispersal across in-stream barriers. *Ecology and Evolution*, 7(2):720–732.

Holt, R. D. and Barfield, M. (2008). Habitat selection and niche conservatism. *Israel Journal of Ecology and Evolution*, 54(3-4):295–309.

Holtmann, B., Lagisz, M., and Nakagawa, S. (2017a). Metabolic rates, and not hormone levels, are a likely mediator of between-individual differences in behaviour: a meta-analysis. *Functional Ecology*, 31(3):685–696.

Holtmann, B., Santos, E. S., Lara, C. E., and Nakagawa, S. (2017b). Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype–environment covariance. *Proceedings of the Royal Society B: Biological Sciences*, 284(1864).

Holway, D. A. and Suarez, A. V. (1999). Animal behavior : an essential component of invasion biology. *Trends in Ecology & Evolution*, 14(8):328–330.

Hosoki, T., Mori, S., Nishida, S., Kume, M., Sumi, T., and Kitano, J. (2020). Erratum: Diversity of gill raker number and diets among stickleback populations in novel habitats created by the 2011 Tōhoku earthquake and tsunami (Evolutionary Ecology Research (2019) 20 (213-230)). *Evolutionary Ecology Research*, 20(4):469–470.

Houston, A. I. and Lang, A. (1998). The ideal free distribution with unequal competitors: The effect of modelling methods. *Animal Behaviour*, 56(1):243–251.

Houston, A. I. and McNamara, J. M. (1988). The ideal free distribution when competitive abilities differ: an approach based on statistical mechanics. *Animal Behaviour*, 36(1):166–174.

Huizinga, M., Ghalambor, C. K., and Reznick, D. N. (2009). The genetic and environmental basis of adaptive differences in shoaling behaviour among populations of Trinidadian guppies, *Poecilia reticulata*. *Journal of Evolutionary Biology*, 22(9):1860–1866.

Huntingford, F. A. (1976). The relationship between anti-predator behaviour and aggression among conspecifics in the three-spined stickleback, *Gasterosteus aculeatus*. *Animal Behaviour*, 24(2):245–260.

Huntingford, F. A. and Wright, P. J. (1993). The development of adaptive variation in predator avoidance in freshwater fishes. *Marine Behaviour and Physiology*, 23(1-4):45–61.

Hutchings, J. A. (2002). *Migration of Freshwater Fishes.*

Huxley, J. S. (1934). A natural experiment on the territorial instinct. *British Birds*, 27(10):270–277.

Ingram, T., Jiang, Y., Rangel, R., and Bolnick, D. I. (2015). Widespread positive but weak assortative mating by diet within stickleback populations. *Ecology and evolution*, 5(16):3352–3363.

Jackson, A. L., Humphries, S., and Ruxton, G. D. (2004). Resolving the departures of observed results from the Ideal Free Distribution with simple random movements. *Journal of Animal Ecology*, 73(4):612–622.

Jeschke, J. M. and Tollrian, R. (2007). Prey swarming: which predators become confused and why? *Animal Behaviour*, 74(3):387–393.

John, O. P. and Robins (2022). *Handbook of personality: Theory and research*. Guilford Press.

Jolles, J. W., Fleetwood-Wilson, A., Nakayama, S., Stumpe, M. C., Johnstone, R. A., and Manica, A. (2014). The role of previous social experience on risk-taking and leadership in three-spined sticklebacks. *Behavioral Ecology*, 25(6):1395–1401.

Jonsson, N. (1991). Influence of water flow, water temperature and light on fish migration in rivers. *Nordic Journal of Freshwater Research*, 66:20–35.

Junge, C., Museth, J., Hindar, K., Kraabøl, M., and Vøllestad, L. A. (2014). Assessing the consequences of habitat fragmentation for two migratory salmonid fishes. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24(3):297–311.

Kaiser, M. I. and Müller, C. (2021). What is an animal personality? *Biology and Philosophy*, 36(1):1–25.

Kawecki, T. J. and Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters*, 7(12):1225–1241.

Kitamura, T., Kume, M., Takahashi, H., and Goto, A. (2006). Juvenile bimodal length distribution and sea-run migration of the lower modal group in the Pacific Ocean form of three-spined stickleback. *Journal of Fish Biology*, 69(4):1245–1250.

