

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

EFFET DES RESSOURCES DISPONIBLES SUR LA STRUCTURE DES TOILES
DE VEUVES NOIRES (*LATRODECTUS HESPERUS*) FEMELLES: EST-CE QUE
LA STRUCTURE DES TOILES EST CONTRAINTE PAR DES COMPROMIS
PHYSIOLOGIQUES?

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RÉSUMÉ

Les individus présentent généralement des différences phénotypiques individuelles qui ont un impact sur leur écologie et qui se maintiennent au cours du temps et entre les contextes. Ce qui maintient la variance dans les traits plastiques comme le comportement est souvent difficile à identifier et départager. Les compromis physiologiques où l'investissement dans un trait bénéfique se traduit par une diminution de l'investissement dans un autre est un des mécanismes pouvant contribuer au maintien des différences entre les individus. Les veuves noires de l'ouest (*Latrodectus hesperus*, Chamberlin & Ivies, 1935) construisent des toiles où elles peuvent tisser des fils avec lesquels elles vont acquérir des ressources ou se défendre contre les prédateurs. Les individus démontrent des différences constantes dans le nombre de ces fils et la présence de compromis pourrait expliquer ces différences individuelles. Les objectifs de ce mémoire étaient (1) d'évaluer les compromis possibles entre les fils de capture pour l'approvisionnement et structuraux pour la défense contre les prédateurs dans les toiles de veuves noires; (2) d'évaluer si la disponibilité de ressources était associée aux différences individuelles dans la structure des toiles; et (3) de décrire comment les différences individuelles dans la structure des toiles ont varié au cours du temps. Pour ce faire nous avons placé en alternance une soixantaine de femelles matures vierges sous trois disponibilités de proies sur une période de huit semaines. Nous les avons laissé tisser une semaine suite à chaque période où nous avons mesuré la structure de la toile toutes les douze heures. Nous avons observé une relation positive entre le nombre de fils structuraux et de capture dans la toile des individus. En cette absence de compromis physiologiques, nous suggérons que le maintien des différences individuelles pourraient être attribuées à différentes stratégies d'histoire de vie ou aux traits avec lesquels la structure de la toile est corrélée. Les ressources disponibles ont affecté les différences individuelles et leur importance au cours du temps. De futures études sur la modulation des différences individuelles au cours du temps par les ressources des individus pourraient nous permettre de mieux comprendre les différences de plasticité entre individus.

Mots clés : *constructions animale, personnalité animale, plasticité phénotypique, phénotype étendu, approvisionnement, différences individuelles, Latrodectus hesperus.*

CHAPITRE I

INTRODUCTION GÉNÉRALE

1.1 Maintien des différences individuelles

L'écologie évolutive étudie les différences phénotypiques et la variance génétique héritable qui y est associée, comme c'est sur ces dernières que la sélection s'applique et que les processus évolutifs prennent place. On étudie les différences phénotypiques entre les espèces et les populations, mais aussi entre les individus (Bell *et al.*, 2009; Bolnick *et al.*, 2003; Dall *et al.*, 2012; Des Roches *et al.*, 2018; Futuyma et Moreno, 1988; Hayes et Jenkins, 1997; Stearns, 1992). Les différences individuelles de phénotype sont souvent hérissables (Dochtermann *et al.*, 2019) et peuvent jouer un rôle écologique important (Bolnick *et al.*, 2011; Des Roches *et al.*, 2018; Moiron *et al.*, 2020; Ovadia et Schmitz, 2002; Pettorelli *et al.*, 2015; Réale *et al.*, 2007; Schmitz *et al.*, 2015; Sih *et al.*, 2004a). Par exemple, les différences de traits entre individus (e.g. comportement, morphologie, spécialisation de niche) a un impact important dans les chaînes trophiques où les traits exprimés par les proies ou les prédateurs façonnent les interactions entre individus et populations et la composition de leur communauté (Beckerman *et al.*, 1997; Bolnick *et al.*, 2011; Des Roches *et al.*, 2018; Ovadia et Schmitz, 2002; Pettorelli *et al.*, 2015; Schmitz *et al.*, 2015). La variation individuelle au sein d'une même population ou communauté va généralement se refléter à l'échelle des populations.

Le phénotype des individus peut cependant varier d'un moment ou d'un contexte à l'autre lorsqu'un individu ajuste son phénotype à son environnement (i.e. plasticité phénotypique). Même pour les traits plastiques comme le comportement, la mesure répétée à travers des contextes et le temps peut révéler des différences individuelles constantes (Dingemanse *et al.*, 2010). Ces différences individuelles constantes de comportement ont été appelées de plusieurs façons, dont 'personnalité' et 'tempérament' (Bell *et al.*, 2009; Réale *et al.*, 2007). Elles ont un impact sur les forces sélectives résultantes (Biro et Stamps, 2008; Des Roches *et al.*, 2018; Moiron *et al.*, 2020), sont héritables (Dochtermann *et al.*, 2014), représentent une portion importante de la variance au sein des populations (Bell *et al.*, 2009) et vont également affecter la composition de la communauté et les interactions trophiques (Beckerman *et al.*, 1997; Sih *et al.*, 2004a).

Les différences entre les individus dans un environnement donné peuvent être réduites ou augmentées par plasticité lorsque les individus ajustent leur phénotype au changement d'un environnement. Comme le phénotype n'est pas constant, la sélection peut avoir peu d'incidence sur l'aptitude si la sélection sur le phénotype est opposée entre environnements. Inversement, la sélection peut également être amplifiée lorsque la plasticité accentue les différences phénotypiques entre les individus dans certains contextes ou que la sélection s'applique conjointement au phénotype et la capacité à être plastique des individus. Par exemple, des comportements exprimés avec constance par les individus ont été associés avec différents niveaux de plasticité (Dingemanse et Wolf, 2010; Via et Lande, 1985). La plasticité peut donc moduler la portion des différences individuelles dans l'expression de traits qui vont se maintenir entre les contextes et au cours du temps (Dingemanse *et al.*, 2010). Les différences individuelles devraient donc être étudiées conjointement avec la plasticité phénotypique qui les

modules (Bell *et al.*, 2009; Dingemanse *et al.*, 2010; Dingemanse et Wolf, 2010; Stamps *et al.*, 2012).

Malgré la plasticité des traits, la sélection devrait favoriser les traits pour lequel l'aptitude est supérieure. Cependant, les différences phénotypiques entre les individus sont souvent maintenues au sein des populations. Des processus tels la sélection perturbatrice vont favoriser des phénotypes s'éloignant de l'expression moyenne, permettant à plusieurs phénotypes différents de persister dans la population. Lorsque la sélection varie beaucoup, que ce soit dans le temps (e.g. saisons, années), dans l'espace (e.g. environnement hétérogène), plusieurs phénotypes peuvent atteindre une aptitude similaire (Desmarais et Tessier, 1999; Stearns, 1992; Via et Lande, 1985). Des différences d'état (e.g. morphologie, métabolisme, régulation neuro-hormonale, ontogénie) entre les individus peuvent également maintenir les différences entre individus. Les différences peuvent aussi être maintenues lorsque que l'aptitude est directement relié à la fréquence des traits dans l'environnement social des individus. Ainsi, plus un trait est exprimé dans la population, moins il est bénéfique à l'aptitude des individus, ce qui favorise une diversité de traits dans la population (Farine *et al.*, 2015; Giraldeau, 1984; Gross, 1991; Marchetti, 2000; Neumann et Schneider, 2016; Olendorf *et al.*, 2006; Réale *et al.*, 2007). La sélection peut aussi être contrainte lorsque des traits sont fortement corrélés et que l'expression bénéfique d'un trait diminue l'aptitude d'un autre (Koolhaas *et al.*, 1999; Laskowski *et al.*, 2021; Lima et Dill, 1990; Moiron *et al.*, 2020; Salzman *et al.*, 2018; Stearns, 1992).

1.2 Compromis physiologiques

Lorsque l'expression de traits bénéfiques comme la reproduction actuelle va se traduire par une diminution d'autres traits comme les reproductions futures (e.g.

approvisionnement vs recherche de partenaire) les individus vont devoir compromettre entre différents traits d'histoire de vie (Horta-Lacueva *et al.*, 2021; Lukas *et al.*, 2021; Sih *et al.*, 2004a). Ces compromis peuvent maintenir des différences entre les individus d'une population. Dans le cas de traits plastiques tels que le comportement, négocier différents comportements peut également affecter l'expression des traits avec lesquels le comportement est intégré. Par exemple un individu étant plus explorateur peut avoir avantage à développer une physiologie favorisant la locomotion (Salzman *et al.*, 2018; Sih *et al.*, 2004b). Les compromis peuvent ainsi s'inscrire entre ces suites de traits ou comportements corrélés appelés 'syndromes comportementaux' ou au sein d'intégration phénotypique où le comportement est intégré avec des séries de traits plus ou moins variables tel que les traits morphologiques ou physiologiques (Dosmann *et al.*, 2015; Horta-Lacueva *et al.*, 2021; Lukas *et al.*, 2021; Royauté *et al.*, 2018; Sih *et al.*, 2004a; Westneat *et al.*, 2011). Ainsi, des comportement comme l'exploration peuvent être fortement corrélés avec la tendance à attaquer. Ce type de corrélation survient lorsque des traits vont être liés par des contraintes (e.g. un comportement plus actif va être associé à des demandes métaboliques plus importantes) ou parce que ces suites de trait contribuent à optimiser l'aptitude résultante des traits séparément de façon additive ou synergique (Biro et Stamps, 2008; Koolhaas *et al.*, 1999; Mathot et Frankenhuis, 2018; Patrick *et al.*, 2017; Salzman *et al.*, 2018; Sih *et al.*, 2004a; Sih *et al.*, 2012).

Les différences entre les individus d'une population peuvent aussi se maintenir lorsque les traits sont soumis à des compromis physiologiques. Lorsque deux ou plusieurs traits bénéfiques à l'aptitude des individus ne peuvent pas être exprimés en même temps ou dépendent des mêmes ressources limitées, l'augmentation de l'expression d'un trait devient associée avec une diminution ou l'absence de l'expression d'un autre. L'étude de la relation entre l'expression de ces trait devrait alors se traduire en une relation

négative (Stearns, 1989; Van Noordwijk et de Jong, 1986). Lors de l'étude de compromis le compromis peut être limité par plusieurs facteurs. Les individus possèdent un temps qui est limité, et doivent donc choisir entre plusieurs options comportementales (Lima et Dill, 1990; Ludwig et Rowe, 1990). Pour le renard roux (*Vulpes vulpes*, (Linnaeus, 1758)) il y a un compromis entre l'approvisionnement et la vigilance en présence de prédateurs (Wikenros *et al.*, 2014). Dans ce cas-ci, le temps est la ressource limitante puisque les renards ne peuvent pas s'approvisionner et être à l'affût en même temps et donc allouer du temps dans un diminue le temps allouable à l'autre. Les individus alternent entre les deux comportements et vont allouer leur temps différemment. Certains individus vont ainsi investir plus de temps à être vigilants que d'autres sur une période donnée. Ce type de compromis est largement étudié dans plusieurs systèmes pour son impact sur l'aptitude phénotypique des individus et la sélection qui en découle (Lima et Dill, 1990; Ludwig et Rowe, 1990; Moiron *et al.*, 2019; Sommer et Schmitz, 2020; Zajitschek et Connallon, 2017). La période de temps observée peut également grandement affecter l'expression de comportement ou les décisions d'allocations des individus. Les traits en intégration phénotypique comme le métabolisme, l'état et la condition de l'individu sont tous des facteurs pouvant influencer les décisions d'allocation d'un individu (Abrams, 1992; Alonzo, 2015; Angilletta Jr *et al.*, 2003; Badyaev, 2005; Careau *et al.*, 2008; Dosmann *et al.*, 2015; Elkin et Reid, 2005; Messina et Fry, 2003; Miller *et al.*, 2019; Stearns, 1989; Tatar et Carey, 1995) et qui vont fluctuer à différentes échelles de temps (Bell et Peeke, 2012; Carroll *et al.*, 2007; Dhellemmes *et al.*, 2020; Trudgill *et al.*, 2005).

Les compromis physiologiques vont donc généralement être limités et modulés par l'état des individus et leurs ressources énergétiques (Dhellemmes *et al.*, 2020). Lorsque les individus ont accès à peu de ressources, ils sont limités dans la quantité de ressources pouvant être allouées aux différents traits. Chez les coréidés, *Narnia*

femorata (Stål, 1870), les femelles peuvent investir dans la croissance des pattes arrières ou les ovaires pour augmenter la locomotion et la reproduction, respectivement (Miller *et al.*, 2019). Les deux traits dépendent de la croissance des tissus qui est limitée par les ressources énergétiques. Les individus ayant des ovaires plus développés ont ainsi des pattes postérieures moins développées et vice versa. Les individus vont souvent allouer leurs ressources différemment aux différents traits en fonction des ressources qu'ils peuvent allouer. Les ressources énergétiques modulent également l'allocation entre des traits, les différences individuelles et le comportement (Beckerman *et al.*, 1997; Lichtenstein *et al.*, 2016; Zajitschek et Connallon, 2017). Différents niveaux de ressources peuvent changer directement la force de la relation entre deux traits compromis ou même enlever la présence de compromis (Körner *et al.*, 2017; Messina et Fry, 2003; Miller *et al.*, 2019; Salzman *et al.*, 2018). Similairement, différents niveaux de ressources pourrait directement changer la façon dont les individus négocient le compromis, ou leur patron d'allocation des ressources entre les deux traits (!!! INVALID CITATION !!! (Elkin et Reid, 2005; Laskowski et al., 2021; Van Noordwijk et de Jong, 1986; Zajitschek et Connallon, 2017)). Comme les compromis sont souvent étudiés à un seul niveau de ressources limitées, il est important de comprendre comment différents niveaux de ressources peuvent affecter le patron d'allocation des individus (Desmarais et Tessier, 1999; Hamel *et al.*, 2009; Körner *et al.*, 2017; Messina et Fry, 2003; Salzman *et al.*, 2018; Sih *et al.*, 2015).

Un défi lors de la mesure d'un compromis physiologique est que la présence d'une trop grande variation dans le niveau de ressources des individus peut masquer la présence de compromis même s'il est présent (Roff et Fairbairn, 2007; Van Noordwijk et de Jong, 1986). Lorsque la variance des ressources est plus importante que celle des choix des individus, le compromis peut être masqué. Un individu ayant plus de ressources peut investir plus dans les traits compromis pour la même proportion d'allocation entre

les traits, l'augmentation de l'allocation dans un trait étant alors accompagnée par l'augmentation dans l'autre trait. Ainsi, pour observer un compromis physiologique, il est nécessaire de s'assurer que les individus aient accès à un niveau similaire de ressources (Roff et Fairbairn, 2007; Van Noordwijk et de Jong, 1986).

1.3 Phénotype étendu

Le phénotype d'un individu peut s'étendre à des traits extérieurs à l'individu qui leur sont spécifiques et affectent leur aptitude (Dawkins, 1982). Ces phénotypes étendus peuvent prendre plusieurs formes telles que le microbiote des individus, les pistes d'approvisionnement de fourmis, ou les ruches d'abeilles (Blamires, 2013; Rosengaus *et al.*, 2011; Royauté *et al.*, 2018; Smith *et al.*, 2015). Les phénotypes étendus peuvent être utiles lors de la mesure des différences individuelles. La constance des différences individuelles des comportements est estimée par la répétabilité. La répétabilité est la proportion de la variance dans le trait observé qui est expliquée par l'identité des individus à travers les contextes ou simplement à travers le temps (Bell *et al.*, 2009; Nakagawa et Schielzeth, 2010). Cependant, mesurer des comportements comme l'agression ou l'exploration à plusieurs reprises peut engendrer de l'habituation chez les animaux mesurés (Biro et Stamps, 2015; Wolak *et al.*, 2012). Afin d'éviter les biais méthodologiques, le comportement peut être mesuré dans des traces physiques en l'absence de l'animal sous forme du phénotype étendu. Comment les individus négocient leur compromis pourrait également être reflété dans leurs constructions. Les individus vont ajuster leur constructions et investir différemment dans les fonctions du phénotype étendu (Blamires, 2010; Royauté *et al.*, 2018; Smith *et al.*, 2015). Ces phénotypes étendus sont généralement plastiques (Blamires, 2010; DiRienzo et Aonuma, 2018) et peuvent directement affecter l'aptitude des individus (Blamires *et*

al., 2018; DiRienzo *et al.*, 2020). Les constructions offrent donc une opportunité d'évaluer la négociation de compromis.

1.4 Objectifs

Les objectifs de ce mémoire sont d'évaluer comment la relation entre le nombre de deux types de fils contenu dans la toile de veuves noires de l'ouest (*Theridiidae*, *Latrodectus hesperus*) varie avec la limitation des ressources et le temps. Les veuves noires de l'ouest construisent des toiles avec lesquelles elles interagissent avec leur environnement. La toile est importante pour l'acquisition de ressources, la défense contre les prédateurs et la reproduction (Schraft *et al.*, 2021). Les individus démontrent des différences constantes dans la structure de leurs toiles et la présence de compromis a un fort potentiel d'y jouer un rôle (Dirienzo et Montiglio, 2016a; Zevenbergen *et al.*, 2008).

