**PAPERS TO READ**

Tremmel M, Müller C: Insect personality depends on environmental conditions. Behavioral Ecology 2013, 24(2):386-392.

van Oers K, de Jong G, van Noordwijk AJ, Kempenaers B, Drent PJ: Contribution of genetics to the study of animal personalities: a review of case studies. Behaviour 2005, 142(9-10):1191-1212.

1. Zajitschek F, Hunt J, Jennions MD, Hall MD, Brooks RC: Effects of juvenile  and adult diet on ageing and reproductive effort of male and female black field crickets Teleogryllus commodus. Functional Ecology 2009, 23(3):602-611.

Réale D, Garant D, Humphries MM, Bergeron P, Careau V, Montiglio P-O: Personality and the emergence of the pace-of-life syndrome concept at the population level. Proc Biol Sci 2010, 365(1560):4051-4063.

Norton W, Bally-Cuif L: Unravelling the proximate causes of the aggression-boldness behavioural syndrome in zebrafish. Behaviour 2012, 149(10-12):1063-1079.

Soares MC, Bshary R, Fusani L, Goymann W, Hau M, Hirschenhauser K, Oliveira RF: Hormonal mechanisms of cooperative behaviour. Proc Biol Sci 2010, 365(1553):2737-2750.

**Diet quality refers to the caloric value and nutritional composition of food and can impact morphology, population dynamics and behaviour of many species** (White 1978, Ishizaki et al. 2001 Bouvier and Hylander 1982). With dynamic ecosystems, diet quality does not remain consistent across all habitats (Tuomainen and Candolin 2011). Behavioural and physiological mechanisms allow individuals to selectively consume food or excrete excesses to meet nutritional and energetic needs (Han and Dingemanse 2015, Senior et al. 2017). In situations where nutritionally limited diets are inescapable, animals will prioritise consumption of the most important nutrients, usually at the cost of another. As a result, individuals can consume an excess of, for example, carbohydrates that exceed the excretion capacity and be converted to lipids (Han and Dingemanse 2017). The subsequent nutritional imbalance influences a multitude of factors, including behaviour (Han and Dingemanse 2017).

Deficient diets are predicted to modify resource allocation as nutrients necessary for growth and maintenance are limited (Johnston 1993). Diet affects metabolic plasticity with nutrient rich/poor diets triggering different gene expression (Mason et al 2016, Rocha et al 2016). The two key nutrients that often have the highest impact on subsequent behaviour are protein and carbohydrate. Carbohydrates are the main source of energy, allowing increased levels of activity and quality reproductive/courting efforts (Maklakov et al. 2008). A limited source will affect high energy behaviours (Han and Dingemanse 2015). High carbohydrate diets also increase metabolic rate, having further implications on the expression of traits with high energy demands such as activity and exploration (Mathot and Dingemanse 2015). Sociability is also influenced by diet quality as it is regulated by neuroendocrine mechanisms (Soares et al 2010). Since poor nutrition has negative effects on neuromuscular development, it is expected that social behaviours will suffer as a result of low quality diets (Akman et al. 2012).

Protein is necessary for growth and muscle development (Bowen et al. 1995). A limited protein supply induces higher cannibalistic rates in some invertebrates as they attempt to supplement the shortage (Simpson et al 2006). Yet, in wolf spiders, the opposite was found to be true with females reared on a high quality diet expressing higher rates of sexual cannibalism (Wilder and Rypstra 2008). The inconsistencies across species emphasises the significance of studying them separately rather than assuming they all follow the same pattern. Individuals with access to more protein tend to mate more frequently (Blay and Yuval 1997), outperforming their protein-limited counterparts. Protein deficient invertebrates become bolder since the cost of boldness is not as great as individuals with sufficient protein levels (Dingemanse and Wolfe 2010). When low quality diets are prevalent, the trade-off between carbohydrate and protein benefits becomes obvious (Simpson et al 2006, Maklakov et al. 2008). Optimal target intakes will not be reached and the individual will prioritise the nutrient that will be most beneficial to their fitness (Han and Dingemanse 2017). Diet quality will impact different species in different ways due to the variation in energetic and nutritional demand (Simpson et al. 2004).

Macronutrient composition and pleiotropic genes generate behavioural correlations where functionally different behaviours are linked (Van Oers et al. 2005). These correlations happen both within- and among-individuals (Han and Dingemanse 2015). Among-individual correlations are influenced by genetics and the environment (Dingemanse and Dochtermann 2013) where the environment alters the expression level of a gene that is linked with a behavioural trait (Filby et al. 2012, Norton et al. 2011). In cases where the gene is pleiotropic, the behavioural changes will be correlated. Thus, environmental effects, such as diet quality, greatly impact behavioural correlations.