Kitano, J., Ishikawa, A., Kume, M., and Mori, S. (2012). Physiological and genetic basis for variation in migratory behavior in the three-spined stickleback, *Gasterosteus aculeatus*. *Ichthyological Research*, 59(4):293–303.

Kitano, J. and Lema, S. C. (2013). Divergence in thyroid hormone concentrations between juveniles of marine and stream ecotypes of the threespine stickleback (*Gasterosteus aculeatus*). *Evolutionary Ecology Research*, 15(2):143–153.

Kitano, J., Lema, S. C., Luckenbach, J. A., Mori, S., Kawagishi, Y., Kusakabe, M., Swanson, P., and Peichel, C. L. (2010). Adaptive divergence in the thyroid hormone signaling pathway in the stickleback radiation. *Current Biology*, 20(23):2124–2130.

Koolhaas, J. M., de Boer, S. F., Coppens, C. M., and Buwalda, B. (2010). Neuroendocrinology of coping styles: Towards understanding the biology of individual variation. *Frontiers in Neuroendocrinology*, 31(3):307–321.

Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W., and Blokhuis, H. J. (1999). Coping styles in animals: current status in behavior and stress-physiology. *Neuroscience Biobehavioral Reviews*, 23(7):925–935.

Kozak, G. M. and Boughman, J. W. (2012). Plastic responses to parents and predators lead to divergent shoaling behaviour in sticklebacks. *Journal of Evolutionary Biology*, 25(4):759–769.

Kraabøl, M., Johnsen, S. I., Museth, J., and Sandlund, O. T. (2009). Conserving iteroparous fish stocks in regulated rivers: The need for a broader perspective! *Fisheries Management and Ecology*, 16(4):337–340.

Krause, J., Krause, S., Arlinghaus, R., Psorakis, I., Roberts, S., and Rutz, C. (2013). Reality mining of animal social systems. *Trends in Ecology and Evolution*, 28(9):541–551.

Krause, J., Ruxton, G. D., Ruxton, G., Ruxton, I. G., et al. (2002). *Living in groups*. Oxford University Press.

Kusakabe, M., Ishikawa, A., Ravinet, M., Yoshida, K., Makino, T., Toyoda, A., Fujiyama, A., and Kitano, J. (2017). Genetic basis for variation in salinity tolerance between stickleback ecotypes. *Molecular Ecology*, 26(1):304–319.

Lacasse, J. and Aubin-Horth, N. (2014). Population-dependent conflict between individual sociability and aggressiveness. *Animal Behaviour*, 87(C):53–57.

Lackey, A. C. and Boughman, J. W. (2017). Evolution of reproductive isolation in stickleback fish. *Evolution*, 71(2):357–372.

Lahti, D. C., Johnson, N. A., Ajie, B. C., Otto, S. P., Hendry, A. P., Blumstein, D. T., Coss, R. G., Donohue, K., and Foster, S. A. (2009). Relaxed selection in the wild. *Trends in Ecology & Evolution*, 24(9):487–496.

Lam, T. J. and Hoar, W. S. (1967). Seasonal effects of prolactin on freshwater osmoregulation of the marine form (*Trachurus*) of the stickleback, *Gasterosteus aculeatus*. *Canadian Journal of Zoology*, 45(4):509–516.

Langenhof, M. R., Apperloo, R., and Komdeur, J. (2016). Small variations in early-life environment can affect coping behaviour in response to foraging challenge in the three-spined stickleback. *PloS one*, 11(2):e0147000.

Langenhof, M. R. and Komdeur, J. (2018). Why and how the early-life environment affects development of coping behaviours. *Behavioral Ecology and Sociobiology*, 72(3):34.

Laskowski, K. L. and Bell, A. M. (2014). Strong personalities, not social niches, drive individual differences in social behaviours in sticklebacks. *Animal behaviour*, 90:287–295.

Legrand, D., Cote, J., Fronhofer, E. A., Holt, R. D., Ronce, O., Schtickzelle, N., Travis, J. M. J., and Clobert, J. (2017). Eco-evolutionary dynamics in fragmented landscapes. *Ecography*, 40(1):9–25.

Lehtonen, J. and Jaatinen, K. (2016). Safety in numbers: the dilution effect and other drivers of group life in the face of danger. *Behavioral Ecology and Sociobiology*, 70(4):449–458.