1.5 Système d'étude (*Latrodectus hesperus*)

Les veuves noires de l'ouest tissent des toiles tridimensionnelles. Ces toiles vont généralement être tissées puis utilisées par les araignées pour une partie importante de leur vie. Elles comportent trois sections (Benjamin et Zschokke, 2003). Un refuge prenant la forme d'un entonnoir est généralement séparé du reste de la toile et se trouve sous une souche ou une plante. Il est constitué d'une couche de soie dense et protège l'araignée et ses œufs contre les prédateurs et les parasitoïdes. La section la plus volumineuse de la toile, le feuillet, est composée d'une matrice de fils parallèles au sol sous laquelle l'araignée se déplace et capture ses proies. Sous le feuillet se situent les fils structuraux soutenant la toile ainsi que les fils de captures à pied collants (Agnarsson, 2004; Blackledge *et al.*, 2005a; Blackledge *et al.*, 2005b). Ces toiles sont

également semi permanentes étant utilisées jusqu'à des saisons complètes (Schraft *et al.*, 2021). Les fils structuraux servent de mécanisme de défense contre les prédateurs. Les fils structuraux transmettent par vibration la présence de prédateurs en plus de servir de barrière physique aux prédateurs comme ils sont ancrés solidement (Vetter *et al.*, 2016; Vibert *et al.*, 2016). Les fils de capture servent à la capture de proies rampantes et sont composés de trois à quatre fils enroulés sous tension munie de gouttes collantes au pied des fils (Agnarsson, 2004; Argintean *et al.*, 2006; Hu *et al.*, 2007). Lorsqu'une proie rampante passe sur un fil de capture, elle se colle aux gouttes et brise l'ancrage du fil qui relâche sa tension, remontant la proie dans la matrice où l'araignée peut la capturer (Agnarsson, 2004; Blackledge *et al.*, 2005a; Blackledge *et al.*, 2005b). L'araignée se déplace alors sur la toile et enroule rapidement la proie avec de la soie collante à l'aide de ses pattes arrières (Dirienzo et Montiglio, 2016a).

Le choix que les veuves noires font dans le tissage des fils sous la toile va généralement affecter la fonction de la toile et différer d'un individu à l'autre (Dirienzo et Montiglio, 2016a, 2016b). La forme de la toile est également associée au comportement de l'araignée sur la toile. Les araignées qui produisent plus de fils collants attaquent plus souvent les stimuli vibratoires appliqués sur leur toile et ceux qui tissent plus de fils structuraux attaquent moins (Dirienzo et Montiglio, 2016a, 2016b). Les veuves noires de l'ouest vont également ajuster leurs toiles en fonction de leurs ressources énergétiques, les individus avec moins de ressources énergétiques vont augmenter les fils collants dans leur toile et ceux avec plus de ressources avoir plus de fil structuraux (Blackledge et Zevenbergen, 2007; Dirienzo et Montiglio, 2016a). La condition développementale des araignées pouvant également affecter leur plasticité (Dirienzo et Montiglio, 2016a). La construction de toile devrait être coûteuse en énergie pour les araignées en général (Craig, 2003; Prestwich, 1977; Tanaka, 1989) et plus précisément pour les espèces de la famille (*Theridiidae*) tissant ce type de toiles capable de préserver

leurs propriétés sur une période prolongée dans des milieux secs (Benjamin et Zschokke, 2003; Blackledge *et al.*, 2005b; Gonzaga *et al.*, 2006). On ignore encore la dynamique des différences individuelles constantes entre les niveaux de ressources et le temps accordé à la construction de phénotype étendu. Comme les veuves noires de l'ouest démontrent des différences constantes dans la structure de leur toile associées aux ressources et que la présence de compromis est probable, ce système présente une opportunité d'observer ces mécanismes peu compris.

CHAPITRE II

EFFECTS OF RESOURCE AVAILABILITY ON THE WEB STRUCTURE OF FEMALE WESTERN BLACK WIDOWS: DO PHYSIOLOGICAL TRADE- OFFS CONSTRAIN WEB STRUCTURE?

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2.1 Abstract

The study of plastic traits such as behavior provides insight into what generates and maintains phenotypic variation among individuals. Negative relationships between traits where expressing one behavior is paired with the decrease of another is one such mechanism where differences between individuals can be maintained. However, few studies have investigated how individual differences in negotiation of a trade-off between two traits may vary over time and resources. Black widow spiders can build webs including structural threads to protect themselves against predators or sticky trap (i.e. 'gumfooted') threads to capture prey. They consistently differ in web structure and the presence of a trade between thread types is likely. The objectives of this study were to (1) assess the relationship between web functions and whether there was a trade-off. We also wanted to (2) assess how food level (resources) affected the individual variation in web function. Our last objective was to (3) describe how individual differences in web structure varied with time. We alternated spiders through 8 weeks where prey abundance varied between 1 cricket every week, every other week, or every three weeks. We then measured the webs the spiders weaved for a week every twelve hours. We did not find evidence for a physiological trade-off between trap and structural threads. We suggest trade-offs in fitness outcome or between traits integrated with web structure could likely maintain individual differences in web structure. However, individual differences in web structure did change with food availability through time. Our study provides insights in the processes maintaining individual differences in web structure.

Key words: animal architecture, animal personality, behavioral syndrome, extended phenotype, foraging, individual differences, *Latrodectus hesperus*.

2.2 Introduction

Behaviour is often highly plastic and varies across environments, but individuals within populations also show consistent differences in their behaviour (Dall *et al.*, 2004; Réale *et al.*, 2007; Sih *et al.*, 2004a) These differences often constitute a large portion of a population's phenotypic variance (Bell, 2012; Bell *et al.*, 2009; Dingemanse et Dochtermann, 2013; Dingemanse et Réale, 2005; Garamszegi *et al.*, 2015), are heritable, and subject to selection (Biro et Stamps, 2008; Dingemanse et Réale, 2005; Dochtermann *et al.*, 2019). Individual differences (or the behavioural profile of individuals) have important consequences for their survival, fecundity, mating success or growth (Montiglio *et al.*, 2016; Patrick *et al.*, 2017; Réale et Festa-Bianchet, 2003; Santostefano *et al.*, 2017);. As a result, we often consider this behavioural variation to be adaptive, and ongoing work investigates when/how ecological conditions generate selection pressures maintaining individual differences in behaviour (Brommer, 2013; Moiron *et al.*, 2020; Nicolaus *et al.*, 2013; Nussey *et al.*, 2007) .

Behavioural differences among individuals could also arise because of constraints in the expression of behaviour (Biro et Stamps, 2008; Réale *et al.*, 2010a; Stamps, 2007; Steinhoff *et al.*, 2020). One major constraint is that individuals often have limited amount of energy or time to express behaviour (Lessels, 1991; Stearns, 1992)(Lessels 1991, Stearns 1992, Olson and Shine 1997). Such physiological trade-offs can maintain individual differences in behavioural traits (Biro et Stamps, 2008; Réale *et al.*, 2010b; Stamps, 2007). The life history trade-off that received the most attention is the one linking survival with reproductive effort(Stearns, 1992). Related to this life history trade-off, several studies have documented a trade-off between predator avoidance and foraging (Cole et Quinn, 2012; Farwell et McLaughlin, 2009; Lima et Dill, 1990; Steinhoff *et al.*, 2020). Predator avoidance might conflict with foraging activity either

because the two behaviours cannot be performed simultaneously, or because foraging activity directly increases predation risk (Abrams, 1992; Lima, 1998; Lima et Dill, 1990; McNamara et Houston, 1987; Sih, 1980; Verdolin, 2006). Thus, there must often be a trade-off between foraging and avoiding predators. When such a trade-off occurs, we expect the two traits to show a negative relationship where individuals with higher values for foraging also express lower values for predator avoidance. For example, there is a trade-off between time spent foraging and time spent on vigilance in the presence of predators in the red fox *Vulpes vulpes* (Wikenros *et al.*, 2014). In this case, different individuals will allocate their time differently. At the level of the population, this may maintain trait variation even in the presence of selection, because individuals with different time allocations might achieve a similar fitness (Roff et Fairbairn, 2007; Stearns, 1992). These individual differences in allocation can be repeatable and consistent across different contexts, which leads to differing behavioural profiles such as consistently bolder (or aggressive) and shy (or defensive) individuals (Dingemanse et Réale, 2005; Réale *et al.*, 2007).

Individual differences in the access to limited resources can mask trade-offs because individuals with more resources can invest more in multiple biological functions compared with individuals with fewer resources (Roff et Fairbairn, 2007; Stearns, 1989; Van Noordwijk et de Jong, 1986). This can mask the negative relationship between traits, or even generate a positive one (Roff et Fairbairn, 2007; Stearns, 1992; Van Noordwijk et de Jong, 1986). Thus, determining whether there is a trade-off between traits requires manipulating and standardizing resource availability among individuals (Roff et Fairbairn, 2007) and measuring the behaviour of individuals repeatedly to assess whether the trade-off exists at the within individual level (Ljungström *et al.*, 2016; Moyes *et al.*, 2006; Moyes *et al.*, 2009; Roff et Fairbairn, 2007) An additional challenge is that individuals can also base their resource allocation on their perceived

abundance of resources. For example, house crickets (*Acheta domesticus*) experiencing different diets during their development grow to negotiate life history trade-offs differently (Royauté et Dochtermann, 2016). An additional layer of complexity exists for labile traits: values of behavioural traits fluctuate over time (Bell et Peeke, 2012; Biro et Stamps, 2015; Carroll *et al.*, 2007; Gomes et Cardoso, 2020) and the magnitude of individual differences in behaviour that one observes depend on the duration over which measurements are made (Montiglio *et al.*, 2010). Hence it is important to ascertain that behaviour is measured at the proper temporal scale to detect potential trade-offs (Körner *et al.*, 2017; Messina et Fry, 2003; Miller *et al.*, 2019; Salzman *et al.*, 2018; Varpe, 2017).

Here, we investigated the temporal dynamic of web building and assessed the importance of a potential trade-off between structures enabling prey capture and structures protecting against predation in females of the western black widow *Latrodectus hesperus* (Chamberlin et Ivie, 1935). Black widow spiders build persistent three-dimensional webs that include structural threads to protect against predators and sticky trap threads to capture preys (Schraft *et al.*, 2021). Females show stable differences in the number and relative proportion of each type of thread that they produce on their web over much of their adult lifespan (Blackledge et Zevenbergen, 2007; Dirienzo et Montiglio, 2016b; Zevenbergen *et al.*, 2008). Web structure affects behaviour, such that the spiders building webs with more trap threads are also more likely to attack vibratory prey cues because of the structure of their web (Dirienzo et Montiglio, 2016b; DiRienzo *et al.*, 2020). Building a web is presumably costly because silk is constituted of proteins and water (Argintean *et al.*, 2006; Blackledge *et al.*, 2005a; Blamires *et al.*, 2014) that are in some spiders limited enough that changes in prey affects protein structure of silk (Blamires, 2010; Blamires *et al.*, 2009; Sandoval, 1994). Individual differences in web structure might arise as a result of individual differences

in resource allocation to each type of threads (Craig, 2003; Prestwich, 1977; Tanaka, 1989). Black widows produce more trap threads when they are hungry or have a lower condition (Dirienzo et Montiglio, 2016a; Zevenbergen *et al.*, 2008), but individuals could differ consistently in how they cope with the costs associated with building different threads and how they negotiate the trade-off between protection and prey capture.

Our objectives were (1) to assess how food abundance affected the relationship between the number of structural and trap threads on black widow webs; (2) to quantify how food abundance affected the magnitude of individual variation in web structure; and (3) to describe how the magnitude of individual differences in web structure varied over time during the web construction phase. We placed each spider in a random order through eight weeks of being fed under a low, intermediate, or ad libitum food treatment. After each treatment, we assessed the number of each type of threads. We monitored web structure every 12 hours for a week. Given prior evidence, we expected spiders in the low food treatments to allocate more silk to trap threads (to increase prey capture) than spiders in the high food treatment (Blackledge et Zevenbergen, 2007; Zevenbergen *et al.*, 2008). If web structure is constrained by a physiological trade-off, we predicted stronger differences in web structure under higher food abundance. We also expected that individual differences in web structure would increase and then stabilize over time during the web construction phase.

2.3 Methods

Study system and husbandry

Western black widow spiders are generalist predators found along the western coast of North America (Schraft *et al.*, 2021). They build three dimensional cobwebs. Those

webs can be separated into three function sections: the refuge, which consists of a dense funnel of silk usually within a confined space; the sheet, which is a mostly horizontal plane where the spiders move around or sit and wait for preys; and the section of threads located under the web where the spiders link threads from the sheet to the ground (Dirienzo et Montiglio, 2016b; Kaston, 1970; Vetter, 1980; Zevenbergen *et al.*, 2008). The threads under the web can either be trap threads used to capture crawling preys or structural threads reinforcing web integrity, create a barrier between, and warn the spider of, potential predators such as birds or mud dauber wasps (Brandley *et al.*, 2016; Irving et Harold Hinman, 1935) or egg predators and parasitoids wasps and flies (Rau, 1935; Vetter *et al.*, 2012).

We used 60 wild-caught virgin female black widow spiders from Davis, California, United-States. We captured individuals around buildings and concrete structures. We brought individuals to the University of Arizona, where they were initially kept for separate experiments prior to this study (DiRienzo, submitted). During these prior experiments, spiders went through two rounds of web building assays for 5 days, followed by an injection treatment. Briefly, we removed the spiders from their web at the end of each round of web building, selected a subset of spiders that were anaesthetised with CO₂ only, or anaesthetised with CO₂ and injected with either dopamine or serotonin. After an hour, each spider was then put back on its original web and underwent three aggression tests over a period of 48 hours. We randomly assigned treatments across spiders and between the two rounds of web building. We then transferred the spiders to our laboratory in Quebec, Canada a month prior to the beginning of this study. We housed spiders in individual plastic containers (946 ml) at 23°C ± 1.50 and 25 % humidity ± 8.94 with a photoperiod of 12h. Spiders were fed a single live house cricket (*Acheta domesticus*) every two weeks before the start of our experiment.

Food treatments

We subjected the spiders to each food abundance treatment for 8 weeks. Previous studies showed that this period is enough to induce changes in condition and web structure (Dirienzo et Montiglio, 2016a, 2016b). The ad libitum treatment involved feeding the spiders with a cricket every week. The restricted treatment involved feeding the spiders a cricket every three weeks. The intermediate treatment involved feeding the spiders a cricket every two weeks. Over the course of the experiment, we subjected each spider to all three treatments in three different orders (restricted/intermediate/ad libitum, intermediate/ad libitum/restricted, ad libitum/restricted/intermediate). At the end of the 8-week food treatment, we weighed spiders using numeric balances (Ohaus Scout 123X) to the closest milligram. We then placed each spider into an individual standardized cardboard frame (31 cm length x 17 cm height x 24 cm width) equipped with a grid of 1.5 in² at the bottom to facilitate counting the number of threads (Fig. 1). We placed each cardboard frame in a larger sterilite™ plastic container (46cm x 31.1cm x 29.2cm). We left the spiders to weave a web for a week before transferring them back to their individual plastic containers (946 ml) to recover for a week without any access to food before initiating the next food treatment.

Web assays and silk measurements

During the web building assays, we assessed web structure over seven days, counting the number of structural and trap threads every 12h using a well-established method (Blackledge et Zevenbergen, 2007; Dirienzo et Montiglio, 2016b; Zevenbergen *et al.*, 2008). We counted the total number of threads as every thread going from the superior sheet of the web to the ground. Trap threads were identified as any threads bearing glue droplets at their foot and structural threads as any other threads that bore no glue droplets. After the spiders were transferred back into their respective plastic containers,

we wrapped the webs around glass sticks and left them for 12 hours in the desiccator. We then weighed them on numeric balances (Sartorius SECURA224-1S) to the closest microgram. We used the measures of spider weight to calculate spider mean weight, weight difference to this average and a relative change in mass index being the percentage of weight difference over the spiders' mean weight (see annex for an example). Spider weight after web building and web weight were not measured for the first trial due to an error.

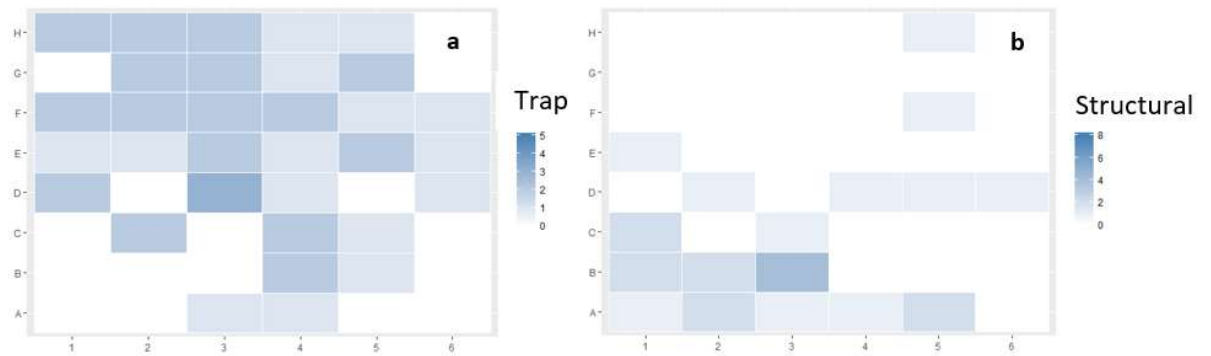


Figure 1 Average count of **a** trap and **b** structural threads in each section of the grid ($N = 135$ webs) in this study, A1 being the refuge.

Measuring body size and condition

We calculated weight loss during web building as the difference between spider mass before and after the week of web building. Three measures of body mass were taken per individual for before and after web building. Due to logistical issues, measurement of a weight before web building couldn't be measured. We used the mean of those all five measures to calculate individual average weight. We then used the ratio of lost mass in during web building over the individual's average weight as an estimate of

relative weight loss by an individual during web building (See supplementary materials).

Statistical analyses

All statistical analyses were conducted using the R program 3.4.3 (R Core Team, 2018).

First, to assess whether web building was costly for individuals and whether the food treatment affected spider condition, we ran linear mixed models analysing spider weight after web building and the relative change in weight after web building varied as a function of food treatment, the treatment order, (i.e. the sequence in which each individual experienced the three food treatments), the block (1 and 2 each being separate weeks), silk mass, spider weight before web building, trap, and structural thread counts (all variables included as fixed effects). Spider weights were centered.

