UNIVERSITÉ DU QUÉBEC À MONTRÉAL

BÉNÉFICES DIRECTS ET INDIRECTS DU CHOIX DE PARTENAIRE CHEZ LE GRILLON DE SABLE (GRYLLUS FIRMUS)

MÉMOIRE

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LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

BSC	Biosafety cabinet
IASC	Théories du conflit sexuel intralocus
ICHH	Hypothèse du handicap de l'immunocompétence
LD50	Dose léthale pour 50% de la population
RMR	« Resting metabolic rate » Taux métabolique au repos
SMI	Scaled mass index

LISTE DES SYMBOLES ET DES UNITÉS

cells/µl	Nombre de cellule par microlitre
n=	Nombre d'observations
µl	Microlitre

RÉSUMÉ

Chez de nombreuses espèces animales, les caractères sexuels secondaires des mâles attirent les femelles et permettraient le signalement honnête de la qualité du mâle. Par contre, les différents bénéfices qui peuvent être obtenus chez la femelle par la sélection de partenaires sexuels sont des concepts importants dans la littérature sur la sélection sexuelle. Dans cette étude, nous utilisons le temps nécessaire à une femelle grillon Gryllus firmus pour monter sur un mâle dans le but de s'accoupler, comme indice global de l'attirance sexuelle. Premièrement, nous étudions si les mâles attirants qui ont une plus grande capacité d'acquisition de ressources. Nous prédisons qu'ils peuvent allouer plus de ressources dans deux traits reliés aux aptitudes phénotypiques malgré le fait que ces traits soient en compétition au niveau des ressources disponibles. Par exemple, nous testons les compromis entre l'attirance sexuelle et la capacité immunitaire. En second, nous observons les bénéfices directs (sur la capacité reproductrice de la femelle) et indirects (sur les aptitudes phénotypiques de sa progéniture) de la sélection de partenaires. Ensuite, nous étudions les concepts des théories du conflit sexuel intralocus où l'accouplement avec des mâles en bonne condition pourrait donner lieu à des bénéfices au niveau des aptitudes phénotypiques, différents selon le sexe des descendants. Finalement, nous observons l'héritabilité de la masse, la taille du pronotum, le SMI, le temps à atteindre la maturité, l'attirance et la capacité immunitaire. Les résultats soulignent que les mâles qui ont atteint le dernier stade de maturation plus rapidement étaient en meilleure condition corporelle. Contrairement à nos prédictions, l'attirance du mâle n'était pas corrélée avec sa capacité de résistance aux infections ou sa longévité. Cependant, les mâles attirants étaient en meilleure condition corporelle et possédaient un plus petit pronotum. Nous n'avons pas observé d'effet de l'attirance du mâle sur la capacité reproductrice de la femelle, par contre, les mâles attirants ont produit des fils de taille supérieure. Le temps pour atteindre la maturité était le seul trait héritable observé. Étudier la sélection sexuelle et le comportement animal permet d'approfondir nos connaissances sur les mécanismes de choix de partenaire et leur importance évolutive.

Mots clés : Attirance, choix de partenaire, héritabilité, immunité, sélection sexuelle

ABSTRACT

A large number of studies discuss the trade-offs between immunity and secondary sexual traits in insects. The implications of attractiveness and whether females gain genetic benefits for their offspring from their mate choice are important factors related to these trade-offs. However, a limited amount of studies used global attractiveness indicators, even if sexual attractiveness involves a large number of traits. In this study, we use a global indicator of male's attractiveness using the latency for a female to mount him and start the copulation in the sand field crickets, *Gryllus firmus*. The objective is to observe the direct and indirect benefits of mate choice. Firstly, we study the relationship between male attractiveness and two fitness-related traits (disease survival and longevity) to test the hypothesis of a positive covariance. Secondly, the female's fecundity, fertility and egg size are used to study the direct benefits a female receives from mate choice. Then, the effects of sire traits on offspring fitness are used to study indirect benefits. Finally, we look into the heritability of our studied traits (mass, pronotum size, scaled mass index, time to reach maturity, attractiveness and disease resistance). In contrast to the hypothesis of females receiving indirect benefits from mate choice, improving offspring viability, we also observe if female mate preferences can affect offspring fitness in sex-specific ways. Our results showed no correlation of attractiveness and our two fitness-related traits. However, attractive males and males who eclosed to adulthood more quickly were in better body condition. We did not find any effect of male attractiveness on female reproductive output. Although, as a potential indirect benefit of mate choice, we observed that attractive males produced bigger sons. The time to reach adulthood was strongly heritable and males who took more time to mature had bigger offspring. This study also emphasizes the importance of further research using global measures of sexual attractiveness and the complexity of indirect benefits studies.

Keywords:, Attractiveness, heritability, immunity, mate choice, sexual selection

INTRODUCTION

Pourquoi et comment le choix du partenaire évolue chez les animaux est un sujet controversé en biologie évolutive (Andersson, 1994; Arnqvist, 2006; Jennions & Petrie, 1997; Kokko *et al.*, 2003). Darwin (1871) fut le premier à suggérer que le choix de partenaire sexuel est un processus important de la sélection sexuelle qui est responsable du développement d'ornements extravagants chez les mâles. Ici, la définition utilisée sera celle caractérisant le choix de partenaire chez la femelle comme le processus où un individu se reproduit non aléatoirement avec un ou plusieurs mâles en fonction de ses préférences (Heisler *et al.*, 1987; Iwasa & Nee, 1991). Le concept de préférence amène un prérequis au niveau de la sélection de partenaire. Pour avoir des préférences qui se conservent évolutivement, les traits privilégiés par les femelles doivent être des agents potentiels de sélection sexuelle chez les mâles (Heisler *et al.*, 1987).

Le choix de partenaire sexuel est un processus composé d'une série d'étapes impliquant des actions énergétiquement coûteuses chez la femelle (Pomiankowski, 1987). Le temps et l'énergie utilisés pour évaluer, localiser les mâles, ainsi que l'augmentation du niveau d'exposition à la prédation sont des coûts pris par les femelles qui sélectionnent les mâles (Westneat & Fox, 2010; Gray, 1999; Pomiankowski, 1987). Malgré les coûts importants liés à cette sélection, une grande variété d'espèces animales ont conservé la sélection de partenaires à travers l'évolution (William E

Wagner, 1998). Il est donc possible, que des bénéfices supérieurs aux coûts sont associés au comportement de sélection.

Les raisons pour lesquelles les femelles trouvent certains mâles plus attirants que d'autres et dignes d'être sélectionnés pour la reproduction, sont un sujet central des études en biologie évolutive. Une hypothèse fondamentale pour expliquer ce phénomène est que les mâles attirants pourvoient un avantage au niveau des aptitudes phénotypiques des femelles ou de leur progéniture (Bonduriansky, 2001; Head *et al.*, 2005; Kirkpatrick, 1982). Cet avantage au niveau des aptitudes phénotypiques pourrait alors égaler et dépasser les coûts associés aux comportements de sélection sexuelle.