Leinonen, T., Herczeg, G., Cano, J. M., and Merilä, J. (2011). Predation-imposed selection on threespine stickleback (gasterosteus aculeatus) morphology: A test of the refuge use hypothesis. *Evolution*, 65(10):2916–2926.

Leinonen, T., McCairns, R. J. S., Herczeg, G., and Merilä, J. (2012). Multiple evolutionary pathways to decreased lateral plate coverage in freshwater threespine sticklebacks. *Evolution*, 66(12):3866–3875.

Lenth, R. V. (2021). *emmeans: Estimated Marginal Means, aka Least-Squares Means*. R package version 1.6.1.

Lescak, E. A., Bassham, S. L., Catchen, J., Gelmond, O., Sherbick, M. L., Van Hippel, F. A., Cresko, W. A., Von Hippel, F. A., and Cresko, W. A. (2015). Evolution of stickleback in 50 years on earthquake-uplifted islands. *Proceedings of the National Academy of Sciences of the United States of America*, 112(52):E7204–E7212.

Lissaman, P. and Shollenberger, C. (1970). Formation flight of birds. *Science*, 168(3934):1003.

Lloyd-Smith, J. O., Schreiber, S. J., Kopp, P. E., and Getz, W. M. (2005). Superspreading and the effect of individual variation on disease emergence. *Nature*, 438(7066):355–359.

Lothian, A. J. and Lucas, M. C. (2021). The role of individual behavioral traits on fishway passage attempt behavior. *Ecology and Evolution*, 11(17):11974–11990.

Luttbeg, B. and Sih, A. (2010). Risk, resources and state-dependent adaptive behavioural syndromes. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365(1560):3977–3990.

Lynch, M., Walsh, B., et al. (1998). Genetics and analysis of quantitative traits.

Mable, B. K. (2019). Conservation of adaptive potential and functional diversity : integrating old and new approaches. *Conservation Genetics*, 20(1):89–100.

Maciejewski, M. F., Jiang, C., Stuart, Y. E., and Bolnick, D. I. (2020). Microhabitat contributes to microgeographic divergence in threespine stickleback. *Evolution*, 74(4):749–763.

Magurran, A. E. and Seghers, B. H. (1994). Predator inspection behaviour covaries With schooling tendency amongst wild guppy, *Poecilia Reticulata*, populations in Trinidad. *Behaviour*, 128(1):121–134.

Marchinko, K. B. (2009). Predation's role in repeated phenotypic and genetic divergence of armor in threespine stickleback. *Evolution*, 63(1):127–138.

Marchinko, K. B. and Schluter, D. (2007). Parallel evolution by correlated response: lateral plate reduction in threespine stickleback. *Evolution*, 61(5):1084–1090.

Marras, S., Killen, S. S., Lindström, J., McKenzie, D. J., Steffensen, J. F., and Domenici, P. (2015). Fish swimming in schools save energy regardless of their spatial position. *Behavioral Ecology and Sociobiology*, 69(2):19–226.

Matsumura, S., Arlinghaus, R., and Dieckmann, U. (2010). Foraging on spatially distributed resources with sub-optimal movement, imperfect information, and travelling costs: departures from the ideal free distribution. *Oikos*, 119(9):1469–1483.

McAdams, D. P. (1992). The five-factor model in personality: A critical appraisal. *Journal of Personality*, 60(2):329–361.

McGhee, K. E. and Bell, A. M. (2014). Paternal care in a fish: epigenetics and fitness enhancing effects on offspring anxiety. *Proceedings of the Royal Society B: Biological Sciences*, 281(1794):20141146.

McGhee, K. E., Feng, S., Leasure, S., and Bell, A. M. (2015). A female's past experience with predators affects male courtship and the care her offspring will receive from their father. *Proceedings of the Royal Society B: Biological Sciences*, 282(1819):20151840.

McGhee, K. E., Pintor, L. M., Suhr, E. L., and Bell, A. M. (2012). Maternal exposure to predation risk decreases offspring antipredator behaviour and survival in threespined stickleback. *Functional Ecology*, 26(4):932–940.