Second, we determined how our food treatments affected web structure. We used mixed models to analyse silk mass (normal error distribution), the number of trap threads, the number of structural threads, the total number of threads (all Poisson error distribution), and the proportion of trap threads relative to the total number of threads (binomial error distribution) in each web as a function of food treatment (restricted, intermediate, ad libitum), the web trial order, and the trial period, (Bates, 2010). We also included individual identity as a random effect to avoid pseudo replication and compute the repeatability of individual differences.

Third, we modelled the relationship between the number of trap threads and the number of structural threads on the webs. We used a generalized linear mixed model analyzing the number of trap threads (Poisson error distribution) as a function of the number of structural threads, the food treatment (restricted, intermediate, ad libitum), and their

interaction. We also included food treatment trial order as fixed effects, trial period and individual identity and date as random effects.

We quantified how between- and within-individual variation in the number of structural and trap threads and the number of threads in total changed over time during the web building phase. We built models analysing the number of threads in total, the number of trap threads, and the number of structural threads (log transformed). We included the scaled time (ordinated categorical variable, using polynomial contrasts), food treatment, the trial period and the order in which we applied the treatments to each spider as fixed effects and individual identity and treatment as random effects. We log-transformed the number of trap and structural threads and the number of threads in total to normalize the distribution of residuals. In these models, residual variance could vary exponentially as a function of time (hereafter, we refer to these variables as variance covariates, see (Pineiro et Bates, 2000b);(Pineiro et Bates, 2000a) also see (Montiglio *et al.*, 2015) and script in supplementary materials. Since for a given time each repeated measurement for an individual was under a different treatment, we also allowed residual variance to vary as a function of the food treatment. This allowed us to quantify changes in the magnitude of individual variance and residual variance over time during web building (associated with the individual identity random effect and residuals respectively). We assessed the statistical significance of these variance covariates using log-likelihood ratio tests comparing the full model to a model excluding the effect or covariate of interest. These tests use a Chi^2 statistic and one degree of freedom. We excluded from this analysis any individual which died during the experiment ($N = 13$) to ascertain that each individual had 3 observations per time slot. Finally, we quantified how the relation between the number trap and structural threads changed at the between- and within-individual level. We built a model analysing the number of trap threads where we included individual mean number of

structural threads, the quadratic of the mean number and the deviation of each web's number of structural threads the individual's average as fixed effects (see (Van de Pol et Wright, 2009); Supplementary materials). We included the deviation of each web nested in individual identity and which number of web's the individual weaved in this experiment (ranging 1 to 3) as random effects. We log-transformed the number of trap and structural threads and the number of threads in total to normalize the distribution of residuals.

We simplified each model in a backward stepwise manner using Akaike's information criterion (AIC) (Burnham et Anderson, 2002). If the models did not differ when an effect was removed, we kept the most parsimonious model. We added an observation level random effect (OLRE) in models with binomial or Poisson error distributions to account for potential over-dispersion (Harrison, 2014, 2015). 95% confidence intervals were obtained through parametric bootstrapping procedures (number of simulations = 1000; (Bates, 2010). Whenever a model included spider weight loss, we removed two females who laid eggs during web building as it is impossible to know how much weight loss was due to being gravid and then laying eggs.

2.4 Results

The food treatment did not affect the weight of spiders after web building (difference between ad libitum and intermediate food treatments: estimate = -1.884 mg, 95% CI = -9.657 : 5.889 , $n = 83$, $t_{1,73} = -0.483$, $P = 0.631$; difference between ad libitum and restricted food treatments: estimate = 2.033 mg, 95% CI = -5.739 : 9.805 , $n = 83$, $t_{1,73} = 0.521$, $P = 0.604$; Table S.1). Spiders lost weight during the web building phase on

average (estimate = 8.160 mg, 95% CI = 5.101:11.219, $n = 85$, $t_{1,73} = 5.317$, $P < 0.0001$; Table S.2). Spiders had less weight when they built more trap threads (trap threads: -0.186, 95% CI = -0.365: -0.007, $t_{1,73} = -2.069$, $P = 0.042$; Table S.1) but not when they built structural threads (structural threads: -0.113, 95% CI = -0.365, 0.139, $t_{1,73} = -0.895$, $P = 0.374$; Table S.1). Spider relative weight loss during web building increased with the number of trap threads that they produced (trap threads: 0.069, 95% CI = -0.012:0.126, $t_{1,73} = 2.399$, $P = 0.019$; Table S.2) but not with the number of structural threads produced (structural threads: 0.035, 95% CI = -0.045, 0.115, $t_{1,73} = 0.873$, $P = 0.386$; Table S.2) nor with and web weight (estimate = -0.871, 95% CI = -1.931:0.189, $n = 83$, $t_{1,73} = -1.637$, $P = 0.106$; Table S.2).

Spiders under the intermediate food treatment weaved lighter webs (difference between ad libitum and intermediate food treatment: estimate = -0.630, 95% CI = -1.161:-0.097, $t_{1,76} = -2.322$; Table S.3). Spider under the restricted food treatment produced webs with a higher proportion of trap threads (difference between ad libitum and restricted food treatments: estimate = 0.731, 95% CI = 0.119:1.323, $n = 135$, $z = 2.339$, $P = 0.019$; Table S.7). Food restrictions did not appear to affect the number of trap threads (difference between ad libitum and restricted estimate = 0.423, 95% CI = -0.118:0.970, $n = 135$, $z = 1.580$, $P = 0.114$; Table S.4) and structural threads (difference between ad libitum and restricted estimate = -0.284, 95% CI = -0.649:0.078, $n = 135$, $z = -1.567$, $P = 0.117$; Table S.5). However, when combining observations with the restricted and intermediate food treatments, we found that the combined treatment led spiders to produce more trap threads (). We did not detect any relationship between the number of trap and structural threads in each of the food treatment (Table 1).

Table 1 Final Poisson linear mixed effect model of the determinants of the number of trap thread ($n = 135$ webs from $N = 45$ individuals). Deviance = 1009.5 on 125 df.

Variance component	Variance	χ^2	df	r	P
Individual	1.737	27.489	1	23.3%	<.000
					1
OLRE	1.309	439.98	1		<.000
					1

Fixed effects	Coef	SE	z value	95% CI	Df	P
Intercept	1.354	0.569	2.378	0.167: 2.481	1(135)	0.017
Food treatment (intermediate) ^a	-0.523	0.506	-1.034	-1.576:- 0.504	1(135)	0.301
Food treatment (Restricted) ^a	0.093	0.510	0.183	-0.946: 1.135	1(135)	0.855
Number of structural threads	-0.007	0.017	-0.409	-0.041:- 0.028	1(135)	0.682
# of structural threads X Food treatment (intermediate) ^a	0.030	0.020	1.516	-0.009: 0.072	1(135)	0.130

# of structural threads X food	0.017	0.022	0.764	-0.028: 0.064	1(135)	0.444
treatment (restricted) ^a						
Order (B) ^b	0.045	0.548	0.083	-1.096:1.126	1(45)	0.934
Order (C) ^b	0.303	0.553	0.548	-0.796:1.454	1(45)	0.584
Block (2) ^c	0.656	0.454	1.445	-0.254:1.602	1(135)	0.148

AIC 1031.

5

Marginal *R*² 0.072

Conditional 0.576

*R*²

Significant *P* values are shown in bold. Order identifies the order in which the spiders underwent the three food treatments (A: Ad libitum, intermediate then restricted; B: Intermediate, restricted then ad libitum and C: Restricted, ad libitum then intermediate).
^aAd libitum taken as reference. ^bOrder A taken as reference. ^cBlock 1 taken as reference.

There was no trade-off between the number of trap threads and the number of structural threads between individuals (estimate = 2.628, 95% CI = 1.065:4.185, $n = 135$, $t_{1,77} = 3.283$, $P = 0.996$; Table S.9; Fig 2) and between each web within individuals (estimate = 0.181, 95% CI = -0.194:0.511, $n = 135$, $t_{1,77} = 1.080$, $P = 0.05$; Table S.9; Fig 2) individual level.

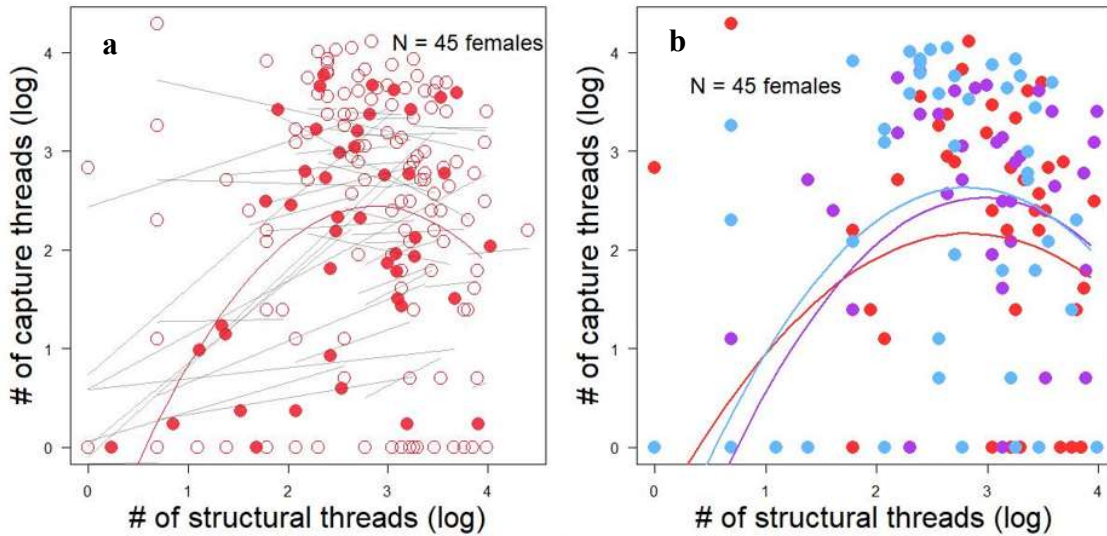


Figure 2 **a** Between individual (red filled dots) and within individual (empty dots) relationship between the number of trap and structural threads (log-transformed) from 45 virgin adult female western black widows. **b** Relationship between the number of trap and structural threads for webs built under ad libitum (red), intermediate (purple) and restricted (blue) food treatment from 45 virgin adult female western black widows.

The number of trap threads ($N = 1890$, linear = 0.442 , 95% CI = 0.415 : 0.469; quadratic = -0.089, 95% CI = -0.110: -0.067; Table 2; Fig 3a)) and the number of structural threads ($N = 1890$, linear = 0.218, 95% CI = 0.202 : 0.235; quadratic = -0.049, 95% CI = -0.065 -0.034 ; Table 3; Fig 3a) increased over time during the web building phase in a quadratic function (LRT= 61.59, df = 1, $P < .0001$ and LRT = 36.83, df = 1, $P < .0001$). Spiders produced more structural threads than trap threads during web building (Fig. 3a).

The average number of trap and structural threads that the spiders produced over time during the web building phase did not differ between treatments (Table 2 & 3; Fig 3b). Individual variance in the number of trap threads varied among the food treatments (LRT = 70.43, df = 4, $P < 0.001$) and initially decreased over time to reach a plateau (quadratic effect of time: LRT = 57.445, df = 3, $P < 0.001$; Table 2). Individual variance in the number of trap threads initially decreased over time to then stabilize around the 120th hour of web building (Fig. 3b; Table S.10). Individual variance was larger than the residual variance (Fig. 3b; Table S.10).

Table 2 Final model of the determinants of the number of trap threads over time (log transformed; $N = 1890$)

Variance component	Variance	LRT	Df	<i>P</i>
Individual	1.575	3176.134	1	<.0001
Food Treatment (nested in ID)	0.972	2064.993	1	<.0001
Residual	0.410			

Variance covariates	Coefficient	LRT	Df	<i>P</i>
Time linear (ad libitum)	-0.717	160.852	3	<.0001
Time linear (intermediate)	-0.081			

Time linear (restricted)	-0.541				
Time quadratic (ad libitum)	-0.028	57.445	3	<.000	1
Time quadratic (intermediate)	0.186				
Time quadratic (restricted)	0.037				

Fixed effects	Coefficient	SE	<i>t</i>	95% CI	Df (residual Df)	<i>P</i>
Intercept	1.215	0.468	2.596	0.297:2.133	1(1752)	0.00
Food treatment (intermediate) ^a	0.042	0.207	0.204	-0.456:0.371	1(87)	0.83

Food treatment	0.309	0.206	1.503	-0.100:0.718	1(87)	0.13
(Restricted) ^a						7
Time linear	0.442	0.014	32.03	0.415:0.469	1(1752)	<.00
(scaled)			6			01
Time quadratic	-0.089	0.011	-	-0.110:-0.068	1(1752)	<.00
(scaled)			8.254			01
Order (B) ^b	-1.343	0.514	-	-2.351:-0.334	1(1752)	0.00
			2.612			9
Order (C) ^b	1.665	0.514	3.238	0.657:2.674	1(1752)	0.00
						1
Block (2) ^c	0.377	0.500	0.753	-0.632:1.386	1(43)	0.45
						6

AIC 3011.936

Significant *P* values are shown in bold. Order identifies the order in which the spiders underwent the three food treatments (A: Ad libitum, intermediate then restricted; B: Intermediate, restricted then ad libitum and C: Restricted, ad libitum then intermediate).
^aAd libitum taken as reference. ^bOrder A taken as reference. ^cBlock 1 taken as reference.

Table 3 Final model of the determinants of the number of structural threads over time (log transformed; *N* = 1890)

Variance component	Variance	LRT	df	<i>P</i> value
Individual	1.223	4801.08	1	<.0001
		3		
Food Treatment(nested in ID)	0.897	3683.25	1	<.0001
		1		
Residual	0.147			
Variance covariates	Coefficient	LRT	df	<i>P</i> value

Time (ad libitum)	-0.581		362.485	3		<.0001
Time (intermediate)	-0.473					
Time (restricted)	-0.105					
Time quadratic(ad libitum)	0.463		463.128	3		<.0001
Time quadratic (intermediate)	0.470					
Timequadratic (restricted)	0.583					

Fixed effects	Coefficient	SE	<i>t</i>	95% CI	Df(residual df)	<i>P</i> value
Intercept	2.229	0.376	5.933	1.492:2.966	1(1752)	<.0001
Food treatment (Intermediate) ^a	-0.271	0.191	-1.419	-0.650:0.109	1(87)	0.1596
Food treatment (Restricted) ^a	-0.286	0.189	-1.509	-0.662:0.091	1(87)	0.1350

Time linear (scaled)	0.218	0.008	26.671	0.202:0.235	1(1752)	<.0001
Time quadratic (scaled)	-0.049	0.008	-6.290	-0.065:-0.034	1(1752)	<.0001
Order (B) ^b	-1.007	0.407	-2.472	-1.806:-0.208	1(1752)	0.0135
Order (C) ^b	1.613	0.408	3.957	0.813:2.412	1(1752)	0.0001
Block (2) ^c	0.193	0.398	0.484	0.193:0.994	1(43)	0.6305
AIC	935.847					

Significant P values are shown in bold. Order identifies the order in which the spiders underwent the three food treatments (A: Ad libitum, intermediate then restricted; B: Intermediate, restricted then ad libitum and C: Restricted, ad libitum then intermediate).

^aAd libitum taken as reference. ^bOrder A taken as reference. ^cBlock 1 taken as reference.

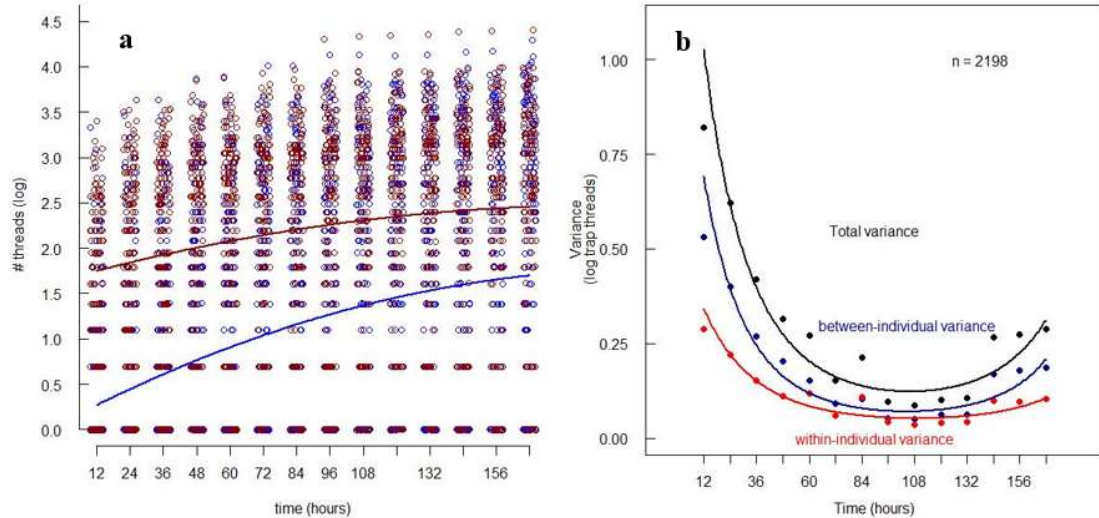


Figure 3 **a** Number of structural (red) and trap (blue) threads overtime. **b** Total (black), between (blue) and within (red) variance in log transformed trap threads over time. Variances were estimated using the residuals from the variance-covariance model in Table 2.