La théorie prédit que les femelles choisissent leur partenaire sexuel afin d'acquérir des ressources matérielles (bénéfices directs) et/ou qu'elles sélectionnent le mâle pour conférer une supériorité génétique à leur progéniture (bénéfices indirects) (Andersson, 1994; Jennions & Petrie, 1997; Kokko *et al.*, 2003; Møller & Jennions, 2001). Si la fécondité ou la viabilité des femelles varie en fonction de leurs préférences de partenaire, ces préférences peuvent évoluer en relation avec les bénéfices directs obtenus. Elles peuvent également évoluer suite à une sélection liée à des traits qui sont génétiquement corrélés à une viabilité génétique plus forte ou un succès reproducteur supérieur pour leur progéniture (Heisler *et al.*, 1987). D'une part, les avantages directs pour une femelle vont améliorer ses capacités de survie et ses aptitudes phénotypiques. Une augmentation de la capacité immunitaire de la femelle (Worthington & Kelly, 2016), de la fertilité (Møller & Jennions, 2001), de la protection contre les prédateurs

(Andersson & Simmons, 2006) ou une augmentation des soins parentaux (Kirkpatrick, 1985) sont des bénéfices directs potentiels suite au choix de partenaire sexuel.

0.1.1 Bénéfices directs et indirects

Les femelles qui effectuent un choix de partenaires peuvent obtenir des bénéfices directs comme une augmentation des soins parentaux (Pomiankowski, 1987), de la fécondité (Savalli & Fox, 1998), des cadeaux nuptiaux (Møller & Jennions 2001), un nombre supérieur d'œufs (Drnevich *et al.*, 2001; Weigensberg, Carriere & Roff, 1998) ou même une augmentation de la capacité de survie aux infections chez la femelle via des composés dans le sperme du mâle (Worthington & Kelly, 2016). Plusieurs traits du sperme peuvent être utilisés pour définir la qualité de ce dernier (Simmons, 2011). Le pH du sperme (Mansour, Ramoun, & Lahnsteiner, 2005), la quantité (Gage & Cook, 1994), la viabilité des spermatozoïdes (Simmons, 2011) et leur motilité sont tous des éléments importants (Choe & Crespi, 1997). Lorsqu'il y a une corrélation positive entre le nombre de descendants et la qualité du sperme, il y a présence de bénéfices directs pour la femelle suite à son choix de partenaire (Simmons, 2011).

D'autre part, la femelle peut recevoir des bénéfices indirects lors de la reproduction. Ceux-ci confèrent un avantage génétique à la progéniture culminant à des aptitudes phénotypiques plus élevé. Ces bénéfices sont dits indirects puisqu'ils affectent les aptitudes phénotypiques de la femelle par le biais d'une augmentation de celui de ses descendants. Il fut démontré que le mâle peut avoir un impact important sur le potentiel immunitaire (Raveh *et al.*, 2014), le niveau d'attirance sexuelle (Head *et al.*, 2005), et le succès reproducteur de sa progéniture (Wedell & Tregenza, 1999). La variation au niveau du succès reproducteur de la femelle est en partie causée par la variation au niveau de la qualité du mâle ainsi que de sa contribution. La condition d'un mâle a un impact sur sa capacité à conférer des avantages directs et indirects (Head *et al.*, 2005; Kirkpatrick & Barton, 1997). Deux questions importantes sont alors comment est-ce que les traits sexuels secondaires signalent honnêtement la qualité d'un mâle par rapport à un autre et comment la femelle optimise sa sélection de partenaires malgré les coûts qui y sont associés.

Les bénéfices indirects peuvent être séparés en trois catégories; les bénéfices au niveau des traits avant la maturation sexuelle (présexuel), les bénéfices sur les traits après la maturation sexuelle (post-sexuel) et les bénéfices au niveau de la fertilité. Lors du choix de partenaire, la femelle peut obtenir des bénéfices indirects présexuels en choisissant un mâle qui lui accorde une progéniture ayant une taille à l'éclosion supérieure (Weigensberg, Carriere, et al., 1998). Un exemple de bénéfice chez la progéniture juvénile influencé par le génotype du père s'est observé chez le poisson *Poecilia reticulata*, par la présence d'une corrélation entre la coloration du père (un trait fortement corrélé à l'attirance sexuelle) et la capacité de sa progéniture à éviter la capture par prédateur (un élément clé à la survie chez cette espèce) (Evans *et al.*, 2004). De plus, le temps de développement des descendants de la femelle peut varier en fonction du mâle qu'elle a choisi (Lailvaux, Hall, & Brooks, 2010; Wedell & Tregenza, 1999). Le temps de développement peut avoir un impact important sur les aptitudes phénotypiques puisqu'un temps de développement plus court peut amener à un plus haut taux de survie jusqu'à la maturation et un succès reproducteur plus élevé (Simmons, 1987). Le choix de partenaire peut aussi mener à l'obtention de bénéfices indirects post-sexuels comme une meilleure résistance aux infections (Hamilton & Zuk, 1982; Raveh *et al.*, 2014) et un niveau d'attirance sexuelle plus élevée chez la progéniture (Head *et al.* 2005). Certaines études semblent observer une corrélation négative entre le temps de développement et le niveau d'attirance, ce qui pourrait expliquer en partie la conservation d'une variation génétique (Lailvaux, Hall, & Brooks, 2010; Rodríguez *et al.*, 2013; Wedell & Tregenza, 1999).

L'importance du choix de partenaire afin d'obtenir des bénéfices indirects fut plus largement discutée lors de l'introduction de l'hypothèse « sexy son » par Weatherhead & Robertson (1979). Cette théorie suggère que les femelles peuvent sélectionner leur partenaire en fonction de leur niveau d'attirance même s'ils offrent des bénéfices directs faibles. Il est hypothétisé que, lorsque la femelle choisit un partenaire attirant, sa progéniture mâle, portant en partie les gènes du père attirant, aura un succès reproducteur élevé (Head *et al.*, 2006; Wedell & Tregenza, 1999). Selon la prémisse que la progéniture acquière une partie de la qualité individuelle du père, l'hypothèse « sexy sons » postule que les femelles se reproduisant avec des mâles attirants obtiendraient des bénéfices via l'augmentation du succès reproducteur de leur progéniture (Weatherhead & Robertson, 1979). Les chercheurs Wedell et Tregenza (1999) ont observé que les grillons mâles (*Gryllus bimaculatus*) avec un succès reproducteur élevé donnent naissance à des fils avec eux aussi un succès reproducteur supérieur.

Cependant, la plupart des études empiriques sur la théorie du choix des partenaires suggèrent que l'évolution est faiblement affectée par la sélection des bénéfices indirecte en comparaison avec l'importance de la sélection directe (Head *et al.*, 2005; Kirkpatrick & Barton, 1997). Il y a présence d'un manque dans la littérature au niveau des relations entre la capacité d'acquisition et les bénéfices indirects qui seraient obtenus par le choix de partenaire. Par ce manque de littérature et l'importance des bénéfices directs, il est difficile d'évaluer l'effet des bénéfices indirects sur le choix de partenaire ainsi que leur dépendance ou indépendance avec les bénéfices directs (Johnstone, 1995).