McKinnon, J. S., Mori, S., Blackman, B. K., David, L., Kingsley, D. M., Jamieson, L., Chou, J., and Schluter, D. (2004). Evidence for ecology's role in speciation. *Nature*, 429(6989):294–298.

Montiglio, P. O., Ferrari, C., and Réale, D. (2013). Social niche specialization under constraints: Personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 368(1618):8–10.

Moran, E. V., Hartig, F., and Bell, D. M. (2016). Intraspecific trait variation across scales: Implications for understanding global change responses. *Global Change Biology*, 22(1):137–150.

Moran, N. P., Mossop, K. D., Thompson, R. M., Chapple, D. G., and Wong, B. B. (2017). Rapid divergence of animal personality and syndrome structure across an arid-aquatic habitat matrix. *Oecologia*, 185(1):55–67.

Mouchet, A., Cole, E. F., Matthysen, E., Nicolaus, M., Quinn, J. L., Roth, A. M., Tinbergen, J. M., van Oers, K., van Overveld, T., and Dingemanse, N. J. (2021). Heterogeneous selection on exploration behavior within and among West European populations of a passerine bird. *Proceedings of the National Academy of Sciences of the United States of America*, 118(28):1–6.

Netz, C., Ramesh, A., Gismann, J., Gupte, P. R., and Weissing, F. J. (2021). christophnetz/time-to-IFD_simulator: Comment on DiNuzzo & Griffen - Simulation code.

Netz, C., Ramesh, A., Gismann, J., Gupte, P. R., and 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.

Nicolaus, M. and Edelaar, P. (2018). Comparing the consequences of natural selection, adaptive phenotypic plasticity, and matching habitat choice for phenotype–environment matching, population genetic structure, and reproductive isolation in meta-populations. *Ecology and Evolution*, 8(8):3815–3827.

Nicolaus, M., Tinbergen, J. M., Bouwman, K. M., Michler, S. P., Ubels, R., Both, C., Kempenaers, B., and Dingemanse, N. J. (2012). Experimental evidence for adaptive personalities in a wild passerine bird. *Proceedings of the Royal Society B: Biological Sciences*, 279(1749):4885–4892.

Nicolaus, M., Tinbergen, J. M., Ubels, R., Both, C., and Dingemanse, N. J. (2016). Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecology Letters*, 19(4):478–486.

Nicolaus, M., Wang, X., Lamers, K. P., Ubels, R., and Both, C. (2022). Unravelling the causes and consequences of dispersal syndromes in a wild passerine. *Proceedings of the Royal Society B*, 289(1974):20220068.

Niemelä, P. T. and Dingemanse, N. J. (2014). Artificial environments and the study of 'adaptive' personalities. *Trends in Ecology Evolution*, 29(5):245–247.

Niemelä, P. T., Tiso, S., and Dingemanse, N. J. (2021). Density-dependent individual variation in male attractiveness in a wild field cricket. *Behavioral Ecology*, 32(4):707–716.

Nussey, D. H., Wilson, A. J., and Brommer, J. E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, 20(3):831–844.

Ostlund-Nilsson, S., Mayer, I., and Huntingford, F. A. (2006). *Biology of the three-spined stickleback*. CRC press.

Páez, D., Brisson-Bonenfant, C., Rossignol, O., Guderley, H., Bernatchez, L., and Dodson, J. (2011). Alternative developmental pathways and the propensity to migrate: a case study in the atlantic salmon. *Journal of Evolutionary Biology*, 24(2):245–255.

Parker, G. (1978). Evolution of competitive mate searching. *Annual review of entomology*, 23(1):173–196.

Parker, G. and Sutherland, W. (1986). Ideal free distributions when individuals differ in competitive ability: phenotype-limited ideal free models. *Animal Behaviour*, 34(4):1222–1242.

Pearish, S., Hostret, L., and Bell, A. M. (2013). Behavioral type–environment correlations in the field: a study of three-spined stickleback. *Behavioual Ecology Sociobiology*, 67(5):765–774.

Piersma, T. and Drent, J. (2003). Phenotypic flexibility and the evolution of organismal design. *Trends in Ecology & Evolution*, 18(5):228–233.

Pigliucci, M. (2005). Evolution of phenotypic plasticity: Where are we going now? *Trends in Ecology and Evolution*, 20(9):481–486.