2.5 Discussion

Here, we tested whether individual differences in web building were the result of a trade-off between different components of the web. We investigated how the silk invested in trap and structural threads (serving for foraging and protection, respectively) varied with food abundance and time. Such trade-offs between foraging and predator avoidance can have important consequences for habitat use (Cowlshaw, 1997),

community structure (Miller et Svensson, 2014; Schmitz, 2007), and life history (Steinhoff *et al.*, 2020). In line with previous work, higher food abundance increased spider condition and resulted in heavier webs with a lower proportion of trap threads (Blackledge et Zevenbergen, 2007; Dirienzo et Montiglio, 2016a; Zevenbergen *et al.*, 2008). However, despite these individual differences in web structure, we did not find evidence for a trade-off between foraging and predator avoidance when food was restricted. Instead, webs with more structural threads also exhibited more trap threads. Interestingly, spiders expressed stronger differences in web structure when they were fed *ad libitum*. Individual differences were also stronger during the initial stages compared with the later stages of web building.

Our first results were that spiders that had access to more food were heavier, produced heavier webs with fewer trap threads. These results confirm that restricting access to food had the intended effect of suppressing body condition and the production of silk (Bucher et Entling, 2011; Nakata, 2009; Sandoval, 1994). They also show that spider responded to the treatment by adjusting the structure of their web, increasing the number of trap threads when food was more limited. These findings are in line with previous studies in our study species reporting that black widow spiders with lower access to food build a higher proportion of trap threads (Blackledge et Zevenbergen, 2007; Dirienzo et Montiglio, 2016a; Zevenbergen *et al.*, 2008) They also echo studies on other taxa reporting that spiders adjust the architecture of their web in response to the abundance of prey (e.g. (Chacon et Eberhard, 1980; Herberstein *et al.*, 2000; Sherman, 1994), which likely reflects a strategy to catch more prey (e.g. (Chacon et Eberhard, 1980; Herberstein et Elgar, 1994). Altogether, our findings and those documented by other studies would suggest that spiders tend to only invest in structures that enhance prey catching, such as trap threads in black widow spiders, when they have high need for food. This strongly suggests that such structures are costly to build

which is supported by our observation that spiders lost more weight the more they built trap threads. This cost is likely to be linked with the expenditure of limited resources such as energy or water content (Benjamin et Zschokke, 2003; Sherman, 1994; Tanaka, 1989; Vollrath *et al.*, 2001), but could also be detrimental to other web functions such as the attraction of mates (Kasumovic et Andrade, 2004; MacLeod et Andrade, 2014) and of the protection against predators and intruders (Moiron *et al.*, 2019; Nakata, 2009; Wikenros *et al.*, 2014).

Trade-offs

There was no effect of the amount of silk (web weight) or the number of threads produced on weight loss during web building. Furthermore, the number of trap thread was independent of the number of structural threads. On the contrary, we found a positive relationship between the number of trap and structural thread at the between-individual level. There was thus no evidence for a cost associated with building a web and no evidence for a trade-off between the two types of threads. Given that our study controlled for differences in resource abundance, this relationship is unlikely to be the result of great variation in resource acquisition masking differences in individual allocation (Van Noordwijk et de Jong, 1986). This challenges our prediction that energetic costs associated with producing silk impose a trade-off between the number of trap and structural threads that female black widows can produce. It has been suggested that a trade-off could maintain individual differences in web structure in black widow spiders, whereby some females invest more in protection and build more structural threads, while others invest more in foraging and build more trap threads (Dirienzo & Montiglio 2016a; Dirienzo & Montiglio 2016c). Such trade-offs are often only observed when individuals have limited access to resources (e.g. (Körner *et al.*, 2017; Messina et Fry, 2003). We note that our food restricted spiders were heavier than previous studies (Blackledge & Zevenbergen 2007; Dirienzo & Montiglio 2016a). It is

thus possible that none of our spiders were limited enough in resources to express a physiological trade-off. Nevertheless, we think that this is unlikely to completely explain the absence of a trade-off given that our food-restricted treatment was severe enough to reduce body weight and alter web structure. .

An alternative explanation is that structural threads not only serve as a protection but are also necessary to support trap threads. This would explain why the number of structural threads was maintained including under restricted food abundance. In supporting of this idea, we observed that all spiders produced more structural threads during the initial phases of web construction, before adding trap threads. Alternatively, other resources, such as water or specific nutrients, may pose greater constraints to web building than limited food abundance. The western black widow spider is a desert specialist (Schraft *et al.*, 2021) and is likely to face limited access to water in its natural habitat. In spiders, water is essential because it is required for silk production (Jin et Kaplan, 2003; Vollrath et Edmonds, 1989; Vollrath et Porter, 2006) and water deprivation could limit the ability to build a web in dry habitats. Likewise, silk production may be limited by specific nutrients that our experiment failed to manipulate adequately. It is acknowledged that particular amino-acids or fatty acids can mediate physiological trade-offs (Grandison et al. 2009, Attisano et al. 2012). Trade-offs have also been reported for particular body sizes but not others (e.g. Rayor and Uetz 1993). Such size-dependent trade-offs, however, should have been detected here, as we have investigated the relationship between trap and structural threads both at the between- and within-individual levels (Ljungström *et al.*, 2016; Roff et Fairbairn, 2007). One avenue for future work is thus to test the effects alternative limiting resources (e.g. water, specific nutrients) on the trade-offs between body condition and silk production (Blamires *et al.*, 2017; Gonzaga *et al.*, 2006; Gregorič *et al.*, 2015; Mayntz *et al.*, 2009).

Individual variation in web structure

Although there was no evidence for a trade-off between the different types of threads, we found significant individual differences in web structure. Thus, the maintenance of variance in web structure does not appear to be a result of a trade-off between the different type of threads. Stable differences in the web structure may result from a trade-off between web structure or web building effort and life history or morphological traits (Stearns, 1992). Stable individual differences can also arise as a result of differences in past experience and developmental plasticity (Stamps et Groothuis, 2010). Since the spiders in our study were caught in the wild, differences in food abundance, prey type, or micro-habitat during development could lead to stable differences in web structure. Future experiments should investigate the effects of developmental conditions on web structure, beyond those of food abundance (Dirienzo et Montiglio, 2016a). The different components of the web could also be under contrasting selective pressures. For example, there may be directional selection under low food conditions to reduce the number of structural threads and increase the number of trap threads. In contrast, under high food conditions, there may be stabilizing selection on the number of structural threads and directional selection to reduce the number of trap threads. Such contrasting patterns of selection will result in multiple combinations of trap and structural threads which provide similar fitness outcomes. This could ultimately allow spiders with different types of webs to coexist and persist within a population (Stearns, 1989). One avenue for future works would thus be to examine the fitness consequences of different types of webs and the possible mechanisms maintaining individual differences in web structure.

Our results show that the abundance of food altered the magnitude of individual differences in web structure, as variation in web structure was greater with increasing food abundance. One explanation for this finding is that the mean and the variance in

the number of each type of threads may not be independent and spiders building more threads may also show more variance in thread number, although we could not detect such a difference. For example, the variance can be constrained by the mean, where a lower mean is mechanically associated with a narrower scope for variation around this mean (e.g. (Houle, 1992; Lande, 1977; Van Valen, 2005)), such as for zero bound count data or for Gaussian data where the standard deviation is proportional to the mean. This would be the case if the abundance of food had a positive effect of the production of silk *and* on the variance in thread number. This was, however, not the case in our study given that we found no difference in silk production between our ad libitum and restricted food treatments. Alternatively, greater food abundance may provide a more favourable environment which could facilitate the full expression of traits and trait differences across individuals. For example, Nicolaus et al. (2013) found that within-individual variance in clutch size were greater under low-density compared to high-density periods, which suggests that favourable (low-density) environments lead to greater variation in the expression of clutch size. One possible mechanism for a reduced magnitude of individual differences under less favourable environments is stronger stabilizing selection (and thus stronger canalising) on the trait under harsher conditions (Gibson et Wagner, 2000). Regardless of the specific mechanisms maintaining individual variation in web structure, our findings suggest that environmental variables, such as resource abundance, may often alter the magnitude of among-individual differences in a population.

Temporal variation in web structure

Variance in web structure decreased over time both at the between- and within-individual levels. When food was limited (i.e. in our intermediate and restricted food treatments), individual differences in the number of threads remained stable over the web building phase. During the initial phase of web building (i.e. the first 84 hours),

individual differences in web structure appeared to be higher for well-fed spiders. For all treatments, part of the high variation during the first hours could be the result of some spiders not starting to build a web right from the start. However, this would not explain the change in the magnitude of individual differences that we observed between treatments. This suggests that the web structure might be time-limited at first. Selection acts on the fitness of phenotypic traits. Similar trait values would thus have similar fitness and the more traits differ, the more room their fitness can differ. Thus, greater differences in the type and number of threads among individuals at the beginning of the web building phase could lead to larger differences in fitness. However, the presence of such differences could be the result of web structure during the first days of web building having little effect on fitness as long as it leads to an optimal structure of the final web. In other words, this would be the case if selection happens on the final web structure, and little on the intermediate steps of web building. The opposite could also be true where stronger contrasting selection maintains higher variance on the initial web structure. Such temporal changes in the short term provide an opportunity to study how selection pressures on the structure of the web, and more generally on developmental traits, change throughout the different stages of the trait expression.

Conclusion

Here we investigated the role of trade-offs in maintaining individual differences in web function and how they varied with access to food and throughout time. Although we found that the abundance of food affected female black widow spiders in their body condition, silk production and the structure, we found no evidence for a trade-off between the different types of threads used to build a web. Despite the absence of a trade-off, there were still significant differences in web structure across individual spiders. We suggest that trade-offs could be costly by factors outside of this study such as water expenditure or other functions, such as investment in reproduction or somatic

maintenance and survival. Our results also show that the magnitude of differences among individuals in web structure can change with variation in food abundance and over time. This finding highlights the importance of considering resource abundance and temporal changes when investigating individual variation. We suggest that constraints caused by both limited food resources and time might be important drivers of individual differences within a population.

2.6 References

Abrams, P.A. (1992) Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptation. *The American Naturalist*, 140, 573-600.

Argintean, S., Chen, J., Kim, M. & Moore, A.M.F. (2006) Resilient silk captures prey in black widow cobwebs. *Applied Physics A: Materials Science and Processing*, 82, 235-241.

Bates, D.M. (2010) *lme4: Mixed-effects modeling with R*. Springer New York.

Bell, A.M. (2012) Animal behaviour: Personality in the wild. *Nature*, 491, 341-342.

Bell, A.M., Hankison, S.J. & Laskowski, K.L. (2009) The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77, 771-783.

Bell, A.M. & Peeke, H.V. (2012) Individual variation in habituation: behaviour over time toward different stimuli in threespine sticklebacks (*Gasterosteus aculeatus*). *Behaviour*, 149, 1339.

Benjamin, S.P. & Zschokke, S. (2003) Webs of theridiid spiders: Construction, structure and evolution. *Biological Journal of the Linnean Society*, 78, 293-305.

Biro, P.A. & Stamps, J.A. (2008) Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, 23, 361-368.

Biro, P.A. & Stamps, J.A. (2015) Using repeatability to study physiological and behavioural traits: Ignore time-related change at your peril. *Animal Behaviour*, 105, 223-230.

Blackledge, T.A., Summers, A.P. & Hayashi, C.Y. (2005) Gumfooted lines in black widow cobwebs and the mechanical properties of spider capture silk. *Zoology*, 108, 41-46.

Blackledge, T.A. & Zevenbergen, J.M. (2007) Condition-dependent spider web architecture in the western black widow, *Latrodectus hesperus*. *Animal Behaviour*, 73, 855-864.

Blamires, S.J. (2010) Plasticity in extended phenotypes: Orb web architectural responses to variations in prey parameters. *Journal of Experimental Biology*, 213, 3207-3212.

Blamires, S.J., Hasemore, M., Martens, P.J. & Kasumovic, M.M. (2017) Diet-induced co-variation between architectural and physicochemical plasticity in an extended phenotype. *Journal of Experimental Biology*, 220, 876-884.

Blamires, S.J., Hochuli, D.F. & Thompson, M.B. (2009) Prey protein influences growth and decoration building in the orb web spider *Argiope keyserlingi*. *Ecological Entomology*, 34, 545-550.

Blamires, S.J., Sahni, V., Dhinojwala, A., Blackledge, T.A. & Tso, I.M. (2014) Nutrient deprivation induces property variations in spider gluey silk. *PLoS ONE*, 9.

Brandley, N., Johnson, M. & Johnsen, S. (2016) Aposematic signals in North American black widows are more conspicuous to predators than to prey. *Behavioral Ecology*, 27, 1104-1112.

Brommer, J.E. (2013) Phenotypic plasticity of labile traits in the wild. *Current Zoology*, 59, 485-505.

Bucher, R. & Entling, M.H. (2011) Contrasting effects of habitat fragmentation, population density, and prey availability on body condition of two orb - weaving spiders. *Ecological Entomology*, 36, 680-685.

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

Carroll, S.P., Hendry, A.P., Reznick, D.N. & Fox, C.W. (2007) Evolution on ecological time-scales. *Functional Ecology*, 21, 387-393.

Chacon, P. & Eberhard, W. (1980) Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey. *Bulletin-British Arachnological Society*.

Chamberlin, R.V. & Ivie, W. (1935) The black widow spider and its varieties in the United States.

Cole, E.F. & Quinn, J.L. (2012) Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1168-1175.

Cowlishaw, G. (1997) Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, 53, 667-686.

Craig, C.L. (2003) *Spiderwebs and silk: tracing evolution from molecules to genes to phenotypes*. Oxford University Press.

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

Dingemanse, N.J. & Dochtermann, N.A. (2013) Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, 82, 39-54.

Dingemanse, N.J. & Réale, D. (2005) Natural selection and animal personality. *Behaviour*, 142, 1159-1184.

Dirienzo, N. & Montiglio, P.O. (2016a) The contribution of developmental experience vs. condition to life history, trait variation and individual differences. *Journal of Animal Ecology*.

Dirienzo, N. & Montiglio, P.O. (2016b) Linking consistent individual differences in web structure and behavior in black widow spiders. *Behavioral Ecology*, 27, 1424-1431.

DiRienzo, N., Schraft, H.A., Montiglio, P.O., Bradley, C.T. & Dornhaus, A. (2020) Foraging behavior and extended phenotype independently affect foraging success in spiders. *Behavioral Ecology*, 31, 1242-1249.

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

Farwell, M. & McLaughlin, R.L. (2009) Alternative foraging tactics and risk taking in brook charr (*Salvelinus fontinalis*). *Behavioral Ecology*, 20, 913-921.

Garamszegi, L.Z., Markó, G., Szász, E., Zsebők, S., Azcárate, M., Herczeg, G. & Török, J. (2015) Among-year variation in the repeatability, within- and between-individual, and phenotypic correlations of behaviors in a natural population. *Behavioral Ecology and Sociobiology*, 69, 2005-2017.

Garant, D., Kruuk, L.E.B., Wilkin, T.A., McCleery, R.H. & Sheldon, B.C. (2005) Evolution driven by differential dispersal within a wild bird population. *Nature*, 433, 60-65.

Gibson, G. & Wagner, G. (2000) Canalization in evolutionary genetics: A stabilizing theory? *BioEssays*, 22, 372-380.

Gomes, A.C.R. & Cardoso, G.C. (2020) The lag-time constraint for behavioural plasticity. *Proceedings of the Royal Society B: Biological Sciences*, 287.

Gonzaga, M.O., Leiner, N.O. & Santos, A.J. (2006) On the sticky cobwebs of two theridiid spiders (Araneae: Theridiidae). *Journal of Natural History*, 40, 293-306.

Gregorič, M., Kuntner, M. & Blackledge, T.A. (2015) Does body size predict foraging effort? Patterns of material investment in spider orb webs. *Journal of Zoology*, 296, 67-78.

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

Harrison, X.A. (2015) A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. *PeerJ*, 3, e1114.

Herberstein, M., Craig, C. & Elgar, M. (2000) Foraging strategies and feeding regimes: web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Evolutionary Ecology Research*, 2, 41-67.

Herberstein, M. & Elgar, M. (1994) Foraging strategies of *Eriophora transmarina* and *Nephila plumipes* (Araneae: Araneoidea): Nocturnal and diurnal orb - weaving spiders. *Australian Journal of Ecology*, 19, 451-457.

Houle, D. (1992) Comparing evolvability and variability of quantitative traits. *Genetics*, 130, 195-204.

Irving, W.G. & Harold Hinman, E. (1935) The blue mud-dauber as a predator of the Black Widow Spider. *Science*, 82, 395-396.

Jin, H.-J. & Kaplan, D.L. (2003) Mechanism of silk processing in insects and spiders. *Nature*, 424, 1057-1061.

Kaston, B.J. (1970) Comparative biology of American black widow spiders. San Diego Soc Natur Hist Trans.

Kasumovic, M.M. & Andrade, M.C. (2004) Discrimination of airborne pheromones by mate-searching male western black widow spiders (*Latrodectus hesperus*): species- and population-specific responses. *Canadian Journal of Zoology*, 82, 1027-1034.

Körner, M., Vogelweith, F., Foitzik, S. & Meunier, J. (2017) Condition-Dependent Trade-Off Between Weapon Size and Immunity in Males of the European Earwig. *Scientific Reports*, 7.

Lande, R. (1977) On comparing coefficients of variation. *Systematic Zoology*, 26, 214-217.

Lessels, C. (1991) The evolution of life history strategies. *Behavioral ecology*, 3rd ed. Oxford: Blackwell Scientific.

Lima, S.L. (1998) Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, 48, 25-34.

Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, 68, 619-640.

Ljungström, G., Stjernstedt, M., Wapstra, E. & Olsson, M. (2016) Selection and constraints on offspring size - number trade - offs in sand lizards (*Lacerta agilis*). *Journal of Evolutionary Biology*, 29, 979-990.

MacLeod, E.C. & Andrade, M.C. (2014) Strong, convergent male mate choice along two preference axes in field populations of black widow spiders. *Animal Behaviour*, 89, 163-169.