Individual animals differ in behaviour consistently within the same population (Bell et al. 2009). Behaviour is considered repeatable when there is variation between individuals and each individual behaves consistently over time (Bell et al. 2009). Behaviours that are linked to energetic needs are predicted to be more plastic as they change in response to the environment (Castellano et al. 2002, Smith and Hunter 2005). That being said, if the behaviour continues to remain consistent after the environmental change, it is still considered repeatable, despite its plasticity. The strength of environmental influences also differs between species, with ectotherms thought to have lower heritability of morphological traits than endotherms (Mousseau and Roff 1987), largely due to their dependence on external factors. Whether repeatability follows the same trend in ectotherms is yet to be completely explored, with preliminary meta-analyses suggesting it does (Bell et al. 2009). However, we know that low quality diets reduce behavioural repeatability in some spider species (Lichtenstein et al. 2016). Males also generally display more repeatability than females, the specific details of which are dependent on the behavioural trait in question (Andrew 1972, Wingfield 1994). However, other studies argue that because of their shared genetic basis, behavioural expressions have little variation (Reddiex et al. 2013). *L. delicata,* specifically, have shown little evidence that suggests sexual differences in behavioural traits and correlations (Michalengeli et al. 2016). Perhaps the differences in nutrient demand induce varied behaviours that impact repeatability in response to environmental changes. While the behaviours remain similar between males and females, the subsequent impacts of diet quality differ.

Diet quality has also been shown to influence behaviour and life history traits (Warner et al. 2007). Nutritional composition in the early stages of an animal’s life relate to behaviours expressed at maturity (Han and Dingemanse 2015), indicating a long term effect. Food available to juveniles determines the proportion of the population that will survive into maturity (White 1978).

The short-term effects have predominately been observed in grazing mammals from an agricultural perspective (Greenwood and Demment 1988, Newman et al. 1994). Their foraging behaviours reinforced selective eating as a means of nutrient compensation. Differences in nutrient availability have been shown to cause changes in courtship behaviours, with reproductive behaviours also being influenced by nutrient balance in food (Maklakov 2008, Bertram et al. 2009). These short-term impacts may have huge implications for subsequent fitness. These impacts need to be explored across all species, rather than a selected few. This project aims to provide insight into the behavioural implications of diet quality in lizards.

**Behavioural impacts of varied diets**

*Han and Dingemanse 2015*

* Low-protein, high-carb diet in crickets: increased calling effort (reproductive behaviour) —> carbs are main energy source. High carb means more muscle and tissue activity
* High protein in Drosophila: ^ mating frequency and courtship.
* High protein in mormon crickets: lower cannibalism
* Activity and exploration predicted to respond to carb levels - high energy behaviours.
* Social behaviours - regulated by neuroendocrine mechanisms [ref 67] .’. affected by protein and carb levels.

*Dingemanse et al 2009*

* Animal personality: Average behaviour of an individual across multiple contexts

*Han and Dingemanse 2017*

* Studies on birds show that early life diet affects personality (namely aggression and exploration)
* **Behavioural stability:** within-individual variation. High quality diets during development may enable individuals to alter their aggression levels in adulthood while the opposite would be true for low quality diets [ref 33 and 34]
* Adult diet changes impacted morphology not personality in crickets
* Adult diet was not enough to offset juvenile high carb diet effects [ref 83]
* Individual differentiation affected by juvenile diet - high protein —> increased male aggression, decreased within-ind variation
* Evidence of aggression and exploration being impacted by early life diet in birds [ref 10] (but what about short term adult diets?)

**Mechanisms**

*Han and Dingemanse 2015*

* Permanent environment. can shape correlations independently from genetics. (Additive effects)
* They can also interact with genes - e.g. environment alters level of gene expression.
* Environment can also affect gene expression that relate to neurotransmitter breakdowns (which are connected to multiple behaviours. [ref 60, 61]
* Activity and exploration predicted to respond to carb levels - high energy behaviours.
* Social behaviours - regulated by neuroendocrine mechanisms [ref 67] .’. affected by protein and carb levels.
* Poor nutrition negatively impacts neuromuscular development .’. predicted to also negatively impact sociality.
* Protein mainly impacts aggression/boldness. Low protein means more aggressive/bold because they have less to lose

*Senior et al 2017*

* Molecular level = variation in coping ability of cells in response to dietary restrictions. e.g. dietary restriction generates variation in mitochondrial DNA replication and associated replication errors .’. somatic decline [see ref 19]
* Individual level = restrictions influence energy and resource allocation >> adopt different life history strategies (variance in longevity). [see ref 20]
* Differences in digestive/post-ingestive physiology which influences variation in efficiency of resource acquisition. [ref 10]

*Soares et al 2010*

* Hormones heavily influence behaviour - especially sociality in regards to aggression —> look up papers to back up diets impact on testosterone/hormone levels
* One hormone impacts different behavioural aspects which depends on life history and social context [ref Winfield 2008]
* Hormones can also affect gene expression rather than having direct impacts on behaviour —> increase/decrease in likelihood of behavioural expression rather than deterministic factors
* Entire paper discusses neurotransmitters, hormones etc as a mechanism for social regulation. Find papers to support diet influence on hormone levels to make this paper viable.