Potticary, A. L. and Duckworth, R. A. (2020). Multiple environmental stressors induce an adaptive maternal effect. *American Naturalist*, 196(4):487–500.

Price, M. V. (1983). Ecological consequences of body size: a model for patch choice in desert rodents. *Oecologia*, 59(2):384–392.

Pritchard, D. J., Hurly, T. A., Tello-Ramos, M. C., and Healy, S. D. (2016). Why study cognition in the wild (and how to test it)? *Journal of the Experimental Analysis of Behavior*, 105(1):41–55.

Quinn, T. P. and Myers, K. W. (2004). Anadromy and the marine migrations of Pacific salmon and trout: Rounsefell revisited. *Reviews in Fish Biology and Fisheries*, 14(4):421–442.

R Core Team (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Raeymaekers, J. A. M., Konijnendijk, N., Larmuseau, M. H. D., Hellemans, B., De Meester, L., and Volckaert, F. A. M. (2014). A gene with major phenotypic effects as a target for selection vs. homogenizing gene flow. *Molecular Ecology*, 23(1):162–181.

Railsback, S. F. and Harvey, B. C. (2002). Analysis of habitat-selection rules using anindividual-based model. *Ecology*, 83(7):1817–1830.

Ramesh, A., Domingues, M. M., Stamhuis, E. J., Groothuis, T. G. G., Weissing, F. J., and 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.

Ramesh, A., Gismann, J., Groothuis, T. G. G., Weissing, F. J., and Nicolaus, M. (2022a). Mesocosm experiments reveal the loss of migratory tendencies in a recently isolated population of three-spined sticklebacks. *bioRxiv*, page 2022.05.09.491155.

Ramesh, A., Groothuis, T. G. G., Weissing, F. J., and Nicolaus, M. (2022b). Habitat fragmentation induces rapid divergence of migratory and isolated sticklebacks. *Behavioral Ecology*, 33(1):167–177.

Ravinet, M. (2021). Patterns of genomic divergence and introgression between Japanese stickleback species with overlapping breeding habitats. *Journal of Evolutionary Biology*, 34(1):114–127.

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., and Montiglio, P. O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560):4051–4063.

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., and Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2):291–318.

Reimchen, T. E. (1980). Spine deficiency and polymorphism in a population of *Gasterosteus aculeatus* : an adaptation to predators? . *Canadian Journal of Zoology*, 58(7):1232–1244.

Reimchen, T. E. (1994). Predators and morphological evolution in threespine stickleback. *The Evolutionary Biology of the Threespine stickleback*, pages 240–276.

Reimchen, T. E., Bergstrom, C., and Nosil, P. (2013). Natural selection and the adaptive radiation of Haida Gwaii stickleback. *Evolutionary Ecology Research*, 15(3):241–269.

Robinson, B. W. (2013). Evolution of growth by genetic accommodation in Icelandic freshwater stickleback. *Proceedings of the Royal Society B: Biological Sciences*, 280(1772).

Sanogo, Y. O., Hankison, S., Band, M., Obregon, A., and Bell, A. M. (2011). Brain transcriptomic response of threespine sticklebacks to cues of a predator. *Brain, Behavior and Evolution*, 77(4):270–285.

Scheiner, S. M. (1993). Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics*, 24(Figure 1):35–68.

Schirmer, A., Herde, A., Eccard, J. A., and Dammhahn, M. (2019). Individuals in space: personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialization. *Oecologia*, 189(3).

Schirmer, A., Hoffmann, J., Eccard, J. A., and Dammhahn, M. (2020). My niche: Individual spatial niche specialization affects within- and between-species interactions. *Proceedings of the Royal Society B: Biological Sciences*, 287(1918).

Schlichting, C. D. (2008). Hidden reaction norms, cryptic genetic variation, and evolvability. *Annals of the New York Academy of Sciences*, 1133(1942):187–203.

Shaw, A. K. (2020). Causes and consequences of individual variation in animal movement. *Movement Ecology*, 8(1):1–12.

Shine, R., Brown, G. P., and Phillips, B. L. (2011). An evolutionary process that assembles phenotypes through space rather than through time. *Proceedings of the National Academy of Sciences*, 108(14):5708–5711.