Mayntz, D., Toft, S. & Vollrath, F. (2009) Nutrient balance affects foraging behaviour of a trap-building predator. *Biology Letters*, 5, 735-738.

McNamara, J.M. & Houston, A.I. (1987) Starvation and predation as factors limiting population size. *Ecology*, 68, 1515-1519.

Messina, F.J. & Fry, J. (2003) Environment - dependent reversal of a life history trade - off in the seed beetle *Callosobruchus maculatus*. *Journal of Evolutionary Biology*, 16, 501-509.

Miller, C.W., Joseph, P.N., Kilner, R.M. & Emberts, Z. (2019) A weapons-testes trade-off in males is amplified in female traits. *Proceedings. Biological sciences*, 286, 20190906-20190906.

Miller, C.W. & Svensson, E.I. (2014) Sexual Selection in Complex Environments. *Annual Review of Entomology*, 59, 427-445.

Moiron, M., Araya-Ajoy, Y.G., Mathot, K.J., Mouchet, A. & Dingemanse, N.J. (2019) Functional relations between body mass and risk-taking behavior in wild great tits. *Behavioral Ecology*, 30, 617-623.

Moiron, M., Laskowski, K.L. & Niemelä, P.T. (2020) Individual differences in behaviour explain variation in survival: a meta-analysis. *Ecology Letters*, 23, 399-408.

Montiglio, P.-O., Garant, D., Thomas, D. & Réale, D. (2010) Individual variation in temporal activity patterns in open-field tests. *Animal Behaviour*, 80, 905-912.

Montiglio, P.O., Garant, D., Pelletier, F. & Réale, D. (2015) Intra-individual variability in fecal cortisol metabolites varies with lifetime exploration and reproductive life history in eastern chipmunks (*Tamias striatus*). *Behavioral Ecology and Sociobiology*, 69, 1-11.

Montiglio, P.O., Wey, T.W., Chang, A.T., Fogarty, S. & Sih, A. (2016) Multiple mating reveals complex patterns of assortative mating by personality and body size. *Journal of Animal Ecology*, 85, 125-135.

Moyes, K., Coulson, T., Morgan, B.J., Donald, A., Morris, S.J. & Clutton - Brock, T.H. (2006) Cumulative reproduction and survival costs in female red deer. *Oikos*, 115, 241-252.

Moyes, K., Morgan, B.J., Morris, A., Morris, S.J., Clutton-Brock, T.H. & Coulson, T. (2009) Exploring individual quality in a wild population of red deer. *Journal of Animal Ecology*, 406-413.

Nakata, K. (2009) To be or not to be conspicuous: the effects of prey availability and predator risk on spider's web decoration building. *Animal Behaviour*, 78, 1255-1260.

Nicolaus, M., Brommer, J.E., Ubels, R., Tinbergen, J.M. & Dingemanse, N.J. (2013) Exploring patterns of variation in clutch size-density reaction norms in a wild passerine bird. *Journal of Evolutionary Biology*, 26, 2031-2043.

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

Patrick, S.C., Pinaud, D. & Weimerskirch, H. (2017) Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. *Journal of Animal Ecology*, 86, 1257-1268.

Pinheiro, J.C. & Bates, D.M. (2000a) Extending the basic linear mixed-effects model. *Mixed-effects models in S and S-PLUS*, 201-270.

Pinheiro, J.C. & Bates, D.M. (2000b) Linear mixed-effects models: basic concepts and examples. *Mixed-effects models in S and S-Plus*, 3-56.

Prestwich, K. (1977) The energetics of web-building in spiders. *Comparative Biochemistry and Physiology--Part A: Physiology*, 57, 321-326.

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rau, P. (1935) The wasp, *Chalybion cyaneum* Fab., preys upon the black widow spider, *Latrodectus mactans* Fab. (Hymen., Araneae). *Entomological News*, 46, 259-260.

Réale, D., Dingemanse, N.J., Kazem, A.J.N. & Wright, J. (2010a) Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 3937-3946.

Réale, D. & Festa-Bianchet, M. (2003) Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, 65, 463-470.

Réale, D., Garant, D., Humphries, M.M., Bergeron, P., Careau, V. & Montiglio, P.-O. (2010b) 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, 4051-4063.

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

Roff, D.A. & Fairbairn, D.J. (2007) The evolution of trade-offs: where are we? *Journal of Evolutionary Biology*, 20, 433-447.

Royauté, R. & Dochtermann, N.A. (2016) When the mean no longer matters: developmental diet affects behavioral variation but not population averages in the house cricket (*Acheta domesticus*). *Behavioral Ecology*, 28, 337-345.

Salzman, T.C., McLaughlin, A.L., Westneat, D.F. & Crowley, P.H. (2018) Energetic trade-offs and feedbacks between behavior and metabolism influence correlations between pace-of-life attributes. *Behavioral Ecology and Sociobiology*, 72.

Sandoval, C. (1994) Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. *Functional Ecology*, 701-707.

Santostefano, F., Wilson, A.J., Niemelä, P.T. & Dingemanse, N.J. (2017) Behavioural mediators of genetic life-history trade-offs: A test of the pace-of-life syndrome hypothesis in field crickets. *Proceedings of the Royal Society B: Biological Sciences*, 284.

Schmitz, O.J. (2007) Predator diversity and trophic interactions. *Ecology*, 88, 2415-2426.

Schraft, H., Jaham, M.D., Toupin, L.P. & Montiglio, P.O. (2021) North American widow spiders (Araneae: Theridiidae). *Arachnology*, 18, 783-802.

Sherman, P.M. (1994) The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. *Animal Behaviour*, 48, 19-34.

Sih, A. (1980) Optimal behavior: can foragers balance two conflicting demands? *Science*, 210, 1041-1043.

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

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

Stamps, J.A. (2007) Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters*, 10, 355-363.

Stearns, S.C. (1989) Trade-offs in life-history evolution. *Functional ecology*, 3, 259-268.

Stearns, S.C. (1992) *The evolution of life histories*.

Steinhoff, P.O.M., Warfen, B., Voigt, S., Uhl, G. & Dammhahn, M. (2020) Individual differences in risk-taking affect foraging across different landscapes of fear. *Oikos*, 129, 1891-1902.

Tanaka, K. (1989) Energetic cost of web construction and its effect on web relocation in the web-building spider *Agelena limbata*. *Oecologia*, 81, 459-464.

Van de Pol, M. & Wright, J. (2009) A simple method for distinguishing within-versus between-subject effects using mixed models. *Animal Behaviour*, 77, 753.

Van Noordwijk, A.J. & de Jong, G. (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. *The American Naturalist*, 128, 137-142.

Van Valen, L. (2005) The statistics of variation. *Variation*, 29-47.

Varpe, Ø. (2017) Life History Adaptations to Seasonality. *Integrative and Comparative Biology*, 57, 943-960.

Verdolin, J.L. (2006) Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology*, 60, 457-464.

Vetter, R.S. (1980) Defensive behavior of the black widow spider *Latrodectus hesperus* (Araneae: Theridiidae). *Behavioral Ecology and Sociobiology*, 7, 187-193.

Vetter, R.S., Vincent, L.S., Itnyre, A.A., Clarke, D.E., Reinker, K.I., Danielsen, D.W.R., Robinson, L.J., Kabashima, J.N. & Rust, M.K. (2012) Predators and parasitoids of egg sacs of the widow spiders, *Latrodectus geometricus* and *Latrodectus hesperus* (Araneae: Theridiidae) in southern California. *The Journal of Arachnology*, 40, 209-214, 206.

Vollrath, F. & Edmonds, D.T. (1989) Modulation of the mechanical properties of spider silk by coating with water. *Nature*, 340, 305-307.

Vollrath, F., Madsen, B. & Shao, Z. (2001) The effect of spinning conditions on the mechanics of a spider's dragline silk. *Proceedings of the Royal Society B: Biological Sciences*, 268, 2339-2346.

Vollrath, F. & Porter, D. (2006) Spider silk as archetypal protein elastomer. *Soft Matter*, 2, 377-385.

Wikenros, C., Ståhlberg, S. & Sand, H. (2014) Feeding under high risk of intraguild predation: Vigilance patterns of two medium-sized generalist predators. *Journal of Mammalogy*, 95, 862-870.

Zevenbergen, J.M., Schneider, N.K. & Blackledge, T.A. (2008) Fine dining or fortress? Functional shifts in spider web architecture by the western black widow *Latrodectus hesperus*. *Animal Behaviour*, 76, 823-829.

CHAPITRE III

CONCLUSION

Les objectifs de ce mémoire étaient d'évaluer comment la relation entre deux fonctions exprimées dans le phénotype étendu de veuves noires de l'ouest varie avec la limitation des ressources et dans le temps. Plus précisément, nos objectifs étaient (1) d'évaluer la relation entre les fils de capture et les fils structurels dans les toiles et s'il y a présence de compromis; (2) d'évaluer comme la disponibilité de ressources était associée aux différences individuelles dans la structure des toiles; et (3) de décrire comment les différences individuelles dans la structure des toiles ont varié avec le temps. À cet effet, nous avons manipulé l'abondance de nourriture accessible à des femelles adultes avant de mesurer la structure de leurs toiles au cours du temps. Nous avons également analysé le patron d'investissement fait par les individus dans deux fonctions différentes de la toile. Cette section détaille les implications générales de nos résultats et discute des limites de notre étude.

3.1 Absence de compromis

Une augmentation du nombre de fils de capture dans la toile des veuves noires était associée à une augmentation du nombre de fils structurels. Comme dans la littérature, le nombre de fils de capture a augmenté lorsque les araignées étaient limitées en ressources (Blackledge *et al.*, 2005b; Blackledge et Zevenbergen, 2007; Zevenbergen *et al.*, 2008). Malgré que les ressources étaient restreintes, la relation était principalement positive. La présence d'un compromis basé sur l'allocation de ressources énergétiques restreintes est peu probable dans les toiles de veuves noires de l'ouest. Cette absence de compromis entre des éléments de la toile remplissant différentes fonctions est soutenue par les résultats d'une étude publiée cette année (Thompson *et al.*, 2020). Les différences de structures de toiles chez les veuves noires de l'ouest ne sont donc pas maintenues par la présence de compromis entre les différents types de fils. Cependant, d'autres mécanismes peuvent maintenir la variance phénotypique comme la présence de stratégies alternatives, des compromis dans les aptitudes résultantes ou des différences ontogéniques méritent d'être explorés. Les bénéfices à l'aptitude de construire une toile favorisant la capture de proies ou la défense contre les prédateurs pourrait correspondre à différentes stratégies. Cela surviendrait si les aptitudes résultantes sont similaires (Stearns, 1989; Wolf *et al.*, 2007). Il est aussi possible que les individus changent leur stratégie en réponse à leur état et aux bénéfices associés (Biro et Stamps, 2008; Desmarais et Tessier, 1999; Ludwig et Rowe, 1990; Stearns, 1992; Wolf *et al.*, 2007; Yasué *et al.*, 2003). Ce changement de stratégie est supporté par l'observation de changement de structure de toile avec les ressources (Blackledge et Zevenbergen, 2007; Dirienzo et Montiglio, 2016a; Zevenbergen *et al.*, 2008) et l'observation d'une augmentation de la défense lorsque les individus pondent par DiRienzo et Aonuma (2018).

L'absence de compromis physiologique soulève également des questions à savoir si les toiles de veuves noires sont réellement coûteuses en énergie comme chez d'autres espèces araignées (Benjamin et Zschokke, 2003; Gregorič *et al.*, 2015; Harmer *et al.*, 2012; Lichtenstein *et al.*, 2016; Prestwich, 1977; Tanaka, 1989). Le coût énergétique de construire une toile chez les araignées est plus important chez les araignées qui tissent une nouvelle toile quotidiennement (Prestwich, 1977). Chez les theridiidae, comme l'indique la relation entre les fils collants et la perte de poids, les coûts les plus importants seraient associés à l'allocation de nutriments limités et d'eau afin de produire et entretenir les fils collants dans des milieux secs (Benjamin et Zschokke, 2003; Blackledge *et al.*, 2005a; Gonzaga *et al.*, 2006; Gregorič *et al.*, 2015). Ainsi, il est possible que le coût ne se produise pas au niveau des réserves énergétiques de l'individu, mais de l'eau, expliquant que nous n'ayons pas détecté de différence dans le coût des toiles.

3.2 Effet de l'abondance des ressources sur les différences individuelles

Des différences d'abondance de ressources dans l'environnement ou de condition entre les individus affectent le comportement des individus (Alonzo, 2015; Auer *et al.*, 2020; Badyaev, 2005; Mayntz *et al.*, 2009; Moiron *et al.*, 2019; Sgrò et Hoffmann, 2004; Sinervo et Svensson, 1998; Sirot et Bernstein, 1996; Tatar et Carey, 1995). Similairement, les différences individuelles peuvent être amplifiées ou diminuées d'un environnement à un autre par plasticité (Alonzo, 2015; Badyaev, 2005; Dingemanse *et al.*, 2010; Dingemanse et Wolf, 2013; Royauté *et al.*, 2019; Royauté *et al.*, 2018; Via et Lande, 1985; Westneat *et al.*, 2011). Dans notre étude nous avons observé des changements au cours du temps de différences individuelles entre les ressources

disponibles. Les ressources disponibles n'ont cependant pas changé la relation entre les deux types de fils retrouvés dans les toiles des veuves noires. Comme pour des études précédentes, les individus montraient des différences constantes de structure de toile, peu importe l'abondance des ressources (DiRienzo et Aonuma, 2018; DiRienzo et Montiglio, 2016a, 2016b; Thompson *et al.*, 2020), et malgré les changements plastiques générés par les traitements. Ainsi, les individus présentent des différences individuelles constantes en plus d'exprimer différents niveaux de plasticité de la structure de la toile en réponse à l'abondance de nourriture (Dingemanse *et al.*, 2010). Cela se traduit par les mêmes individus exprimant plus ou moins de différences en fonction des ressources disponibles. Il serait donc possible que la plasticité chez les veuves noires dépende de l'état (e.g. énergie, perception de l'environnement) des individus. Ce type d'interaction entre état et niveau de plasticité a déjà été observé dans d'autres études (Alonzo, 2015; Blamires *et al.*, 2017; Dingemanse et Wolf, 2013; Neumann et Schneider, 2016; Royauté *et al.*, 2019).

Cependant, il est difficile de quantifier la variance générée par les différences d'abondance de ressources sur la relation des traits compromis (Desmarais et Tessier, 1999; Körner *et al.*, 2017; Messina et Fry, 2003; Miller *et al.*, 2019; Tatar et Carey, 1995). Dans notre étude, les veuves noires de l'Ouest montrent des différences individuelles et de plasticité entre niveaux de ressources indépendamment de la relation entre deux fonctions bénéfiques. Cela concorde avec d'autres systèmes, comme pour les coléoptères femelles (*Dendroctonus ponderosae*), chez lesquels les ressources énergétiques n'affectent pas les décisions d'allocation prise par les individus (Elkin et Reid, 2005). Cependant, ce genre d'observation diffère du modèle de rétroaction entre état et compromis retrouvé plus généralement dans la littérature (Laskowski *et al.*, 2021; Ludwig et Rowe, 1990; Messina et Fry, 2003; Ngo *et al.*, 2021; Salzman *et al.*, 2018; Van Noordwijk et de Jong, 1986).

3.3 Effet du temps sur les différences individuelles

Notre étude montre que les différences individuelles dans la structure de la toile ont changé au cours du temps alloué au tissage des toiles des veuves noires. Cette relation a également différé avec les ressources disponibles aux individus. La plupart des études mesurant les différences individuelles utilisent la répétabilité. La répétabilité est utilisée pour estimer la constance des différences individuelles au cours du temps ou les entre contextes. Cependant, des questions ont été soulevées sur la constance de la répétabilité à travers le temps (Biro et Stamps, 2015; Hayes et Jenkins, 1997; McGraw et Wong, 1996). On sait que l'expression des traits peut changer à travers le temps (e.g. changement de saisons) (Bell et Peeke, 2012; Dhellemmes *et al.*, 2020; Ludwig et Rowe, 1990). Les différences individuelles peuvent également changer sur le plus court terme, comme chez les cerfs élaphe (*Cervus elaphus*) où le temps de la journée joue un rôle important dans la sélection d'habitats et la négociation de compromis (Godvik *et al.*, 2009). Il est possible que la plasticité possible à différents moments de tissage et de ressources ait été sujet à différentes contraintes. Des ressources limitées peut par exemple restreindre la plasticité phénotypique comme les mécanismes proximaux sont restreinte dans leur action par le manque d'énergie (Alonzo, 2015; Moyes *et al.*, 2009). La plasticité peut être plus ou moins canalisé en fonction de plusieurs facteurs comme la sélection, l'environnement ainsi que les contraintes sur les corrélation génétiques entre les traits (Badyaev, 2005; Dingemanse et Wolf, 2013; Gebhardt et Stearns, 1993; Hau et Goymann, 2015; Nylin et Gotthard, 1998; Royauté *et al.*, 2019; Sinervo et Svensson, 1998; Stearns *et al.*, 1991). Notre étude suggère également que le temps est un élément important lorsqu'on interprète la répétabilité d'un comportement, comme les différences individuelles ont changé avec le temps accordé sur une période restreinte dans notre étude (Biro et Stamps, 2015). Particulièrement pour les

phénotypes étendus comme nous savons peu sur l'effet du temps accordé sur ces derniers.