0.1.2 Signalisation sexuelle

Les mâles qui possèdent des ornements extravagants pour la sélection sexuelle sont généralement ceux qui seront préférés pour la reproduction et sélectionnés par les femelles. Selon certaines théories, ces traits pourraient signaler de la condition d'un mâle (Johnstone, 1995; Zahavi, 1975). Cette théorie suppose que, si un mâle peut produire et maintenir un trait large ou exagéré, il devrait alors être de bonne condition ou il serait en condition générale supérieure (Hamilton & Zuk, 1982; Kirkpatrick, 1996; Pomiankowski, 1987). En d'autres mots, si le mâle possède un génotype qui lui permet d'afficher et de maintenir des signaux sexuels extravagants, il aurait alors suffisamment de ressources disponibles pour en allouer à d'autres traits liés aux aptitudes phénotypiques. Par conséquent, lors de la reproduction avec un mâle qui possède des signaux héritables et une qualité supérieure, la progéniture hériterait du génotype de qualité du père et les aptitudes phénotypiques des descendants sera supérieur (Andersson, 1986; Bonduriansky, 2001; Wedell & Tregenza, 1999). Plusieurs études se sont concentrées sur les corrélations potentielles entre la condition du mâle et l'intensité des signalements par ornements (Blount *et al*, 2003; Hunt *et al.*, 2004;

Johnstone, 1995; Kodric-Brown & Brown, 1984; A.P Møller & Jennions, 2001; Parker, 1983). L'expression des traits sexuels secondaires pourrait être dépendante de la condition du mâle et s'il y a présence d'une variance entre les mâles au niveau d'un trait qui est corrélé à leur capacité d'apporter des bénéfices à la femelle, le choix de partenaire aura un impact potentiel sur les aptitudes phénotypiques des femelles (Andersson, 1994; Møller & Jennions, 2001; Møller & Pomiankowski, 1993; Pomiankowski, 1987).

Les préférences au niveau du choix de partenaire des femelles seraient dépendant des coûts et bénéfices obtenus lors de cette sélection dans une situation où les ornements des mâles sont une représentation honnête de leur qualité (Pomiankowski, 1987). Ce choix ne peut s'exprimer que lorsqu'il y a présence d'une variation suffisante entre les mâles pour que les femelles aient la capacité de détecter les différences entre les individus (Rodríguez *et al.*, 2013). Puisque les individus varient dans leur condition potentielle de partenaire, le comportement de choix de partenaire permettrait à la femelle de sélectionner un mâle de qualité supérieure par rapport aux autres individus (Parker, 1983).

Il est important de noter que le choix de partenaire sexuel effectué par les femelles ne s'effectue pas seulement par le choix de reproduction avec un mâle ou un autre, mais aussi par la résistance aux mâles non sélectionnés. La femelle se reproduira alors avec les mâles qui surpassent sa réticence et elle résistera aux autres individus (Rosenthal & Servedio, 1999). Un aspect important de la sélection de partenaire est le choix cryptique qui consiste en une sélection pré et post fécondation que les femelles effectuent pour contrôler le succès d'insémination du mâle avec lequel elles se reproduisent (Eberhard, 1996). Chez certains insectes, la femelle peut choisir le temps total de reproduction en fonction du mâle, ce qui peut affecter la quantité de sperme reçu et donc le succès reproducteur du mâle (Thornhill, 1983). Chez les grillons, la femelle peut activement retirer le spermatophore qui est attaché de manière externe lors de la reproduction (Bussière *et al.*, 2006). Ce choix cryptique actif amène l'élimination ou la réduction de la taille des éjaculats suite à l'ingestion du spermatophore, ce qui réduit le succès reproducteur du mâle (Bussière *et al.*, 2006). Au niveau post copulatoire, certaines femelles peuvent, par exemple, effectuer une sélection sur le sperme utilisé pour la fécondation de ses œufs (discriminant complètement ou partiellement un mâle) ainsi qu'influencer le développement zygotique et les soins parentaux post zygotiques (Thornhill, 1983). Les mécanismes impliqués dans le choix cryptique des femelles varient d'une espèce à l'autre et sont difficilement observables puisqu'une grande partie d'entre eux se produit à l'intérieur de l'appareil reproducteur de la femelle (Eberhard, 1996). Néanmoins, ils sont un vecteur important de sélection sexuelle.

0.1.3 Immunité

De nombreuses études ont démontré la présence de compromis chez un individu entre l'investissement dans les caractères sexuels secondaires et la capacité immunitaire (Adamo, Jensen, & Younger, 2001; Folstad & Karter, 1992; Kelly & Jennions, 2009; Leman *et al.*, 2009; López, 1998; McKean & Nunney, 2001; McNamara, Wedell, & Simmons, 2013; Tregenza, Simmons, Wedell, & Zuk, 2006). Ces compromis peuvent être occasionnés par le coût important du maintien d'un système immunitaire efficace

(Gershman *et al.*, 2010; Rantala & Roff, 2006). L'immunocompétence est l'un des nombreux facteurs qui participent à l'estimation de la qualité individuelle et des aptitudes phénotypiques (Folstad & Karter, 1992; Shoemaker & Adamo, 2007). La capacité immunitaire est donc basée sur des compromis où il y a présence d'une covariance négative entre les traits de résistance aux infections et les autres traits liés aux aptitudes phénotypiques (Jacot, Scheuber, & Brinkhof, 2004). Seuls les individus dont l'état de santé est le moins affecté par les effets négatifs d'un défi immunitaire pourront se permettre l'affichage de signaux sexuels coûteux et d'investir profusément dans leur niveau d'attirance (Jacot *et al.*, 2005). Les individus qui seraient alors favorisés par la sélection devraient avoir la capacité de répondre à diverses circonstances (comme un défi immunitaire) en altérant le niveau d'investissement entre les différents traits liés à ses aptitudes phénotypiques (Shoemaker & Adamo, 2007).

Selon la théorie de la sélection sexuelle médiée par les parasites, l'expression de traits sexuels secondaires révèle aux femelles la capacité du mâle à monter une réponse immunitaire (Hamilton & Zuk, 1982). Les signaux sexuels des mâles dépendent de l'état individuel et ils sont énergiquement coûteux à effectuer. Par conséquent, la qualité du signal tend à être diminuée lors d'une infection bactérienne (Jacot *et al.*, 2004). La théorie de la sélection sexuelle médiée par les parasites se construit sur le principe que les femelles choisissent leurs partenaires en fonction de traits sexuels secondaires indicatifs d'une capacité de résistance aux parasites. Cette sélection est effectuée afin d'octroyer à sa progéniture des gènes de résistance et de protection contre la transmission du parasite (Hamilton & Zuk 1982). Il est aussi hypothétisé que la femelle sélectionne ces traits pour choisir des partenaires sains ayant une plus grande capacité d'assistance au niveau des soins parentaux (Clayton, 1991). Alors, les femelles pourraient obtenir une progéniture avec une plus grande capacité immunitaire lors de la sélection avec des mâles attirants (Folstad & Karter, 1992; Hamilton & Zuk, 1982).