Sih, A. (2013). Understanding variation in behavioural responses to human-induced rapid environmental change: A conceptual overview. *Animal Behaviour*, 85(5):1077–1088.

Sih, A., Bell, A., and Johnson, J. C. (2004). Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, 19(7):372–378.

Sih, A., Cote, J., Evans, M., Fogarty, S., and Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15(3):278–289.

Sih, A., Ferrari, M. C., and Harris, D. J. (2011). Evolution and behavioural responses to human-induced rapid environmental change. *Evolutionary Applications*, 4(2):367–387.

Sih, A., Mathot, K. J., Moirón, M., Montiglio, P.-O., Wolf, M., and Dingemanse, N. J. (2015). Animal personality and state–behaviour feedbacks: a review and guide for empiricists. *Trends in ecology & evolution*, 30(1):50–60.

Smallegange, I. M. and van der Meer, J. (2009). The distribution of unequal predators across food patches is not necessarily (semi) truncated. *Behavioral Ecology*, 20(3):525–534.

Snijders, L., Krause, S., Tump, A. N., Breuker, M., Ortiz, C., Rizzi, S., Ramnarine, I. W., Krause, J., and Kurvers, R. H. (2021). Causal evidence for the adaptive benefits of social foraging in the wild. *Communications Biology*, 4(1):1–8.

Snyder, R. J. (1991). Migration and life histories of the threespine stickleback: evidence for adaptive variation in growth rate between populations. *Environmental Biology of Fishes*, 31(4):381–388.

Sol, D., Timmermans, S., and Lefebvre, L. (2002). Behavioural flexibility and invasion success in birds. *Animal Behaviour*, 63(3):495–502.

Sommer-Trembo, C., Petry, A. C., Gomes Silva, G., Vurusic, S. M., Gismann, J., Baier, J., Krause, S., Iorio, J. d. A. C., Riesch, R., and Plath, M. (2017). Predation risk and abiotic habitat parameters affect personality traits in extremophile populations of a neotropical fish (*Poecilia vivipara*). *Ecology and Evolution*, 7(16):6570–6581.

Soriano-Redondo, A., Gutiérrez, J. S., Hodgson, D., and Bearhop, S. (2020). Migrant birds and mammals live faster than residents. *Nature Communications*, 11(1):1–8.

Spencer, H. G., Kennedy, M., and Gray, R. D. (1995). Patch choice with competitive asymmetries and perceptual limits: the importance of history. *Animal Behaviour*, 50(2):497–508.

Spiegel, O., Leu, S. T., Bull, C. M., and Sih, A. (2017). What's your move? Movement as a link between personality and spatial dynamics in animal populations. *Ecology Letters*, 20(1):3–18.

Stamps, J. and Groothuis, T. G. G. (2010a). The development of animal personality: relevance, concepts and perspectives. *Biological Reviews*, 85(2):301–325.

Stamps, J. A. and Groothuis, T. G. G. (2010b). Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 365(1560):4029–4041.

Stander, P. E. (1992). Cooperative hunting in lions: the role of the individual. *Behavioral ecology and sociobiology*, 29(6):445–454.

Stein, L. R. and Bell, A. M. (2014). Paternal programming in sticklebacks. *Animal Behaviour*, 95:165–171.

Stein, L. R. and Bell, A. M. (2015). Consistent individual differences in paternal behavior: a field study of three-spined stickleback. *Behavioral Ecology and Sociobiology*, 69(2):227–236.

Stein, L. R. and Bell, A. M. (2019). The role of variation and plasticity in parental care during the adaptive radiation of three-spine sticklebacks. *Evolution*, 73(5):1037–1044.

Stein, L. R., Bukhari, S. A., and Bell, A. M. (2018). Personal and transgenerational cues are nonadditive at the phenotypic and molecular level. *Nature Ecology Evolution*, 2(8):1306–1311.

Stockwell, C. A., Hendry, A. P., and Kinnison, M. T. (2003). Contemporary evolution meets conservation biology. *Trends in Ecology and Evolution*, 18(2):94 –101.

Stoffel, M. A., Nakagawa, S., and Schielzeth, H. (2017). rptr: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 8(11):1639–1644.

Sudo, R. and Tsukamoto, K. (2015). Migratory restlessness and the role of androgen for increasing behavioral drive in the spawning migration of the japanese eel. *Scientific Reports*, 5(1):1–7.