Dans notre étude, l'interaction entre le temps accordé au tissage de toiles et les ressources disponibles a modulé les différences de structure de toile entre les individus (i.e. différences de plasticité). Nous ne connaissons pas complètement les processus générant des différences de plasticité chez les individus ni le rôle de ces différences sur les processus évolutifs (Alonzo, 2015; Dingemanse et Wolf, 2013; DiSciullo et Basolo, 2020; Fanson *et al.*, 2021; Thompson *et al.*, 2020; Thys *et al.*, 2021; Urbánková *et al.*, 2020). Comme dans notre étude, les ressources disponibles ou l'état des individus peuvent être une source de variation à travers la plasticité (DiSciullo et Basolo, 2020; Fanson *et al.*, 2021). Cependant, notre étude démontre une relation entre l'effet des ressources sur la plasticité conjointement avec le temps qui est rarement étudié. Ce type de relation pourrait être également présent à de plus grandes échelles de temps ou de contextes.

3.4 Limites de l'étude

Notre prise de mesure des toiles s'effectuait en comptant le nombre de fils touchant au sol sous les toiles. Cette méthode ne prend pas en compte toute la partie aérienne de la toile. Cela limite notre estimation de l'investissement dans la défense contre les prédateurs des araignées. Une des structures les plus défensives de leur toile est le refuge qui prend la forme d'un tunnel de soie, qui peut varier beaucoup en densité et pourrait représenter une grande part de l'investissement en soie dans les toiles. Estimer la densité des parties aériennes de toiles auraient cependant demandé d'utiliser des méthodes en dehors des capacités de cette étude, comme mesurer la densité de fils à l'aide de photographie et du programme imagej (Blackledge et Zevenbergen, 2007;

Schneider *et al.*, 2012) ou d'effectuer des tests de résistance au déchirement du refuge (Koski *et al.*, 2013) ou une dissection des parties de la toile pour la pesée.

Comme pour les différences d'état mesurées dans notre étude, il est probable que les différences individuelles observées reflètent des différences dans les traits intégrés avec la structure de la toile que nous n'avons pas mesurés (Mathot et Frankenhuis, 2018). Par exemple, nous savons que le comportement et la morphologie des araignées peuvent covarier avec la structure de la toile (Dirienzo et Montiglio, 2016a, 2016b).

Il est possible les ressources énergétiques n'étaient pas assez limitées pour pouvoir observer le compromis physiologique (Körner *et al.*, 2017; Messina et Fry, 2003). Si notre expérience avait créé plus de restrictions de condition entre les individus, il aurait été possible d'observer la présence d'un compromis physiologique présent seulement lorsque les ressources sont limitées. Restreindre la masse des individus à un niveau similaire aux individus dans d'autres études aurait été désirable (Blackledge et Zevenbergen, 2007; Dirienzo et Montiglio, 2016a; Zevenbergen *et al.*, 2008).

Bien que les phénotypes étendus offrent une opportunité de mesurer le comportement des individus en leur absence et d'éviter d'induire des biais dus à l'habitation, nos mesures répétées dans le temps ne nous ont pas permis de mesurer les toiles en l'absence des individus. Effectivement, en effectuant des mesures à tous les 12h, il est possible que les individus aient été stressés par la prise de mesure. Cependant, l'effet de mesurer les toiles visuellement sur le comportement de tissage de toile des individus reste peu compris. De plus, si un stress a été engendré il devrait être équivalent pour l'ensemble des individus dans notre étude et ne pas générer des différences que notre étude ne prend pas en compte. Les mesures étaient également limitées à sept jours. Il est probable que les tendances observées dans le temps différent au-delà des sept jours et donc que notre étude n'ait pas été en mesure de les observer.

Un des objectifs de cette étude était d'évaluer la présence de compromis ou d'une relation directe entre les types de fils dans les toiles des veuves noires. Cette relation était absente dans cette étude, et potentiellement chez les veuves noires de l'ouest, ce qui a empêché d'évaluer l'impact des ressources et du temps sur un compromis physiologique, un autre objectif de l'étude.

3.5 Directions futures

Maintenant que l'on sait que les différences individuelles et la plasticité ont été modulées par les ressources disponibles et le temps, il est d'autant plus d'intérêt d'étudier l'impact de ces facteurs sur les compromis. Comme un compromis physiologique n'était pas présent dans notre étude, il serait intéressant le mesurer dans un système où il y a présence d'un compromis entre des traits. Cependant, les changements de plasticité et de différences individuelles ne sont pas toujours associés à un changement de relation entre les traits (Elkin et Reid, 2005). Il serait intéressant de déterminer dans quels contexte les ressources énergétiques affectent ou non l'allocation entre les traits.

Notre étude montre que le temps sur une période restreinte affecte les différences individuelles et l'amplitude de la plasticité engendrée par une variation de contexte (i.e. ressources disponibles). Tout comme les études sur l'expérience ontogénique, une étude reliant l'interaction entre le temps à grande échelle (e.g. saisons, années) et les ressources ou autres contextes nous permettrait de mieux comprendre leur incidence sur les différences individuelles et la variation de plasticité.

Effectuer une étude afin d'analyser l'effet des ressources et du temps sur une période plus longue nous permettrait de mieux comprendre l'effet de ces derniers sur une période plus représentative de la durée d'utilisation par les araignées de leur toile. Nos observations offrent l'opportunité d'étudier comment elles pourraient dépendre de mécanismes générant des différences individuelles et de plasticité. Une étude subséquente de terrain mesurant la sélection sur les individus pourrait nous permettre de déterminer si les changements plastiques apportés par les individus à leurs toiles sont adaptatifs. Effectivement, s'il y a sélection directionnelle forte dans un contexte, il est probable que seuls les individus exprimant une faible variance autour du phénotype bénéfique soient favorisés.

Il est probable que la fonction de défense de la toile mesurée dans notre étude varie avec le statut reproducteur des veuves noires et que l'investissement dans cette fonction se produit principalement dans le refuge de la toile. Notre étude utilisait seulement des femelles vierges afin de contrôler pour l'effet de l'état reproducteur. Cependant, mesurer cette variable conjointement avec l'effort d'approvisionnement comme mesuré ici permettrait d'évaluer la négociation de compromis entre les reproductions actuelles et futures des veuves. Ce type d'étude offrirait des opportunités d'observer un compromis entre traits d'histoire de vie en relation avec des différences d'état et la variation entre les individus et leur plasticité.

ANNEXE A

INFORMATIONS SUPPLÉMENTAIRES AU CHAPITRE II

Relative weight loss index:

$$\frac{(\textit{Weight before web building} - \textit{Weight after web building}) * 100}{\textit{Average weight}}$$

Table S.1 Final linear model of the determinants of spider weight after weight building ($n = 83$ webs from $N = 43$ individuals) $F_{9, 73} = 536.5$, p-value: $< 2.2e-16$

Fixed effects	Coefficient	SE	t value	P
(Intercept)	4.005	4.822	0.830	0.409
Intermediate treatment	-1.884	3.900	-0.483	0.631
Restricted treatment	2.033	3.900	0.521	0.604
Web mass	2.101	1.671	1.257	0.213
Spider weight before web building	0.881	0.017	52.639	<.0001
Number of trap threads	-0.186	0.090	0.042	0.042
Number of structural threads	-0.113	0.126	0.374	0.374
Trial order B	-3.006	3.812	0.433	0.433
Trial order C	-7.974	3.764	0.038	0.038
Trial 2	0.068	2.768	0.981	0.981
AIC	1101.8			
R2	0.985			
Adjusted R2	0.983			

Significant P values are shown in bold.

Table S.2 Final linear model of the determinants of relative spider weight loss during weight building ($n = 83$ webs from $N = 43$ individuals). $F_{9,73} = 2.939$, p-value: 0.004961

Fixed effects	Coefficient	SE	t value	P
(Intercept)	8.160	1.535	5.317	<.0001
Intermediate treatment	-0.293	1.241	-0.236	0.814
Restricted treatment	-1.533	1.241	-1.235	0.221
Web mass	-0.871	0.532	-1.637	0.106
Spider weight before web building	0.021	0.005	3.914	0.0002
Number of trap threads	0.069	0.029	2.399	0.019
Number of structural threads	0.035	0.040	0.873	0.386
Trial order B	0.691	1.213	0.570	0.571
Trial order C	2.056	1.198	1.717	0.090
Trial 2	-0.190	0.881	-0.216	0.830
AIC	469.83			
R^2	0.266			
Adjusted R^2	0.175			

Significant P values are shown in bold. Orders are the order under which the spiders underwent food treatments (A : Ad libitum, intermediate then restricted; B : Intermediate, restricted then ad libitum and C : Restricted, ad libitum then intermediate)

Table S.3 Final linear mixed model of the determinants of web mass ($n = 83$ webs from $N = 43$ individuals). $F_{9,73} = 2.939$, p-value: 0.004961

Random effects	Variance	χ^2	df	r	P
Individual	1.103	15.497	1	60.14%	<.0001
Residual	0.731				

Fixed effects	Coefficient	SE	t value	95% CI
(Intercept)	2.215	0.434	5.110	1.390, 3.041
Intermediate treatment	-0.630	0.271	-2.322	-1.161, -0.097
Restricted treatment	-0.510	0.270	-1.886	-1.049, 0.012
Trial order B	0.340	0.470	0.724	-0.557, 1.232
Trial order C	0.526	0.473	1.111	-0.376, 1.427
Trial 2	0.266	0.373	0.714	-0.445, 0.977
AIC	261.68			
Marginal R^2	0.640			
Conditional R^2	0.096			

Significant P values are shown in bold. Orders are the order under which the spiders underwent food treatments (A : Ad libitum, intermediate then restricted; B : Intermediate, restricted then ad libitum and C : Restricted, ad libitum then intermediate)

Table S.4 Final generalized poisson linear mixed model of the determinants of the number of trap threads ($n = 135$ webs from $N = 45$ individuals). Deviance = 1013.2

Random effects	Variance	χ^2	df	r	P
Individual	1.740	27.213	1	22.8%	<.0001
OLRE	1.328	470.41	1		<.0001

Fixed effects	Coefficient	SE	z value	95% CI	P
(Intercept)	1.113	0.445	2.499	0.174:1.991	0.013
Intermediate treatment	0.122	0.271	0.450	-0.424:0.677	0.653
Restricted treatment	0.423	0.268	1.580	-0.118:0.970	0.114
Trial order B	0.188	0.545	0.345	-0.951:1.270	0.730
Trial order C	0.399	0.546	0.731	-0.681:1.542	0.465
Trial 2	0.687	0.454	1.513	-0.222:1.632	0.130
AIC	1029.2				

Marginal R2 0.054

Conditional R2 0.565

Significant P values are shown in bold. Orders are the order under which the spiders underwent food treatments (A : Ad libitum, intermediate then restricted; B : Intermediate, restricted then ad libitum and C : Restricted, ad libitum then intermediate)

Table S.5 Final generalized poisson linear mixed effect model of the determinants of the number of structural threads ($n = 135$ webs from $N = 45$ individuals). Deviance = 1089.7

Random effects	Variance	χ^2	df	r	P
Individual	0.400	13.283	1	25.8%	=0.0002
OLRE	0.650	381.18	1		<.0001

Fixed effects	Coefficient	SE	z value	95% CI	P
(Intercept)	2.489	0.242	10.306	2.000:2.967	<.0001
Intermediate treatment	-0.279	0.184	-1.514	-0.649:0.087	0.130
Restricted treatment	-0.285	0.182	-1.567	-0.649:0.078	0.117
Trial order B	0.177	0.291	0.608	-0.423:0.751	0.543

Trial order C	0.333	0.292	1.141	-0.247:0.931	0.254
Trial 2	0.194	0.242	0.803	-0.290:0.686	0.422
AIC	1105.7				
Marginal R2	0.041				
Conditional R2	0.382				

Significant P values are shown in bold. Orders are the order under which the spiders underwent food treatments (A : Ad libitum, intermediate then restricted; B : Intermediate, restricted then ad libitum and C : Restricted, ad libitum then intermediate)

Table S.6 Final generalized poisson linear mixed effect model of the determinants of the number of threads ($n = 135$ webs from $N = 45$ individuals). Deviance = 1260.3

Random effects	Variance	χ^2	df	r	P
Individual	0.602	26.097	1	37.4%	<.0001
OLRE	0.555	460.36	1		<.0001

Fixed effects	Coefficient	SE	z value	95% CI	P
(Intercept)	3.020	0.261	11.571	2.493:3.540	<.0001
Intermediate treatment	-0.265	0.168	-1.583	-0.604:0.066	0.114
Restricted treatment	-0.012	0.164	-0.076	-0.342:0.315	0.940
Trial order B	0.113	0.325	0.348	-0.566:0.748	0.728
Trial order C	0.273	0.326	0.837	-0.368:0.946	0.403

Trial 2	0.311	0.270	1.155	-0.229:0.859	0.248
AIC	1276.3				
Marginal R2	0.043				
Conditional R2	0.524				

Significant P values are shown in bold. Orders are the order under which the spiders underwent food treatments (A : Ad libitum, intermediate then restricted; B : Intermediate, restricted then ad libitum and C : Restricted, ad libitum then intermediate)

Table S.7 Final generalized binomial linear mixed effect model of the determinants of the proportion of trap threads ($n = 135$ webs from $N = 45$ individuals). Deviance = 828.61

Random effects	Variance	χ^2	df	r	P
Individual	1.548	18.253	1	16.6%	<.0001
OLRE	1.653	401.53	1		<.0001

Fixed effects	Coefficient	SE	z value	95% CI	P
(Intercept)	-1.351	0.453	-2.985	-2.142:-0.549	0.003
Intermediate treatment	0.397	0.319	1.246	-0.234:1.089	0.213
Restricted treatment	0.731	0.312	2.339	0.115:1.376	0.019
Trial order B	0.125	0.551	0.228	-1.032:1.184	0.820
Trial order C	-0.096	0.556	-0.173	-1.333:0.982	0.863

Trial 2	0.507	0.461	1.100	-0.407:1.376	0.271
AIC	844.6				
Marginal R2	0.045				
Conditional R2	0.071				

Significant P values are shown in bold. Orders are the order under which the spiders underwent food treatments (A : Ad libitum, intermediate then restricted; B : Intermediate, restricted then ad libitum and C : Restricted, ad libitum then intermediate)

Table S.8 Final model of the determinants of the number of threads over time (log transformed; $N = 1890$)

Variance component	Variance	LRT	Df		<i>P</i>
Individual	1.496	4409.583	1		<.0001
Food Treatment (nested in ID)	0.857	3035.087	1		<.0001
Residual	0.209				

Variance covariates	Coefficient	LRT	Df		<i>P</i>
Time linear (ad libitum)	-0.628	391.480	3		<.0001
Time linear (intermediate)	-0.590				
Time linear (restricted)	-0.160				
Time quadratic (ad libitum)	0.265	232.689	3		<.0001
Time quadratic (intermediate)	0.321				
Time quadratic (restricted)	0.441				

Fixed effects	Coefficient	SE	<i>t</i>	95% CI	Df (residual Df)
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Intercept	2.626	0.439	5.979	1.765:3.487	1(1752)
Food treatment	-0.326	0.183	-1.785	-0.689:0.037	1(87)
(intermediate) ^a					
Food treatment (Restricted) ^a	-0.082	0.181	-0.452	-0.442:0.278	1(87)
Time linear (scaled)	0.357	0.010	35.043	0.337:0.377	1(1752)
Time quadratic (scaled)	-0.072	0.009	-8.364	-0.089:-0.055	1(1752)
Order (B) ^b	-1.262	0.484	-2.609	-2.211:-0.313	1(1752)
Order (C) ^b	1.774	0.484	3.664	0.824:2.723	1(1752)
Block (2) ^c	0.270	0.471	0.572	-0.681:1.221	1(43)
AIC	1592.71				

Significant P values are shown in bold. Order identifies the order in which the spiders underwent the three food treatments (A: Ad libitum, intermediate then restricted; B: Intermediate, restricted then ad libitum and C: Restricted, ad libitum then intermediate).

^aAd libitum taken as reference. ^bOrder A taken as reference. ^cBlock 1 taken as reference.

Table S.9 Linear mixed effect model of the determinants of trap threads by between and within individual variance in number of structural threads (log transformed; $N = 135$)

Random effects	Variance	df
Individual	0.794	2(45)
Structural thread deviance (nested in ID)	0.339	
Web number	0.083	1(3)
Residuals	0.740	

Fixed effects	Coefficient	SE	t value
(Intercept)	-1.296	0.940	-1.379
Mean number of structural threads	2.628	0.800	3.283
Deviance of the number of structural threads to the mean	0.181	0.168	1.080
Mean number of structural threads (Squared)	-0.463	0.168	-2.749

Table S.10 Linear models of the determinants of residual variability (log transformed; $N = 135$; Residual extracted from Model of Table 2)

Fixed effects	Total Variability				Between Individual variability				Within individual variability		
	Coefficient	SE	t value	<i>P</i>	Coefficient	SE	t value	<i>P</i>	Coefficient	SE	t value
(Intercept)	-1.406	0.081	-17.393	<.0001	-0.920	0.064	-14.460	<.0001	-1.898	0.071	-26.895
Time (scaled)	-0.417	0.054	-7.772	<.0001	-0.388	0.042	-9.188	<.0001	-0.336	0.047	-7.163

Time quadratic (scaled)	0.162	0.060	2.682	0.021	0.139	0.048	2.920	0.014	0.108	0.053	2.046
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BIBLIOGRAPHIE

. (!!! INVALID CITATION !!! (Elkin et Reid, 2005; Laskowski et al., 2021; Van Noordwijk et de Jong, 1986; Zajitschek et Connallon, 2017)).

Abrams, P. A. (1992). Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptation. *The American Naturalist*, 140(4), 573-600.

Agnarsson, I. (2004). Morphological phylogeny of cobweb spiders and their relatives (Araneae, Araneoidea, Theridiidae). *Zoological Journal of the Linnean Society*, 141(4), 447-626.

Alonzo, S. H. (2015). Integrating the how and why of within-individual and among-individual variation and plasticity in behavior. *Current opinion in behavioral sciences*, 6, 69-75.