Une autre hypothèse est que la présence d'un compromis énergétique entre la capacité immunitaire et les traits sexuels secondaires résulte en une évolution vers un génotype optimal qui n'est pas nécessairement garant d'une meilleure capacité immunitaire, mais plutôt d'une balance entre défense et reproduction (Antonovics & Thrall, 1994; Sheldon & Verhulst, 1996). Les coûts d'une réponse immunitaire peuvent aussi se représenter sous forme de comportement. Par exemple, chez les grillons *Gryllus texensis*, les individus réduiraient leur taux d'alimentation après une infection bactérienne et consommeraient des aliments plus faibles en gras. La raison de ce comportement pourrait être de réduire le besoin de transport des nutriments dans le corps pour favoriser la réponse immunitaire (Adamo *et al.*, 2010). L'anorexie lors d'une infection est un comportement qui pourrait améliorer la capacité immunitaire en réduisant les coûts énergétiques liés à la digestion (Kyriazakis, Tolkamp, & Hutchings, 1998). Par exemple, les souris infectés qui étaient autorisées à être anorexiques ont une mortalité plus faible et une durée de survie supérieure que les souris dont l'alimentation était forcée (Murray & Murray, 1979).

Si la condition d'un mâle ou son habilité à acquérir des ressources nécessaires à toutes ses fonctions primaires biologiques est héritable, alors sa progéniture devrait aussi avoir un niveau d'attirance sexuelle et une immunité supérieure (Andersson, 1986; Møller & Alatalo, 1999; Wedell & Tregenza, 1999). Donc, les femelles qui sélectionnent des mâles avec de meilleurs signaux sexuels auraient des aptitudes phénotypiques accrues via celui de leur progéniture (Head, Hunt, & Brooks, 2006; Jennions & Petrie, 1997; Kokko *et al.*, 2003). Si cela s'avère être le cas, alors ceci expliquerait partiellement pourquoi les femelles préfèrent s'accoupler avec des mâles qui possèdent des signaux sexuels extravagants.

0.1.4 Longévité

La longévité d'un individu est une partie importante de ses aptitudes phénotypiques. Une longévité supérieure peut mener à un nombre accru de reproductions (Banks & Thompson, 1987; Newton, 1989; Nicola Saino *et al.*, 2012). Néanmoins, il est aussi possible qu'une haute activité sexuelle ou un signal sexuel plus intense puisse réduire la longévité des individus (Hunt *et al.*, 2004; Okada *et al.*, 2011). Le taux métabolique au repos (RMR) d'un individu joue un rôle majeur au niveau de la disponibilité des ressources pour le signalement sexuel (Biro & Stamps, 2012; Nilsson, 2002). Un individu ayant un RMR faible aura un coût de maintien somatique réduit, ce qui permettrait l'allocation d'un plus grand nombre de ressources à d'autres activités métaboliques (Reinhold, 1999). Chez le grillon *Gryllodes sigillatus,* il y a présence d'une corrélation négative entre RMR et longévité, ce qui signifierait que les individus actifs meurent plus jeunes (Okada *et al.*, 2011). Le même type de corrélation négative entre RMR et longévité est aussi présent chez le nématode *Caenorhabditis elegans* (Van Voorhies & Ward, 1999), la souris *Mus musculus* L. (Duarte & Speakman, 2014) et multiple espèces d'oiseaux (Furness & Speakman, 2008). De plus, les grillons mâles *Teleogryllus commodus* qui chanteraient plus fréquemment auraient une longévité significativement plus courte, mais un succès reproducteur plus important de par leur niveau d'attirance sexuelle (Hunt *et al.*, 2004). En somme, la présence de compromis entre attirance sexuelle et longévité pourrait être un signalement de la qualité d'un individu, de sa capacité à acquérir des ressources et de son utilisation de ces ressources.

0.1.5 Capture génétique, « good genes »

Lors du choix de partenaire sexuel, si les femelles choisissent des mâles en fonction de traits exprimant honnêtement leur condition, le succès reproducteur élevé de ces mâles conduirait à la fixation des traits et l'épuisement de la variation génétique entre les mâles (Rowe & Houle, 1996). Cette fixation annulerait les bénéfices du choix de partenaire. Pourtant, le choix de partenaire est maintenu chez de nombreuses espèces. Ce paradoxe est connu sous le nom de « Lek paradox » où il y a présence de variation génétique malgré la forte sélection préférentielle des femelles pour certains traits (Rowe & Houle, 1996).

L'hypothèse de capture génétique explique le maintien de la variance génétique interindividuelle pour les traits qui sont sous la sélection sexuelle (Rowe & Houle, 1996). Cette théorie indique que les traits affichés par les mâles sont coûteux et qu'ils sont exprimés en fonction de la condition générale de l'individu (Tomkins *et al.*, 2004). La condition d'un mâle impliquerait une vaste proportion de son génome. Parce que la condition est influencée par les allèles qui ont un effet sur la capacité d'un individu à acquérir et utiliser des ressources, le nombre total de loci influençant la condition est particulièrement large et donc propice aux mutations (Rowe & Houle, 1996). Toute mutation affectant la condition globale d'un individu aura par conséquent des effets sur l'expression de traits sexuels secondaires, ce qui amène une grande variété génétique et phénotypique entre les individus (Andersson, 1986). Une bonne condition fait référence à un animal qui possède plus de réserves énergétiques et la condition est généralement un indicateur de l'état de santé de l'animal (Schulte-Hosteddem, Millar, & Hickling, 2001).

Si les mâles augmentent leur niveau d'attirance sexuelle en investissant plus et que les coûts d'investissement sont moins proportionnellement élevés pour les mâles ayant un bassin de ressource supérieur, il y aura présence d'une covariance entre l'expression de traits sexuels secondaires et la condition du mâle qui pourra évoluer via la sélection sexuelle (Tomkins *et al.*, 2004). La théorie de capture génétique permet d'expliquer le mécanisme sous-jacent des modèles « good genes » (Møller & Alatalo, 1999) prédisant la covariance positive entre les traits sexuels secondaires et les aptitudes phénotypiques de la progéniture. Selon ces modèles, la progéniture des mâles sexuellement attirants aura des aptitudes phénotypiques supérieurs (Møller & Alatalo, 1999). De plus, deux traits dépendants de la condition chez un individu peuvent être positivement corrélés. Cette corrélation dépendra du niveau de variance génétique entre les individus dans leur capacité d'acquisition et d'allocation de ressources (Houle, 1991).

0.1.6 Acquisition et allocation de ressources

Pour étudier comment les traits sexuels secondaires signalent honnêtement la condition d'un mâle et les bénéfices que la femelle obtient lors de la sélection d'un partenaire sexuel attirant, il est important de comprendre ce qui contribue aux aptitudes phénotypiques d'un individu. La reproduction est un élément clé qui contribue à ces aptitudes, mais elle est atteignable à un certain coût, ce qui occasionne une réduction des ressources potentielles octroyées à d'autres composantes des aptitudes phénotypiques (Andersson & Simmons, 2006). Cette distribution des ressources limitées de l'individu est causée par l'allocation des ressources où, par exemple, une capacité de survie sera plus faible en réponse à une augmentation au niveau de l'effort de reproduction (Reznick, Nunney, & Tessier, 2000). La divergence au niveau des traits entre les individus est soumise à deux processus conjointement liés, soit la capacité d'acquérir des ressources et subséquemment l'allocation différentielle de ces ressources entre les divers traits (van Noordwijk & de Jong, 1986). La sélection sexuelle sera influencée différemment si la variance génétique entre les individus est plus élevée dans leur capacité d'acquérir des ressources ou plutôt dans leur allocation de ces ressources (van Noordwijk & de Jong, 1986).