Sutherland, W. J. (1985). Distribution of unequal competitors. *Behavioural Ecology: Ecological Consequences of Adaptive Behaviour*.

Sutherland, W. J. and Parker, G. A. (1992). The relationship between continuous input and interference models of ideal free distributions with unequal competitors. *Animal Behaviour*, 44(PART 2):345–355.

Svanback, R. and Bolnick, D. I. (2007). Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B: Biological Sciences*, 274(1611):839–844.

Taborsky, B., Guyer, L., and Demus, P. (2014). Prudent habitat choice: a novel mechanism of size-assortative mating. *Journal of Evolutionary Biology*, 27(6):1217–1228.

Taylor, E. B. and Donald McPhail, J. (2000). Historical contingency and ecological determinism interact to prime speciation in sticklebacks, gasterosteus. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 267(1460):2375–

2384.

Thorlacius, M. and Brodin, T. (2018). Investigating large-scale invasion patterns using-small scale invasion successions—phenotypic differentiation of the invasive round goby (*Neogobius melanostomus*) at invasion fronts. *Limnology and Oceanography*, 63(2):702–713.

Thorlacius, M., Hellström, G., and Brodin, T. (2015). Behavioral dependent dispersal in the invasive round goby, *Neogobius melanostomus* depends on population age. *Current Zoology*, 61(3):529–542.

Toscano, B. J., Gatto, J., and Griffen, B. D. (2014). Effect of predation threat on repeatability of individual crab behavior revealed by mark-recapture. *Behavioral Ecology and Sociobiology*, 68(3):519–527.

Tregenza, T. (1995). Building on the ideal free distribution. *Advances in ecological research*, 26:253–307.

Treherne, J. E. and Foster, W. A. (1982). Group size and anti-predator strategies in a marine insect. *Animal Behaviour*, 30(2):536–542.

Trompf, L. and Brown, C. (2014). Personality affects learning and trade-offs between private and social information in guppies, *Poecilia reticulata*. *Animal Behaviour*, 88:99–106.

Tudorache, C., Blust, R., and Boeck, G. D. (2007). Swimming capacity and energetics of migrating and non-migrating morphs of three-spined stickleback Gasterosteus aculeatus L. and their ecological implications. *Journal of Fish Biology*, 71(5):1448–1456.

Tuomainen, U. and Candolin, U. (2011). Behavioural responses to human-induced environmental change. *Biological Reviews*, 86(3):640–657.

Van de Pol, M., Pen, I., Heg, D., and Weissing, F. J. (2007). Variation in habitat choice and delayed reproduction: adaptive queuing strategies or individual quality differences? *The American Naturalist*, 170(4):530–541.

Van Den Bos, R., Jolles, J. W., and Homberg, J. R. (2013). Social modulation of decision-making: a cross-species review. *Frontiers in Human Neuroscience*, 7:301.

Van Gestel, J. and Weissing, F. J. (2018). Is plasticity caused by single genes? *Nature*, 555(7698):E19–E20.

Van Gils, J. A., Dekinga, A., Spaans, B., Vahl, W. K., and Piersma, T. (2005). Digestive bottleneck affects foraging decisions in red knots, *Calidris canutus*. ii. patch choice and length of working day. *Journal of Animal Ecology*, 74(1):120–130.

Van Oers, K., Mueller, J. C., Bell, A. M., Aubin-Horth, N., Taller, C., Gesti, G. D. E., Éxito, H. D. E., Garíca-Pintos, A., Caballero, G., Piñeiro, P., Anderson, N., and Ones, D. (2010). Evolutionary genomics of animal personality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560):3991–4000.

Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S. M., Schlichting, C. D., and Van Tienderen, P. H. (1995). Adaptive phenotypic plasticity: consensus and controversy. *Trends in ecology & evolution*, 10(5):212–217.

Wagner, G. P. and Altenberg, L. (1996). Perspective: complex adaptations and the evolution of evolvability. *Evolution*, 50(3):967–976.

Walker, J. A. and Bell, M. A. (2000). Net evolutionary trajectories of body shape evolution within a microgeographic radiation of threespine sticklebacks, (*Gasterosteus aculeatus*). *Journal of Zoology*, 252(3):293–302.