*Norton et al. 2011*

* Mutation of the gene encoding fibroblast growth factor receptor 1a (fgfr1a) increases aggression, boldness and exploration in adult zebrafish.
* Check ref Bell 2005 and Bell and Sih 2007
* Again, find references that show how diet influences growth factor/neurotransmitter levels
* States that a combination of genetic/hormonal constraint and environmental conditions controls expression of behavioural syndromes —> Very small part of the paper. Literally one sentence.
* Behavioural assays are sensitive to changes in feeding regimen, diet, lighting condition etc [ref Wahlsten et al 2006; Burgess and Granato 2008)

**Variance and behavioural correlations**

*Han and Dingemanse 2015*

* Nutritional balance affects among-individual variance
* **Gene pleiotropy:** One gene controls multiple phenotypes
* **Linkage disequilibrium:** Genes affecting one phenotype are correlated with another gene
* Environmental conditions also affect expression of gene pleiotropy .’. strength of correlation.
* Permanent environment. can shape correlations independently from genetics. (Additive effects)

*Norton et al. 2011*

* Aggression, boldness and exploration in a novel environment shown to be linked

*Senior et al 2015*

* between-individual variance in fitness-related traits are higher on a single food diet.
* Results suggest that selection on traits correlated with nutritional requirements is weak in heterogenous env.
* Mixed diet = most individuals able to reach IT. Single food diet = Some individuals get closer to IT than others .’. higher variance in fitness

*Dingemanse et al. 2009*

* Personality and individual plasticity might be linked [ref 7, 26, 27]. Mouse aggression level example = ref 29. Link to vertebrates since many studies have been done on inverts.
* Argues that to understand both animal personality and individual plasticity, they need to be studied in conjunction —> enables future research to answer harder questions. i.e. why selection favours specific links between the two.

**Significance**

*Han and Dingemanse 2015*

* Most studies done on invertebrates, few experimental
* Diversity of intake targets across taxa - effects of diet restriction will also be diverse
* Extreme scenarios could happen to a population where dispersion is limited.
* Sexual differences are predicted since there are sex specific nutritional needs —> All female population used

*Senior et al 2015*

* Justifies between-individual variance as a research topic - drives selection and adaptation. Also sheds light on how numerous species co-exist
* Sex differences - foraging priorities and diet requirements [ref Lihoreau et al. 2015 and Maklakov et al 2008 for examples]
* Mentions the most beneficial IT (evolutionary fitness)

*Han and Dingemanse 2017*

* Males and females differ in their response to nutritional environment because of differing nutritional preferences [ref 26 36-39]
* Suggests cricket females require more protein as they preferentially fed on protein rich diets when given the choice - however no significant sex differences in mean behavioural levels in response to diet. High protein need because egg production. [ref 39]
* sequential testing may have carry on effects

*Van Oers et al. 2013*

* Most genetic studies on personality traits have been carried out on lab grown populations and do not capture the evolutionary processes that may have shaped these traits
* Argues that variation is genetic and is maintained by natural selection

**FOCUS FOR LAST PARAGRAPH**

AIMS

* Test short term impacts of diet quality on L. delicata sociality, neophobia and activity.
* Observe behavioural correlations between traits and among-individual variance - do they persist in nutrient-limited environments?

PREDICTIONS

* Sociability is expected to be higher in the low nutrient group based on previous studies that showed similar results in invertebrates. Individuals fed a higher quality diet are expected to be more active and neophobic than their nutrient-poor counterparts. (Han and Dingemanse 2015)
* Nutritional balance affects among-individual variance (Han and Dingemanse 2015). Increase in inter individual variance when on single food diet (Senior et al 2015)

**TO THINK ABOUT**

* Add clarity/questions/predictions etc
* Experimental design in a figure —> flowchart?
* Intro: 3-3.5 pages (1.5 spaced)
* Methods: Detailed – add track editing stuff
* Results: 1 pageish
* Discussion: 3-4 pages (1.5 spaced)
* Maybe add male and female dependent on how it goes?

***Discussion maybe***

* + - Trophic level of consumer is important to consider
    - Fitness trait under observation may be the most important moderator - Single food diet had a particularly high impact on the variance in longevity and reproductive traits. Suggests considerable between-individual variation in the ITs associated with these traits
    - Animals should display exploratory behaviours especially when facing nutritional imbalance. [ref day et al 1998; Houston et al 2011]