Lorsqu'il y a présence d'une plus grande variance au niveau de l'allocation des ressources, les individus auront une divergence dans leur capacité à offrir des bénéfices directs aux femelles pendant la reproduction (Simmons, 2011). Néanmoins, si les mâles varient principalement dans leur capacité d'acquisition de ressources, la capacité d'obtention de bénéfices génétiques indirects pour la femelle différera entre ses partenaires potentiels (Simmons 2011). Les mâles qui ont une capacité d'acquisition de ressource supérieure, donneront une progéniture qui, elle aussi, aura un bassin de ressources plus élevé (si les traits liés à l'acquisition sont héritables). Avec un plus grand nombre de ressources disponibles, il est estimé que les descendants seront en meilleure condition (Rowe & Houle, 1996), ce qui résulte en bénéfices indirects pour la femelle (van Noordwijk & de Jong 1986).

Si les individus varient génétiquement principalement dans leur allocation de ressource, il y aura présence de corrélations négatives entre les traits liés aux aptitudes phénotypiques (van Noordwijk & de Jong 1986). Les corrélations négatives sont présentes puisqu'un individu qui investis majoritairement dans le trait A, pourra moins investir dans le trait B. Si la variance entre les individus, au niveau d'une population, est causé par des allocation de ressources divergentes, les choix de partenaire impliquera lui aussi des compromis entre trait A et B pour la progéniture (si les traits sont héritable). Tandis que s'ils varient principalement dans leur capacité d'acquisition de ressources, il y aura présence d'une corrélation positive entre deux traits liés aux aptitudes phénotypiques de l'individu puisque la qualité de leurs gènes leur accorde une capacité supérieure à obtenir et transformer les ressources (van Noordwijk & de Jong 1986). Dans cette situation, les mâles ayant un plus grand bassin de ressources pourront investir plus dans leurs traits sexuels secondaires (Møller & De Lope, 1994). Subséquemment, les mâles attirants, porteurs de ces gènes qui accordent une meilleure capacité d'acquisition de ressources, donneront à leur progéniture des gènes qui affectent positivement les traits liés à leur aptitudes phénotypiques. Donc, les femelles sélectionnant les mâles attirants recevraient des bénéfices indirects via le choix de partenaire (Simmons 2011).

Si les individus varient génétiquement principalement dans leur capacité d'acquisition de ressource, la théorie de van Noordwijk & de Jong (1986) prédit la présence d'une covariation positive entre deux traits liés aux aptitudes phénotypiques. Les mâles ayant un bassin de ressources plus important pourront investir dans deux traits liés aux aptitudes phénotypiques qui compétitionnent pour les ressources (van Noordwijk & de Jong 1986). Ils pourraient, par exemple, avoir plus de ressources pour être attirants face aux femelles via l'expression de traits sexuels secondaire et ils auraient conjointement une meilleure capacité immunitaire (Hunt *et al.*, 2004; Kelly, Telemeco, & Bartholomay, 2015). En alliant l'hypothèse de la sélection sexuelle médiée par les parasites à une situation où les individus varieraient génétiquement principalement dans leur capacité d'acquérir des ressources, il y aurait présence d'une covariation positive entre la capacité immunitaire et l'expression de traits sexuels secondaires. Ceci permettrait aux femelles d'obtenir des bénéfices indirects par le choix de partenaire en se basant sur l'expression des traits sexuels secondaires comme signalement de la qualité. La présence de corrélation positive entre les traits sexuels secondaires et l'immunité fut observée dans plusieurs études empiriques (Blount *et al.*, 2003; Jacobs & Zuk, 2011; Kelly & Jennions, 2009; Rantala & Kortet, 2004; Saino, Bolzern, & Møller, 1997).

0.1.7 Conflit sexuel

Les bénéfices indirects obtenus par le choix de partenaire peuvent avoir des effets différents d'un descendant a l'autre. Ceci implique que les gènes obtenus suite à la reproduction avec un mâle en condition supérieure, pourraient avoir des effets bénéfiques sur une partie de la progéniture et néfaste sur l'autre (van Doorn, 2009). Selon ce concept du conflit sexuel intralocus, les mâles et les femelles peuvent avoir une différente expression optimale pour un même trait, conséquemment les génotypes amenant des aptitudes phénotypiques élevé chez un mâle, ne seront pas nécessairement garant de qualité chez la femelle (Katsuki *et al.*, 2012). La sélection de partenaire soumise à un conflit sexuel intralocus est alors associée à une corrélation génétique entre les deux sexes, qui pourrait conduire au ralentissement ou à la limitation de la capacité d'évolution du sexe antagoniste. Cette situation peut entraîner une corrélation intersexuelle négative des aptitudes phénotypiques (van Doorn, 2009). Néanmoins, une synthèse d'études faite sur 114 articles et chapitres de livres a conclus que la majorité des corrélations génétiques exprimées chez les mâles et femelles pour des traits homologues sont positives (Poissant, Wilson, & Coltman, 2010).

La divergence entre les sexes et l'anisogamie conduit à des optima spécifiques au sexe pour de nombreux traits liés à sélection sexuelle. Ce concept peut néanmoins mener à des adaptations indépendantes entre les sexes et une spécialisation (Chapman, Bangham, & Rowe, 2003). Le conflit intralocus peut aussi apporter des coûts supérieurs au niveau du choix de partenaire, puisque la reproduction avec un mâle de qualité pourrait entraîner une progéniture mâle et femelle de qualité opposée. Par exemple, il est fréquent que les mâles puissent sacrifier leur longévité dans l'objectif d'avoir un succès reproducteur accru, alors que le succès reproducteur des femelles est limité par le temps. Ici, une longévité supérieure n'aura pas le même impact au niveau des aptitudes phénotypiques des mâles et des femelles (Bonduriansky *et al.*, 2008).

CHAPITRE I

THE DIRECT AND INDIRECT BENEFITS TO FEMALES OF MATING WITH SEXUALLY ATTRACTIVE MALES

The different benefits obtained through mate choice have been the focus of a large number of sexual selection studies. Whether females gain genetic benefits for their offspring depending on their mate choice is a contentious subject. In this study we use a global indicator of male's attractiveness using the latency for a female to mount him and start the copulation in the sand field crickets, *Gryllus firmus* to observe the potential direct and indirect benefits of mate choice. Firstly, we study if attractive males have a superior disease resistance and longevity. Secondly, we observe the direct and indirect benefits of the female's mate choice and the effects of sire's traits on offspring. Finally, we look into a potential intralocus sexual conflict and the heritability of mass, pronotum size, scaled mass index, time to reach maturity, attractiveness and disease resistance. We observed that males who eclosed to adulthood more quickly were in better body condition but contrary to prediction, a male's attractiveness was not correlated with his disease resistance or longevity. Attractive males were also in better body condition and their pronotum was smaller. Male attractiveness did not seem to impact female's reproductive output, but attractive males produced bigger sons. The time to reach maturity was strongly heritable and males who matured slower had offspring of superior size. Our results emphasize the complexity to observe the indirect genetic benefits from mate choice and the need for further research on the use of global measures of sexual attractiveness.

1.1 Introduction

Few topics in evolutionary biology are as controversial as why females prefer mates that display showy, and presumably costly, ornaments (Andersson, 1994; Arnqvist, 2006; Jennions & Petrie, 1997; Kirkpatrick, 1996; Kokko *et al.*, 2003). A common explanation is that costly male ornaments advertise the potential benefits that a female would receive by mating with that male. The controversy, however, surrounds whether costly mate choice evolves via direct (i.e. material) or indirect (i.e. genetic) benefits.