Angilletta Jr, M. J., Wilson, R. S., Navas, C. A. et James, R. S. (2003). Tradeoffs and the evolution of thermal reaction norms. *Trends in Ecology and Evolution*, 18(5), 234-240.

- Argintean, S., Chen, J., Kim, M. et Moore, A. M. F. (2006). Resilient silk captures prey in black widow cobwebs. *Applied Physics A: Materials Science and Processing*, 82(2), 235-241.
- Auer, S. K., Solowey, J. R., Rajesh, S. et Rezende, E. L. (2020). Energetic mechanisms for coping with changes in resource availability. *Biology Letters*, 16(11).
- Badyaev, A. V. (2005). Stress-induced variation in evolution: From behavioural plasticity to genetic assimilation. *Proceedings of the Royal Society B: Biological Sciences*, 272(1566), 877-886.
- Bates, D. M. (2010). *lme4: Mixed-effects modeling with R* : Springer New York.
- Beckerman, A. P., Uriarte, M. et Schmitz, O. J. (1997). Experimental evidence for a behavior-mediated trophic cascade in a terrestrial food chain. *Proceedings of the National Academy of Sciences of the United States of America*, 94(20), 10735-10738.
- Bell, A. M. (2012). Animal behaviour: Personality in the wild. *Nature*, 491(7424), 341-342.
- Bell, A. M., Hankison, S. J. et Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, 77(4), 771-783.
- Bell, A. M. et Peeke, H. V. (2012). Individual variation in habituation: behaviour over time toward different stimuli in threespine sticklebacks (*Gasterosteus aculeatus*). *Behaviour*, 149(13-14), 1339.

- Benjamin, S. P. et Zschokke, S. (2003). Webs of theridiid spiders: Construction, structure and evolution. *Biological Journal of the Linnean Society*, 78(3), 293-305.
- Biro, P. A. et Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, 23(7), 361-368.
- Biro, P. A. et Stamps, J. A. (2015). Using repeatability to study physiological and behavioural traits: Ignore time-related change at your peril. *Animal Behaviour*, 105, 223-230.
- Blackledge, T. A., Summers, A. P. et Hayashi, C. Y. (2005a). Gumfooted lines in black widow cobwebs and the mechanical properties of spider capture silk. *Zoology*, 108(1), 41-46.
- Blackledge, T. A., Swindeman, J. E. et Hayashi, C. Y. (2005b). Quasistatic and continuous dynamic characterization of the mechanical properties of silk from the cobweb of the black widow spider *Latrodectus hesperus*. *Journal of Experimental Biology*, 208(10), 1937-1949.
- Blackledge, T. A. et Zevenbergen, J. M. (2007). Condition-dependent spider web architecture in the western black widow, *Latrodectus hesperus*. *Animal Behaviour*, 73(5), 855-864.
- Blamires, S. J. (2010). Plasticity in extended phenotypes: Orb web architectural responses to variations in prey parameters. *Journal of Experimental Biology*, 213(18), 3207-3212.
- Blamires, S. J. (2013). Spider webs as extended phenotypes. Dans *Spiders: Morphology, Behavior and Geographic Distribution* (p. 47-70).

- Blamires, S. J., Hasemore, M., Martens, P. J. et Kasumovic, M. M. (2017). Diet-induced co-variation between architectural and physicochemical plasticity in an extended phenotype. *Journal of Experimental Biology*, 220(5), 876-884.
- Blamires, S. J., Hochuli, D. F. et Thompson, M. B. (2009). Prey protein influences growth and decoration building in the orb web spider *Argiope keyserlingi*. *Ecological Entomology*, 34(5), 545-550.
- Blamires, S. J., Martens, P. J. et Kasumovic, M. M. (2018). Fitness consequences of plasticity in an extended phenotype. *Journal of Experimental Biology*, 221(4).
- Blamires, S. J., Sahni, V., Dhinojwala, A., Blackledge, T. A. et Tso, I. M. (2014). Nutrient deprivation induces property variations in spider gluey silk. *PLoS ONE*, 9(2).
- Bolnick, D. I., Amarasekare, P., Araújo, M. S., Bürger, R., Levine, J. M., Novak, M., . . . Vasseur, D. A. (2011). Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution*, 26(4), 183-192.
- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. et Forister, M. L. (2003). The ecology of individuals: Incidence and implications of individual specialization. *American Naturalist*, 161(1), 1-28.
- Brandley, N., Johnson, M. et Johnsen, S. (2016). Aposematic signals in North American black widows are more conspicuous to predators than to prey. *Behavioral Ecology*, 27(4), 1104-1112.
- Brommer, J. E. (2013). Phenotypic plasticity of labile traits in the wild. *Current Zoology*, 59(4), 485-505.

- Bucher, R. et Entling, M. H. (2011). Contrasting effects of habitat fragmentation, population density, and prey availability on body condition of two orb - weaving spiders. *Ecological Entomology*, 36(6), 680-685.
- Burnham, K. P. et Anderson, D. R. (2002). A practical information-theoretic approach. *Model selection and multimodel inference*, 2.
- Careau, V., Thomas, D., Humphries, M. M. et Réale, D. (2008). Energy metabolism and animal personality. *Oikos*, 117(5), 641-653.
- Carroll, S. P., Hendry, A. P., Reznick, D. N. et Fox, C. W. (2007). Evolution on ecological time-scales. *Functional Ecology*, 21(3), 387-393.
- Chacon, P. et Eberhard, W. (1980). Factors affecting numbers and kinds of prey caught in artificial spider webs, with considerations of how orb webs trap prey. *Bulletin-British Arachnological Society*.
- Chamberlin, R. V. et Ivie, W. (1935). The black widow spider and its varieties in the United States.
- Cole, E. F. et Quinn, J. L. (2012). Personality and problem-solving performance explain competitive ability in the wild. *Proceedings of the Royal Society B: Biological Sciences*, 279(1731), 1168-1175.
- Cowlishaw, G. (1997). Trade-offs between foraging and predation risk determine habitat use in a desert baboon population. *Animal Behaviour*, 53(4), 667-686.
- Craig, C. L. (2003). *Spiderwebs and silk: tracing evolution from molecules to genes to phenotypes* Oxford University Press.

- Dall, S. R. X., Bell, A. M., Bolnick, D. I. et Ratnieks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecology Letters*, 15(10), 1189-1198.
- Dall, S. R. X., Houston, A. I. et McNamara, J. M. (2004). The behavioural ecology of personality: Consistent individual differences from an adaptive perspective. *Ecology Letters*, 7(8), 734-739.
- Dawkins, R. (1982). *The extended phenotype* (vol. 8) Oxford university press Oxford.
- Des Roches, S., Post, D. M., Turley, N. E., Bailey, J. K., Hendry, A. P., Kinnison, M. T., . . . Palkovacs, E. P. (2018). The ecological importance of intraspecific variation. *Nature Ecology and Evolution*, 2(1), 57-64.
- Desmarais, K. H. et Tessier, A. J. (1999). Performance trade-off across a natural resource gradient. *Oecologia*, 120(1), 137-146.
- Dhellemmes, F., Finger, J.-S., Laskowski, K. L., Guttridge, T. L. et Krause, J. (2020, 2020/04/01/). Comparing behavioural syndromes across time and ecological conditions in a free-ranging predator. *Animal Behaviour*, 162, 23-33.
- Dingemanse, N. J. et Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: Mixed-effect modelling approaches. *Journal of Animal Ecology*, 82(1), 39-54.
- Dingemanse, N. J., Kazem, A. J. N., Réale, D. et Wright, J. (2010, 2010/02/01/). Behavioural reaction norms: animal personality meets individual plasticity. *Trends in Ecology & Evolution*, 25(2), 81-89.

- Dingemanse, N. J. et Réale, D. (2005). Natural selection and animal personality. *Behaviour*, 142(9), 1159-1184.
- Dingemanse, N. J. et 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. et Wolf, M. (2013). Between-individual differences in behavioural plasticity within populations: Causes and consequences. *Animal Behaviour*, 85(5), 1031-1039.
- DiRienzo, N. et Aonuma, H. (2018, 4//). Plasticity in extended phenotype increases offspring defence despite individual variation in web structure and behaviour. *Animal Behaviour*, 138, 9-17.
- Dirienzo, N. et Montiglio, P. O. (2016a). The contribution of developmental experience vs. condition to life history, trait variation and individual differences. *Journal of Animal Ecology*.
- Dirienzo, N. et Montiglio, P. O. (2016b). Linking consistent individual differences in web structure and behavior in black widow spiders. *Behavioral Ecology*, 27(5), 1424-1431.
- DiRienzo, N., Schraft, H. A., Montiglio, P. O., Bradley, C. T. et Dornhaus, A. (2020). Foraging behavior and extended phenotype independently affect foraging success in spiders. *Behavioral Ecology*, 31(5), 1242-1249.
- DiSciullo, R. A. et Basolo, A. L. (2020). Body size, but not age-at-maturation or context, affects the expression of predator-induced behavioural plasticity in female green swordtails (*Xiphophorus hellerii*). *Ethology*, 126(3), 320-332.

- Dochtermann, N. A., Schwab, T., Anderson Berdal, M., Dalos, J. et Royauté, R. (2019). The Heritability of Behavior: A Meta-analysis. *Journal of Heredity*, 110(4), 403-410.
- Dochtermann, N. A., Schwab, T. et Sih, A. (2014). The contribution of additive genetic variation to personality variation: Heritability of personality. *Proceedings of the Royal Society B: Biological Sciences*, 282(1798).
- Dosmann, A., Brooks, K. C. et Mateo, J. M. (2015). Evidence for a mechanism of phenotypic integration of behaviour and innate immunity in a wild rodent: Implications for animal personality and ecological immunology. *Animal Behaviour*, 101, 179-189.
- Elkin, C. M. et Reid, M. L. (2005). Low energy reserves and energy allocation decisions affect reproduction by Mountain Pine Beetles, *Dendroctonus ponderosae*. *Functional Ecology*, 19(1), 102-109.
- Fanson, B. G., Fanson, K. V. et Biro, P. A. (2021). Macronutrient composition and availability affects repeatability of fly activity through changes in among- and within-individual (residual) variation. *Evolutionary Ecology*.
- Farine, D. R., Montiglio, P.-O. et Spiegel, O. (2015, 2015/10/01/). From Individuals to Groups and Back: The Evolutionary Implications of Group Phenotypic Composition. *Trends in Ecology & Evolution*, 30(10), 609-621.
- Farwell, M. et McLaughlin, R. L. (2009). Alternative foraging tactics and risk taking in brook charr (*Salvelinus fontinalis*). *Behavioral Ecology*, 20(5), 913-921.
- Futuyma, D. J. et Moreno, G. (1988). The evolution of ecological specialization. *Annual review of ecology and systematics*. Vol. 19, 207-233.

- Garamszegi, L. Z., Markó, G., Szász, E., Zsebök, S., Azcárate, M., Herczeg, G. et Török, J. (2015). Among-year variation in the repeatability, within- and between-individual, and phenotypic correlations of behaviors in a natural population. *Behavioral Ecology and Sociobiology*, 69(12), 2005-2017.
- Gebhardt, M. D. et Stearns, S. C. (1993). Phenotypic plasticity for life history traits in *Drosophila melanogaster*. I. Effect on phenotypic and environmental correlations. *Journal of Evolutionary Biology*, 6(1), 1-16.
- Gibson, G. et Wagner, G. (2000). Canalization in evolutionary genetics: A stabilizing theory? *BioEssays*, 22(4), 372-380.
- Giraldeau, L.-A. (1984). Group foraging: the skill pool effect and frequency-dependent learning. *The American Naturalist*, 124(1), 72-79.
- Godvik, I. M. R., Loe, L. E., Vik, J. O., Veiberg, V., Langvatn, R. et Mysterud, A. (2009). Temporal scales, trade-offs, and functional responses in red deer habitat selection. *Ecology*, 90(3), 699-710.
- Gomes, A. C. R. et Cardoso, G. C. (2020). The lag-time constraint for behavioural plasticity. *Proceedings of the Royal Society B: Biological Sciences*, 287(1926).
- Gonzaga, M. O., Leiner, N. O. et Santos, A. J. (2006). On the sticky cobwebs of two theridiid spiders (Araneae: Theridiidae). *Journal of Natural History*, 40(5-6), 293-306.
- Gregorič, M., Kuntner, M. et Blackledge, T. A. (2015). Does body size predict foraging effort? Patterns of material investment in spider orb webs. *Journal of Zoology*, 296(1), 67-78.

- Gross, M. R. (1991). Evolution of alternative reproductive strategies: frequency-dependent sexual selection in male bluegill sunfish. *Philosophical Transactions - Royal Society of London, B*, 332(1262), 59-66.
- Hamel, S., Côté, S. D., Gaillard, J. M. et Festa - Bianchet, M. (2009). Individual variation in reproductive costs of reproduction: High - quality females always do better. *Journal of Animal Ecology*, 78(1), 143-151.
- Harmer, A. M. T., Kokko, H., Herberstein, M. E. et Madin, J. S. (2012). Optimal web investment in sub-optimal foraging conditions. *Naturwissenschaften*, 99(1), 65-70.
- Harrison, X. A. (2014). Using observation-level random effects to model overdispersion in count data in ecology and evolution. *PeerJ*, 2, e616.
- Harrison, X. A. (2015). A comparison of observation-level random effect and Beta-Binomial models for modelling overdispersion in Binomial data in ecology & evolution. *PeerJ*, 3, e1114.
- Hau, M. et Goymann, W. (2015). Endocrine mechanisms, behavioral phenotypes and plasticity: Known relationships and open questions. *Frontiers in Zoology*, 12(1).
- Hayes, J. P. et Jenkins, S. H. (1997). Individual variation in mammals. *Journal of Mammalogy*, 78(2), 274-293.
- Herberstein, M., Craig, C. et Elgar, M. (2000). Foraging strategies and feeding regimes: web and decoration investment in *Argiope keyserlingi* Karsch (Araneae: Araneidae). *Evolutionary Ecology Research*, 2(1), 41-67.

- Herberstein, M. et Elgar, M. (1994). Foraging strategies of *Eriophora transmarina* and *Nephila plumipes* (Araneae: Araneoidea): Nocturnal and diurnal orb - weaving spiders. *Australian Journal of Ecology*, 19(4), 451-457.
- Horta-Lacueva, Q. J. B., Benhaïm, D., Morrissey, M. B., Snorrason, S. S. et Kapralova, K. H. (2021). Animal personality adds complexity to the processes of divergence between sympatric morphs of Arctic charr. *Animal Behaviour*, 175, 57-73.
- Houle, D. (1992). Comparing evolvability and variability of quantitative traits. *Genetics*, 130(1), 195-204.
- Hu, X., Yuan, J., Wang, X., Vasanthavada, K., Falick, A. M., Jones, P. R., . . . Vierra, C. A. (2007). Analysis of aqueous glue coating proteins on the silk fibers of the cob weaver, *Latrodectus hesperus*. *Biochemistry*, 46(11), 3294-3303.
- Irving, W. G. et Harold Hinman, E. (1935). The blue mud-dauber as a predator of the Black Widow Spider. *Science*, 82(2130), 395-396.
- Jin, H.-J. et Kaplan, D. L. (2003). Mechanism of silk processing in insects and spiders. *Nature*, 424(6952), 1057-1061.
- Kaston, B. J. (1970). Comparative biology of American black widow spiders. *San Diego Soc Natur Hist Trans.*
- Kasumovic, M. M. et Andrade, M. C. (2004). Discrimination of airborne pheromones by mate-searching male western black widow spiders (*Latrodectus hesperus*): species- and population-specific responses. *Canadian journal of zoology*, 82(7), 1027-1034.

- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., . . . Blokhuis, H. J. (1999). Coping styles in animals: Current status in behavior and stress- physiology. *Neuroscience and Biobehavioral Reviews*, 23(7), 925-935.
- Körner, M., Vogelweith, F., Foitzik, S. et Meunier, J. (2017). Condition-Dependent Trade-Off Between Weapon Size and Immunity in Males of the European Earwig. *Scientific Reports*, 7(1).
- Koski, K. J., Akhenblit, P., McKiernan, K. et Yarger, J. L. (2013). Non-invasive determination of the complete elastic moduli of spider silks. *Nature Materials*, 12(3), 262-267.
- Lande, R. (1977). On comparing coefficients of variation. *Systematic Zoology*, 26(2), 214-217.
- Laskowski, K. L., Moiron, M. et Niemelä, P. T. (2021). Integrating Behavior in Life-History Theory: Allocation versus Acquisition? *Trends in Ecology and Evolution*, 36(2), 132-138.
- Lessels, C. (1991). The evolution of life history strategies. *Behavioral ecology*, 3rd ed. Oxford: Blackwell Scientific.
- Lichtenstein, J. L. L., DiRienzo, N., Knutson, K., Kuo, C., Zhao, K. C., Brittingham, H. A., . . . Pruitt, J. N. (2016). Prolonged food restriction decreases body condition and reduces repeatability in personality traits in web-building spiders. *Behavioral Ecology and Sociobiology*, 70(11), 1793-1803.
- Lima, S. L. (1998). Nonlethal effects in the ecology of predator-prey interactions. *Bioscience*, 48(1), 25-34.