Wang, I. J. and Bradburd, G. S. (2014). Isolation by environment. *Molecular Ecology*, 23(23):5649–5662.

Ward, A. J., Thomas, P., Hart, P. J., and Krause, J. (2004). Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, 55(6):561–568.

Wark, A. R., Greenwood, A. K., Taylor, E. M., Yoshida, K., and Peichel, C. L. (2011a). Heritable differences in schooling behavior among threespine stickleback populations revealed by a novel assay. *PLoS ONE*, 6(3).

Wark, A. R., Wark, B. J., Lageson, T. J., and Peichel, C. L. (2011b). Novel methods for discriminating behavioral differences between stickleback individuals and populations in a laboratory shoaling assay. *Behavioral Ecology and Sociobiology*, 65(5):1147–1157.

Webster, M. M. and Ward, A. J. (2011). Personality and social context. *Biological Reviews*, 86(4):759–773.

Wiig, E., Reseland, J. E., Østbye, K., Haugen, H. J., and Vøllestad, L. A. (2016). Variation in lateral plate quality in threespine stickleback from fresh, brackish and marine water: A micro-computed tomography study. *PLoS ONE*, 11(10):e0164578.

Wilson, A. D. M. and Godin, J.-G. J. (2009). Boldness and behavioral syndromes in the bluegill sunfish, *Lepomis macrochirus*. *Behavioral Ecology*, 20(2):231–237.

Wolf, M., van Doorn, G. S., Leimar, O., and Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, 447(7144):581–584.

Wolf, M., Van Doorn, G. S., and Weissing, F. J. (2011). On the coevolution of social responsiveness and behavioural consistency. *Proceedings of the Royal Society B: Biological Sciences*, 278(1704):440–448.

Wolf, M., Van Doorn, G. S., Weissing, F. J., van Doorn, G. S., and Weissing, F. J. (2008). Evolutionary emergence of responsive and unresponsive personalities. *Proceedings of the National Academy of Sciences*, 105(41):15825–15830.

Wolf, M. and Weissing, F. J. (2010). An explanatory framework for adaptive personality differences. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560):3959–3968.

Wolf, M. and Weissing, F. J. (2012). Animal personalities: consequences for ecology and evolution. *Trends in Ecology & Evolution*, 27(8):452–461.

Wong, B. and Candolin, U. (2015). Behavioral responses to changing environments. *Behavioral Ecology*, 26(3):665–673.

Wund, M. A., Baker, J. A., Clancy, B., Golub, J. L., and Foster, S. A. (2008). A test of the "flexible stem" model of evolution: ancestral plasticity, genetic accommodation, and morphological divergence in the threespine stickleback radiation. *The American Naturalist*, 172(4):449–462.

Wund, M. A., Valena, S., Wood, S., and Baker, J. A. (2012). Ancestral plasticity and allometry in threespine stickleback reveal phenotypes associated with derived, freshwater ecotypes. *Biological Journal of the Linnean Society*, 105(3):573–583.

Yiou, P., Cattiaux, J., Faranda, D., Kadygrov, N., Jézéquel, A., Naveau, P., Ribes, A., Robin, Y., Thao, S., van Oldenborgh, G. J., et al. (2020). Analyses of the northern european summer heatwave of 2018. *Bulletin of the American Meteorological Society*, 101(1):S35–S40.

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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.

Behavioral Ecology, 33(1), 167-177.

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.

4. **Ramesh, A.**, Vijayan, S., Sreedharan, S., Somanathan, H., & Uma, D. (2016). Similar yet different: differential response of a praying mantis to ant-mimicking spiders. Biological Journal of the Linnean Society, 119(1), 158-165.

Manuscripts under review (pre-print available)

5. **Ramesh, A.***, Gismann, J.*, Groothuis, T. G., Weissing, F. J., & Nicolaus, M. (2022). Mesocosm experiments reveal the loss of migratory tendencies in a recently isolated population of three-spined sticklebacks. bioRxiv. https://doi.org/10.1101/2022.05.09.491155.

6. Netz, C., **Ramesh, A.**, & Weissing, F. J. (2022). Ideal free distribution of unequal competitors: spatial assortment and evolutionary diversification of competitive ability. bioRxiv. https://doi.org/10.1101/2022.06.27.497704.

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