Direct benefits are hypothesized to improve female fitness because males signal their ability to provide the female with superior resources, good parental care or access to better territories (Andersson, 1994; Kirkpatrick & Barton, 1997; Kirkpatrick, 1985, 1996; Møller & Jennions, 2001). Costly mate choice can also evolve if females gain indirect benefits for their offspring from their mate choice. Models of sexual selection generally propose that male secondary sexual characters advertise a male's general condition and genetic quality (Folstad & Karter, 1992; Smith, 1991; Weatherhead & Robertson, 1979; Zahavi, 1975) and so, by preferring more-attractive males, females are expected to improve the viability and health of their offspring (Simmons, 1987). The indirect benefits of mate choice are expected to be small relative to the direct benefits that females gain by mating with an attractive male (Kirkpatrick & Barton, 1997; Kirkpatrick, 1996). However, empirical studies do indeed support the hypothesis that female preferences can improve the viability of their offspring. For example, offspring sired by attractive males had increased longevity in *Parus major* (Norris, 1993), offspring of field crickets *Gryllus bimaculatus* showed lower risk of mortality (i.e. lower variance in survival) (Simmons, 1987) and faster development to adulthood was observed in the fish *Poecilia reticulata* (Reynolds & Gross, 1992), the cockroach *Nauphoeta cinereal* (Moore, 1994) and tree frogs *Hyla versicolor* (Welch, Semlitsch, & Gerhardt, 1998). Also, sons of sexually attractive crickets *Gryllus bimaculatus* showed superior reproductive success (Wedell & Tregenza, 1999) and offspring sired by *Pavo cristatus* peacocks having more eyespots on their tail survived better than offspring sired by males having fewer eyespots (Petrie, 1994).

These examples highlight the additive genetic benefits of mate choice. Nonadditive genetic benefits via compatible or complementary genes can confer greater disease resistance on offspring (Howard & Lively, 2004). When female mate with males with whom they share the fewest alleles across loci, females produce heterozygous descendants with particular combinations of maternal and paternal alleles that can affect offspring fitness (e.g. by masking deleterious alleles) (Mays Jr & Hill, 2004).

In contrast to the hypothesis that female preferences generally improve offspring viability (e.g. good genes hypothesis), considerable empirical and theoretical evidence has accumulated over the past several decades showing that female mate preferences can affect offspring fitness in sex-specific ways (e.g. Parker, 1979; Rice, 2000; Chippindale, Gibson and Rice, 2001; Bussière *et al.*, 2006; Foerster *et al.*, 2007; Katsuki *et al.*, 2012). This situation will arise whenever the two sexes have different evolutionary optima for a given trait (i.e. the conflict trait); a phenomenon called intra-locus conflict arises when the same genetic locus influences the conflict trait in males and females. Therefore, under this hypothesis alleles that are beneficial (e.g. confer greater sexual attractiveness) in males should be detrimental in females and vice versa but often empiricists test an effect in one sex only (Gibson, Chippindale, & Rice, 2002). The predicted negative correlation between father and daughter fitness does not necessarily mean that sexy fathers will produce sexy sons as this will depend on the species' sex determination system. In both the XY (and XO; e.g. crickets) and ZW (e.g. birds) chromosomal sex-determination systems, the daughters of females preferring attractive males will suffer fitness costs (but the costs are less in the ZW system) (van Doorn, 2009). Although sons in XY systems will never inherit their father's attractiveness if the trait is X-linked, sons in ZW system will inherit their father's attractiveness if the trait is Z-linked (Albert & Otto, 2005). Therefore, the sexy son hypothesis (the Fisher process) is more likely to be supported in ZW rather than XY (or XO) systems (van Doorn, 2009). Contrary to this prediction, however, Head *et al.* (2006) found that male *Acheta domesticus* crickets (an XO system) having greater sexual attractiveness sired sons with greater sexual attractiveness. Similarly, Fedorka and Mousseau (2004) found that successful male *Allonemobius socius* crickets sired sons with significantly higher mating success but daughters with significantly lower reproductive success than unsuccessful males. Because males do not transmit their X chromosome to their sons, these results indicate that the sexually antagonistic variation was likely autosomally inherited. The frequency of autosomal inheritance of sexually selected traits among animal taxa is not known but evidence suggests that X-linked inheritance is very common (Reinhold, 1998).

One trait that plays a significant role in conferring superior fitness to offspring is immunocompetence, which is defined as the ability of an individual to immunologically resist pathogens or parasites (Goldsby, Kindt, & Osborne, 2000). Multiple studies have shown that the expression of sexual traits trades-off with immunity (Ahmed *et al.*, 2002; Blount *et al.*, 2003; Gershman *et al.*, 2010; Jacot *et al.*, 2004; McKean & Nunney, 2008; McNamara *et al.*, 2013; Rantala, Vainikka, & Kortet, 2003; Rolff & Siva-Jothy, 2002). This is not surprising because individuals need to supply all of their fitness-related traits from a single pool of resources (van Noordwijk & de Jong, 1986). However, van Noordwijk and de Jong (1986) highlighted that some individuals will have a greater pool of resources (i.e. be in better condition: Rowe and Houle, 1996) than other males due to superior resource-acquisition. If males differ in their pool of available resources while similarly partitioning their resources amongst fitness-related traits, then the expression of any two traits will positively covary among individuals. Thus, for example, the expression of the sexually selected trait(s) will covary with immunocompetence. Indeed, theories of parasite-mediated sexual selection posit that females inspect male ornaments in order to gather reliable and honest information on the male immune system because males with superior ornaments should have superior immunocompetence (Andersson, 1994; Andersson, 1986; Hamilton & Zuk, 1982; Kodric-Brown & Brown, 1984; Parker, 1983; Rowe & Houle, 1996; Sheldon *et al.*, 1997). Therefore, by choosing males with more-elaborate sexual signals, females accrue indirect benefits in the form of heritable resistance to disease for their offspring (Hamilton & Zuk, 1982). Although there are few empirical examples supporting this hypothesis, Raveh *et al.* (2014) showed that more-attractive house mice *Mus musculus musculus* sired offspring having enhanced disease resistance to *Salmonella enterica* and Barber *et al.* (2001) showed that the offspring of more brightly coloured male sticklebacks *Gasterosteus aculeatus* had greater survivorship to infection by *S. solidus* (Barber *et al.*, 2001).

In this study, we examine the relationship between sexual attractiveness and fitness-related traits in male crickets *Gryllus firmus* (Orthoptera: Gryllidae), and then test whether this relationship affects female mate choice for direct and indirect fitness benefits. In crickets, preferred song components correlate positively with haemocyte load (Ryder & Siva-Jothy, 2000) and encapsulation (Rantala & Kortet, 2003; Simmons, Zuk, & Rotenberry, 2005), two important components of cricket immunocompetence. These results indicate that female choice might select males with higher pathogen resistance ability. In addition, mating with attractive males might benefit sons more than daughters. In the cricket, *Allonemobius socius*, successful sires (i.e. males that were chosen by the female and completed the copulation) produced sons with higher mating success, but daughters with reduced fecundity (Fedorka & Mousseau, 2004).