- Lima, S. L. et Dill, L. M. (1990). Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian journal of zoology*, 68(4), 619-640.
- Linnaeus, C. v. (1758). Systema Naturae per regna tria naturae. Secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. *Editio*, 1(10), 823.
- Ljungström, G., Stjernstedt, M., Wapstra, E. et Olsson, M. (2016). Selection and constraints on offspring size - number trade - offs in sand lizards (*Lacerta agilis*). *Journal of evolutionary biology*, 29(5), 979-990.
- Ludwig, D. et Rowe, L. (1990). Life-history strategies for energy gain and predator avoidance under time constraints. *American Naturalist*, 135(5), 686-707.
- Lukas, J., Kalinkat, G., Miesen, F. W., Landgraf, T., Krause, J. et Bierbach, D. (2021). Consistent Behavioral Syndrome Across Seasons in an Invasive Freshwater Fish. *Frontiers in Ecology and Evolution*, 8.
- MacLeod, E. C. et Andrade, M. C. (2014). Strong, convergent male mate choice along two preference axes in field populations of black widow spiders. *Animal Behaviour*, 89, 163-169.
- Marchetti, C. (2000). Individual differences in the use of social information in foraging by captive great tits. *Animal Behaviour*, 60, 131-140.
- Mathot, K. J. et Frankenhuis, W. E. (2018). Models of pace-of-life syndromes (POLS): a systematic review. *Behavioral Ecology and Sociobiology*, 72(3).

- Mayntz, D., Toft, S. et Vollrath, F. (2009). Nutrient balance affects foraging behaviour of a trap-building predator. *Biology Letters*, 5(6), 735-738.
- McGraw, K. O. et Wong, S. P. (1996). Forming inferences about some intraclass correlation coefficients. *Psychological methods*, 1(1), 30.
- McNamara, J. M. et Houston, A. I. (1987). Starvation and predation as factors limiting population size. *Ecology*, 68(5), 1515-1519.
- Messina, F. J. et Fry, J. (2003). Environment - dependent reversal of a life history trade - off in the seed beetle *Callosobruchus maculatus*. *Journal of evolutionary biology*, 16(3), 501-509.
- Miller, C. W., Joseph, P. N., Kilner, R. M. et Emberts, Z. (2019). A weapons-testes trade-off in males is amplified in female traits. *Proceedings. Biological sciences*, 286(1908), 20190906-20190906.
- Miller, C. W. et Svensson, E. I. (2014). Sexual Selection in Complex Environments. *Annual Review of Entomology*, 59(1), 427-445.
- Moiron, M., Araya-Ajoy, Y. G., Mathot, K. J., Mouchet, A. et Dingemanse, N. J. (2019). Functional relations between body mass and risk-taking behavior in wild great tits. *Behavioral Ecology*, 30(3), 617-623.
- Moiron, M., Laskowski, K. L. et Niemelä, P. T. (2020). Individual differences in behaviour explain variation in survival: a meta-analysis. *Ecology Letters*, 23(2), 399-408.
- Montiglio, P.-O., Garant, D., Thomas, D. et Réale, D. (2010). Individual variation in temporal activity patterns in open-field tests. *Animal Behaviour*, 80(5), 905-912.

- Montiglio, P. O., Garant, D., Pelletier, F. et Réale, D. (2015). Intra-individual variability in fecal cortisol metabolites varies with lifetime exploration and reproductive life history in eastern chipmunks (*Tamias striatus*). *Behavioral Ecology and Sociobiology*, 69(1), 1-11.
- Montiglio, P. O., Wey, T. W., Chang, A. T., Fogarty, S. et Sih, A. (2016). Multiple mating reveals complex patterns of assortative mating by personality and body size. *Journal of Animal Ecology*, 85(1), 125-135.
- Moyes, K., Coulson, T., Morgan, B. J., Donald, A., Morris, S. J. et Clutton - Brock, T. H. (2006). Cumulative reproduction and survival costs in female red deer. *Oikos*, 115(2), 241-252.
- Moyes, K., Morgan, B. J., Morris, A., Morris, S. J., Clutton-Brock, T. H. et Coulson, T. (2009). Exploring individual quality in a wild population of red deer. *Journal of Animal Ecology*, 406-413.
- Nakagawa, S. et Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: A practical guide for biologists. *Biological Reviews*, 85(4), 935-956.
- Nakata, K. (2009). To be or not to be conspicuous: the effects of prey availability and predator risk on spider's web decoration building. *Animal Behaviour*, 78(5), 1255-1260.
- Neumann, R. et Schneider, J. M. (2016). Socially cued developmental plasticity in web-building spiders. *BMC Evolutionary Biology*, 16(1).
- Ngo, K. S., R-Almási, B., Barta, Z. et Tökölyi, J. (2021). Experimental manipulation of body size alters life history in hydra. *Ecology Letters*, 24(4), 728-738.

- Nicolaus, M., Brommer, J. E., Ubels, R., Tinbergen, J. M. et Dingemanse, N. J. (2013). Exploring patterns of variation in clutch size-density reaction norms in a wild passerine bird. *Journal of Evolutionary Biology*, 26(9), 2031-2043.
- Nussey, D. H., Wilson, A. J. et Brommer, J. E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, 20(3), 831-844.
- Nylin, S. et Gotthard, K. (1998) Plasticity in life-history traits. : *Vol. 43. Annual Review of Entomology* (pp. 63-83).
- Olendorf, R., Rodd, F. H., Punzalan, D., Houde, A. E., Hurt, C., Reznick, D. N. et Hughes, K. A. (2006). Frequency-dependent survival in natural guppy populations. *Nature*, 441(7093), 633-636.
- Ovadia, O. et Schmitz, O. J. (2002). Linking individuals with ecosystems: Experimentally identifying the relevant organizational scale for predicting trophic abundances. *Proceedings of the National Academy of Sciences of the United States of America*, 99(20), 12927-12931.
- Patrick, S. C., Pinaud, D. et Weimerskirch, H. (2017). Boldness predicts an individual's position along an exploration–exploitation foraging trade-off. *Journal of Animal Ecology*, 86(5), 1257-1268.
- Pettorelli, N., Hilborn, A., Duncan, C. et Durant, S. M. (2015) Individual Variability: The Missing Component to Our Understanding of Predator-Prey Interactions. : *Vol. 52. Advances in Ecological Research* (pp. 19-44).
- Pinheiro, J. C. et Bates, D. M. (2000a). Extending the basic linear mixed-effects model. *Mixed-effects models in S and S-PLUS*, 201-270.

- Pinheiro, J. C. et Bates, D. M. (2000b). Linear mixed-effects models: basic concepts and examples. *Mixed-effects models in S and S-Plus*, 3-56.
- Prestwich, K. (1977). The energetics of web-building in spiders. *Comparative Biochemistry and Physiology--Part A: Physiology*, 57(3), 321-326.
- R Core Team. (2018). R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*.
- Rau, P. (1935). The wasp, *Chalybion cyaneum* Fab., preys upon the black widow spider, *Latrodectus mactans* Fab.(Hymen., Araneae). *Entomological News*, 46(10), 259-260.
- Réale, D., Dingemanse, N. J., Kazem, A. J. N. et Wright, J. (2010a). Evolutionary and ecological approaches to the study of personality. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365(1560), 3937-3946.
- Réale, D. et Festa-Bianchet, M. (2003). Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, 65(3), 463-470.
- Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V. et Montiglio, P.-O. (2010b). 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. et Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, 82(2), 291-318.

- Roff, D. A. et Fairbairn, D. J. (2007, 2007/03/01). The evolution of trade-offs: where are we? *Journal of Evolutionary Biology*, 20(2), 433-447.
- Rosengaus, R. B., Zecher, C. N., Schultheis, K. F., Brucker, R. M. et Bordenstein, S. R. (2011). Disruption of the termite gut microbiota and its prolonged consequences for fitness. *Applied and environmental microbiology*, 77(13), 4303-4312.
- Royauté, R. et Dochtermann, N. A. (2016). When the mean no longer matters: developmental diet affects behavioral variation but not population averages in the house cricket (*Acheta domesticus*). *Behavioral Ecology*, 28(1), 337-345.
- Royauté, R., Garrison, C., Dalos, J., Berdal, M. A. et Dochtermann, N. A. (2019). Current energy state interacts with the developmental environment to influence behavioural plasticity. *Animal Behaviour*, 148, 39-51.
- Royauté, R., Wilson, E. S., Helm, B. R., Mallinger, R. E., Prasifka, J., Greenlee, K. J. et Bowsler, J. H. (2018). Phenotypic integration in an extended phenotype: among-individual variation in nest-building traits of the alfalfa leafcutting bee (*Megachile rotundata*). *Journal of Evolutionary Biology*, 31(7), 944-956.
- Salzman, T. C., McLaughlin, A. L., Westneat, D. F. et Crowley, P. H. (2018). Energetic trade-offs and feedbacks between behavior and metabolism influence correlations between pace-of-life attributes. *Behavioral Ecology and Sociobiology*, 72(3).
- Sandoval, C. (1994). Plasticity in web design in the spider *Parawixia bistriata*: a response to variable prey type. *Functional Ecology*, 701-707.
- Santostefano, F., Wilson, A. J., Niemelä, P. T. et Dingemanse, N. J. (2017). Behavioural mediators of genetic life-history trade-offs: A test of the pace-of-

life syndrome hypothesis in field crickets. *Proceedings of the Royal Society B: Biological Sciences*, 284(1864).

Schmitz, O. J. (2007). Predator diversity and trophic interactions. *Ecology*, 88(10), 2415-2426.

Schmitz, O. J., Buchkowski, R. W., Burghardt, K. T. et Donihue, C. M. (2015) Functional Traits and Trait-Mediated Interactions. Connecting Community-Level Interactions with Ecosystem Functioning. : *Vol. 52. Advances in Ecological Research* (pp. 319-343).

Schneider, C. A., Rasband, W. S. et Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of image analysis. *Nature methods*, 9(7), 671-675.

Schraft, H., Jaham, M. D., Toupin, L. P. et Montiglio, P. O. (2021). North American widow spiders (Araneae: Theridiidae). *Arachnology*, 18(7), 783-802.

Sgrò, C. M. et Hoffmann, A. A. (2004). Genetic correlations, tradeoffs and environmental variation. *Heredity*, 93(3), 241-248.

Sherman, P. M. (1994). The orb-web: an energetic and behavioural estimator of a spider's dynamic foraging and reproductive strategies. *Animal Behaviour*, 48(1), 19-34.

Sih, A. (1980). Optimal behavior: can foragers balance two conflicting demands? *Science*, 210(4473), 1041-1043.

Sih, A., Bell, A. et Johnson, J. C. (2004a). Behavioral syndromes: An ecological and evolutionary overview. *Trends in Ecology and Evolution*, 19(7), 372-378.

- Sih, A., Bell, A. M., Johnson, J. C. et Ziemba, R. E. (2004b). Behavioral syndromes: An integrative overview. *Quarterly Review of Biology*, 79(3), 241-277.
- Sih, A., Cote, J., Evans, M., Fogarty, S. et Pruitt, J. (2012). Ecological implications of behavioural syndromes. *Ecology Letters*, 15(3), 278-289.
- Sih, A., Mathot, K. J., Moirón, M., Montiglio, P. O., Wolf, M. et Dingemanse, N. J. (2015). Animal personality and state-behaviour feedbacks: A review and guide for empiricists. *Trends in Ecology and Evolution*, 30(1), 50-60.
- Sinervo, B. et Svensson, E. (1998). Mechanistic and selective causes of life history trade-offs and plasticity. *Oikos*, 83(3), 432-442.
- Sirod, E. et Bernstein, C. (1996). Time sharing between host searching and food searching in parasitoids: State-dependent optimal strategies. *Behavioral Ecology*, 7(2), 189-194.
- Smith, M. L., Ostwald, M. M. et Seeley, T. D. (2015). Adaptive tuning of an extended phenotype: Honeybees seasonally shift their honey storage to optimize male production. *Animal Behaviour*, 103, 29-33.
- Sommer, N. R. et Schmitz, O. J. (2020). Differences in prey personality mediate trophic cascades. *Ecology and Evolution*, 10(17), 9538-9551.
- Stål, C. (1870). *Enumeratio Hemipterorum: Bidrag till en förteckning öfver alla hittills kända Hemiptera, jemte systematiska meddelanden* PA Norstedt.
- Stamps, J. et Groothuis, T. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biological Reviews*, 85(2), 301-325.

- Stamps, J. A. (2007). Growth-mortality tradeoffs and 'personality traits' in animals. *Ecology Letters*, 10(5), 355-363.
- Stamps, J. A., Briffa, M. et Biro, P. A. (2012). Unpredictable animals: Individual differences in intraindividual variability (IIV). *Animal Behaviour*, 83(6), 1325-1334.
- Stearns, S., de Jong, G. et Newman, B. (1991). The effects of phenotypic plasticity on genetic correlations. *Trends in Ecology and Evolution*, 6(4), 122-126.
- Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional ecology*, 3(3), 259-268.
- Stearns, S. C. (1992). *The evolution of life histories*.
- Steinhoff, P. O. M., Warfen, B., Voigt, S., Uhl, G. et Dammhahn, M. (2020). Individual differences in risk-taking affect foraging across different landscapes of fear. *Oikos*, 129(12), 1891-1902.
- Tanaka, K. (1989). Energetic cost of web construction and its effect on web relocation in the web-building spider *Agelena limbata*. *Oecologia*, 81(4), 459-464.
- Tatar, M. et Carey, J. R. (1995). Nutrition mediates reproductive trade-offs with age-specific mortality in the beetle *Callosobruchus maculatus*. *Ecology*, 76(7), 2066-2073.
- Thompson, C. H., Rodríguez, R. L. et Sergi, C. (2020). Repeatability but no short-term plasticity in the web architecture of *Latrodectus hesperus* western black widow spiders (Araneae: Theridiidae). *Ethology*, 126(3), 313-319.

- Thys, B., Pinxten, R. et Eens, M. (2021). Long-term repeatability and age-related plasticity of female behaviour in a free-living passerine. *Animal Behaviour*, 172, 45-54.
- Trudgill, D. L., Honek, A., Li, D. et Van Straalen, N. M. (2005). Thermal time - Concepts and utility. *Annals of Applied Biology*, 146(1), 1-14.
- Urbánková, G., Šíchová, K., Riegert, J., Horsley, R., Mladěnková, N., Starck-Lantová, P. et Sedláček, F. (2020). Lifetime low behavioural plasticity of personality traits in the common vole (*Microtus arvalis*) under laboratory conditions. *Ethology*, 126(8), 812-823.
- Van de Pol, M. et Wright, J. (2009). A simple method for distinguishing within-versus between-subject effects using mixed models. *Animal behaviour*, 77(3), 753.
- Van Noordwijk, A. J. et de Jong, G. (1986). Acquisition and allocation of resources: their influence on variation in life history tactics. *The American Naturalist*, 128(1), 137-142.
- Van Valen, L. (2005). The statistics of variation. *Variation*, 29-47.
- Varpe, Ø. (2017). Life History Adaptations to Seasonality. *Integrative and Comparative Biology*, 57(5), 943-960.
- Verdolin, J. L. (2006). Meta-analysis of foraging and predation risk trade-offs in terrestrial systems. *Behavioral Ecology and Sociobiology*, 60(4), 457-464.

- Vetter, R. S. (1980). Defensive behavior of the black widow spider *Latrodectus hesperus* (Araneae: Theridiidae). *Behavioral Ecology and Sociobiology*, 7(3), 187-193.
- Vetter, R. S., Penas, L. M. et Hoddle, M. S. (2016). Laboratory refugia preferences of the brown widow spider, *Latrodectus geometricus* (Araneae: Theridiidae). *Journal of Arachnology*, 44(1), 52-57.
- Vetter, R. S., Vincent, L. S., Itnyre, A. A., Clarke, D. E., Reinker, K. I., Danielsen, D. W. R., . . . Rust, M. K. (2012). Predators and parasitoids of egg sacs of the widow spiders, *Latrodectus geometricus* and *Latrodectus hesperus* (Araneae: Theridiidae) in southern California. *The Journal of Arachnology*, 40(2), 209-214, 206.
- Via, S. et Lande, R. (1985). Genotype-environment interaction and the evolution of phenotypic plasticity. *Evolution*, 39(3), 505-522.
- Vibert, S., Scott, C. et Gries, G. (2016). Vibration transmission through sheet webs of hobo spiders (*Eratigena agrestis*) and tangle webs of western black widow spiders (*Latrodectus hesperus*). *Journal of Comparative Physiology A: Neuroethology, Sensory, Neural, and Behavioral Physiology*, 202(11), 749-758.
- Vollrath, F. et Edmonds, D. T. (1989). Modulation of the mechanical properties of spider silk by coating with water. *Nature*, 340(6231), 305-307.
- Vollrath, F., Madsen, B. et Shao, Z. (2001). The effect of spinning conditions on the mechanics of a spider's dragline silk. *Proceedings of the Royal Society B: Biological Sciences*, 268(1483), 2339-2346.
- Vollrath, F. et Porter, D. (2006). Spider silk as archetypal protein elastomer. *Soft Matter*, 2(5), 377-385.

Westneat, D. F., Hatch, M. I., Wetzel, D. P. et Ensminger, A. L. (2011). Individual variation in parental care reaction norms: Integration of Personality and plasticity. *American Naturalist*, 178(5), 652-667.

Wikenros, C., Ståhlberg, S. et Sand, H. (2014). Feeding under high risk of intraguild predation: Vigilance patterns of two medium-sized generalist predators. *Journal of Mammalogy*, 95(4), 862-870.

Wolak, M. E., Fairbairn, D. J. et Paulsen, Y. R. (2012). Guidelines for estimating repeatability. *Methods in Ecology and Evolution*, 3(1), 129-137.

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

Yasué, M., Quinn, J. L. et Cresswell, W. (2003). Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in Redshanks. *Functional Ecology*, 17(6), 727-736.

Zajitschek, F. et Connallon, T. (2017). Partitioning of resources: the evolutionary genetics of sexual conflict over resource acquisition and allocation. *Journal of Evolutionary Biology*, 30(4), 826-838.

Zevenbergen, J. M., Schneider, N. K. et Blackledge, T. A. (2008). Fine dining or fortress? Functional shifts in spider web architecture by the western black widow *Latrodectus hesperus*. *Animal Behaviour*, 76(3), 823-829.