First, we test the parasite-mediated sexual selection hypothesis that if the genetic variance in resource acquisition is greater than the variance in resource allocation then males having greater sexual attractiveness should acquire more nutritional resources for allocation to competing fitness-related traits (e.g. sexual signaling, immunocompetence) than less attractive males. This hypothesis, therefore, predicts that more-attractive males should be more disease resistant than less attractive males. Secondly, we test the hypothesis that this positive covariance between male attractiveness and immunocompetence provides females with the means to acquire indirect genetic benefits for their offspring in the form of disease resistance. We predict that more-attractive fathers will sire offspring having greater disease resistance than less-attractive fathers. Our experimental design will also allow us to test the more general condition-dependent hypothesis that if males reliably signal their genetic quality (i.e. the ability to acquire more resources), then females choosing to mate with more-attractive males will acquire good genes for their offspring, including genes promoting attractiveness (i.e. produce sexy sons) and viability (e.g. development time, size at maturity). We predict that more-attractive fathers will sire more-attractive sons as well as offspring having faster development and larger size at maturity (two traits that promote survival in crickets) than the offspring of less-attractive fathers. Finally, rearing sons and daughters of known sire-attractiveness also permits us to test whether genes conferring sexual attractiveness in males are sexually antagonistic. We predict that intralocus sexual conflict will be absent in crickets because sexual antagonism will preclude the production of immunocompetent daughters by attractive males, which is contrary to the expectation that females are more immunocompetent than males across animal taxa (Rolff, 2001; Zuk & McKean, 1996). The presence of intralocus sexual conflict would be marked by attractive sires having sons with greater disease resistance than daughters (if there is autosomal trait linkage; Fedorka and Mousseau 2004) or daughter and sire disease resistance being negatively correlated (if sex traits are X-linked). If females receive direct benefits via ejaculate components (Worthington & Kelly, 2016), then females mating with more-attractive males should have greater reproductive success (in the form of fertility, fecundity or egg size) than females who mate with less-attractive males.

1.2 Methods

1.2.1 Cricket rearing and husbandry

The sand field crickets, *Gryllus firmus*, used in this experiment were the descendants of crickets originally collected in Florida by K.A. Judge (MacEwan University, Edmonton, Alberta, Canada). Individuals were reared in an environmental chamber at Université du Québec à Montréal (UQAM), Québec, Canada under standard conditions (28°C, 50% relative humidity, 12h light:12h dark-light cycle). Crickets were maintained in groups of 50-100 individuals in 70L plastic bins containing several cotton-plugged water vials and *ad libitum* cat food (Iams™ Proactive Health™), and layers of egg cartons for shelter. Penultimate-instar nymphs were isolated into individual plastic deli containers (approximative length: 17cm, width:11.8cm, height: 5.4cm) with cat food, a water vial, and a small piece of egg carton, and maintained under standard environmental conditions.

1.2.2 Body mass, pronotum, time to mature of parents and offspring

A total of 699 individuals reached maturity. Individually housed nymphs were checked daily for newly-eclosed adults. At eclosion to adulthood, we recorded the date to calculate the time required to reach adulthood and we weighed the cricket to the nearest 0.1 mg on a Sartorius Secura 224-1S analytical balance. Length of the pronotum (a proxy of structural size in crickets; Kelly, Tawes & Worthington, 2014) was measured in the middle of the individuals as the distance from the anterior to posterior extremities of the pronotum and the width was measured as the distance between the right and left edges of the pronotum. Pronotum size was measured after the cricket's death. Preserved insects were digitally photographed with a Leica MS5 microscope (Leica Microsystems Inc., Concord, ON, Canada) and an SC170 HD camera. The LAS V4.5.5 software (Leica Application Suite) was used to digitally stamp a scale bar on each picture. Finally, these pictures were imported into ImageJ (Java 1.6.0_65, National Institutes of Health, USA) to measure the pronotum length.

1.2.3 Attractiveness trials

Even though most studies on sexual attractiveness in crickets have focused on one or a small subset of male traits or signals, attractiveness is thought to comprise numerous behavioral, chemical and physiological traits (Bussière *et al.*, 2006; Shackleton, Jennions, & Hunt, 2005; Simmons *et al.*, 2013). Factors like the body size (Bertram & Rook, 2012), coloration (Milinski & Bakker, 1990), different variables of the courtship songs; like chirp rate or amplitude (Holzer, Jacot, & Brinkhof, 2003; Simmons *et al.*, 2013; Tregenza *et al.*, 2006), call frequency (Hunt et al., 2004) or pheromone profile (Tregenza & Wedell, 1997) influence sexual attractiveness.

In *Gryllus firmus,* females appear to control mate choice and males follow a stereotypical pattern of courtship behavior. Males will start by touching the female with their antennas and slowly moves towards the female presenting their back. Males will then produce a courtship song after an established contact with a female (Simmons *et al.*, 2013). Cricket's courtship songs are also energetically expensive for males to produce and are believed to convey information about the male quality (Zuk, Rebar, & Scott, 2008). If the female accepts the male, she will mount him, align her genital organs and the male will proceed to the insertion of an epiphallus into the female's genital chamber. After a few seconds, if the female stays mounted on the male, the male will withdraw the epiphallus and only the spermatophore will stay attached to the female (Bussière *et al.*, 2006).

A more comprehensive approach to study mate choice than using specific sexual secondary traits in *Gryllus firmus* is to conduct no-choice tests. No-choice trials are a reliable predictor of a male's mating success (Bussière *et al.*, 2006). No-choice tests allow females to select their partner based on all the physical and chemicals cues males offer. In tests where the female has a choice, male-male competition should be avoided if the objective is to striclty study female mate choice and not male-male competition (Shackleton et al., 2005). However, tests that allow choice and control for male-male interactions usually place the males behind glass or mesh. In those tests, the lack of physical contact with the female can lead to the males behaving abnormally and/or the female having reduced information about the male (Shackleton et al., 2005). The value used to observe the level of sexual attractiveness of a male in this test is the time needed for a female to mount the male. Virgin individuals were used and they were tested between 7 to 14 days after reaching the last instar. The female cricket was placed into a 10cm diameter round plastic container 10 minutes before the male to acclimate. The bottom of the container was covered with filter paper and changed between each trial. The male was then placed within 2cm of the female in the container. The time from the moment the male was introduced in the same habitat as the female until she mounted him and stayed mounted for over 5 seconds was noted as the time to mount. These trials were done between 9 am and 1 pm in a quiet dark room. The only light source used during the trials was a red light to facilitate the manipulations.

Using the time to mount as a variable is an effective way to estimate the level of sexual attractiveness of a male (Bateman 1998; Head *et al.* 2005; Shackleton *et al.* 2005; Bussière *et al.* 2006). Female mated status (mated or virgin) can influence mate choice and their latency to mate (Savalli & Fox, 1998). Females and males were used only once per trial to make sure each individuals were tested during their first sexual encounter. The scaled mass index (SMI) is a reliable index of body condition in crickets (Kelly, Tawes & Worthington, 2014). Here, SMI was calculated for 419 individuals using body mass and pronotum length.

1.2.4 Eggs and offspring

After the attractiveness trials and the completion of the copulation, crickets were left together for 15 minutes. Each female was placed individually into a 2-L plastic container with 30g of moist sand for 5 days to allow them to lay eggs. After the attractiveness trial, males were placed in individual deli-cups and then either received a host resistance test (see below) or observed until death to determine longevity (see below). After 5 days, females were frozen and the sand containing the eggs was delicately placed in a plastic tray with 200mL of water to maintain eggs in a moist environment. From this sample, 10 eggs were preserved in ethanol (95%) and kept in the freezer for later measurements of length and width (using methods described above). Egg size was used as a measure of egg quality because egg size is a proxy for egg investment and therefore egg quality (Stahlschmidt & Adamo, 2015). Egg size can also be correlated to offspring size at hatching and other early fitness related traits in crickets (Weigensberg, Carrière, & Roff, 1998). An additional 40 eggs were replaced in moist sand and checked daily until hatching. The percentage of eggs that hatched was used as a measure of female fertility. The day of hatching was recorded for each offspring. Families of hatchlings were kept in a 2-L container with food, water, and shelter until their penultimate instar (families larger than 10 hatchlings were kept in 6-L containers). Size at maturity and time to maturity were recorded for each offspring. The sand was then dried at room temperature, the eggs sieved out and counted to obtain a measure of total fecundity. Two females were removed from the dataset because they did not mount the male within the 2-hour limit. A total of 54 couples was observed for fecundity and fertility. Only 49 females were assessed for egg size because 5 females laid fewer than 40 eggs. For each female, 10 eggs were measured for a total of 490 eggs.

1.2.5 Disease resistance

Immunocompetence is a complex trait to measure due to its numerous components (Rantala & Roff, 2005; Saino *et al*., 1997). A common approach used by workers is to assay multiple effector systems such as encapsulation capacity (Cotter & Wilson, 2002; Simmons, 2011), phenoloxidase activity (Mucklow *et al.*, 2004), gamma globulin levels (Saino *et al*., 1997) and lysozyme-like activity (Adamo, 2004) just to name a few. Another method is to challenge the immune system and measure the effects of the challenge on some fitness-related trait with the expectation that individuals suffering smaller decreases have better immunocompetence. The best method, however, is to directly test the resistance of a host by infecting it with a living pathogen which allows the estimation of the immune system as a whole (Adamo, 2004). We measured the immunocompetence of *G. firmus* in this study by using host resistance tests. We measured survival of individual crickets after injection (2µl volume) with an LD50 dose of *Serratia marcescens* ($2.5\text{x}10^5$ cells/µl). We use *S. marcescens* because it is a common soil microbe and potentially a natural pathogen of G. *firmus* (Shelley A Adamo et al., 2001; Stevenson, 1959). On the day after an attractiveness trial, we used a 10µL Hamilton® syringe to inject crickets with *Serratia marcescens* (Carolina Biological Supply Company, Burlington, North Carolina) through the pronotal membrane under the pronotum. Injections were carried out under sterile conditions in a biosafety cabinet (BSC). Crickets were then isolated in individual containers in an incubator at 28°C with the survival status (0=dead, 1=alive) being recorded after 24 h. We could test the disease resistance of 17 families only due to permitting issues;

consequently, we tested the longevity of the remaining 22 families. Eleven females failed to have any offspring hatch and one female did not lay eggs.

1.2.6 Statistical analysis

First, the relation between attractiveness (as the independent variable) and the time to reach adulthood (response variable) was assessed by a Poisson generalized linear mixed-effects model. We also tested if pronotum length and the scaled mass index of attractive males were significantly different than unattractive males using a generalized linear mixed-effects model with pronotum length and scaled mass index as fixed effects and the male ID as random effect. The response variables were the pronotum length and scaled mass index while the independent variable was the attractiveness. We also tested the prediction that attractiveness positively covary with disease resistance by using a generalized binomial linear model with male attractiveness (independent) and disease resistance (response) as fixed effects and male ID as random effect. A similar model was run with pronotum length, SMI (independent variables) and disease resistance (response variable) as fixed effects and male ID as the random effect. Likewise, to test the prediction that attractive males have a superior longevity, we ran a negative generalized binomial linear model with male attractiveness (independent variable) and longevity (response variable) as fixed effects and male ID as random effect. To measure if pronotum length and SMI covaries with longevity we ran another similar model using the pronotum length and the SMI (independent variables) and longevity (response variable) as a fixed effects and male ID as random effect. We ran Poisson regressions when our response variable was count data. When testing the disease resistance as a response variable, we used binomial models because each of our independent disease resistance trial resulted in two possible outcomes (either 1 if the cricket survived, or 0 if he died). It is important to note that we use this direction of effects (e.g. disease resistance as a response and attractiveness as the independent variable) because we are testing the variance in resource allocation. We are predicting that males having greater sexual attractiveness should acquire more nutritional resources for allocation to competing fitness-related traits, therefore, more-attractive males should be more disease resistant than less attractive males. We are not testing if greater disease resistance is more attractive to females.

Second, we measured female fertility, fecundity and egg size in separate models. These measurements are used to study the direct benefits females gain from mate choice. We reduced egg length and width to a principal component (PC1) to obtain a measure of egg size. We ran three models to test the effect of female morphology on her reproductive output. We used a Poisson generalized linear mixed-effects model to measure the relationship between fecundity and female morphology using the total number of eggs (response variable), female SMI, female pronotum width and female pronotum length (independent variables) as fixed effects and female ID as a random effect. The same model was done for fertility by replacing the total number of eggs by the total number of descendants. Then, we ran a linear mixed-effects model to measure the relationship between egg size and female morphology using the PC1 of egg size (response variable) with the same independent variables and random effect than the last two models. To measure the effect of male traits on female reproduction we ran another three models. We ran a Poisson generalized linear mixed-effects using the total number of eggs (response variable), the mate SMI, mate attractiveness and mate pronotum length (independent variables) as fixed effects and mate ID as a random effect. The same model was done for fertility by replacing the total number of eggs by the total number of offspring. Then, we ran a linear mixed-effects model to measure the relationship between egg size and mate traits using the egg size (response variable) with the same independent variables and random effect the last two models. We also did three models to test the difference between reduced and full models. The first Poisson generalized linear mixed-effects model used fecundity (response variable), egg size, mate attractiveness, mate pronotum length, mate SMI, female pronotum length and female SMI (independent variables) as fixed effect and family as random effect. The second model was a Poisson generalized linear mixed-effects model using the same fixed and random effect but fecundity was replaced by fertility as the response variable. Lastly, the egg size (as the response variable) was tested with a linear mixed-effects using male attractiveness, male pronotum length, male SMI, female pronotum length, female SMI, female fertility and female fecundity as independent variables and family as random effect.

Third, we tested the prediction that attractive males would sire offspring of higher quality using linear mixed-effects models for mass, pronotum length, scaled mass index and attractiveness. Poisson generalized linear mixed-effects models were done to observe offspring's time to eclose to adulthood in function of sire's traits and generalized binominal linear models for offspring's time to eclose to adulthood in function of offspring's disease resistance. Sire traits were entered as the independent variables and offspring traits as the response variables. In these models, the mass, pronotum length, scaled mass index, attractiveness and time to eclose to adulthood were the fixed effects and the family was used as the random factor. All the models were firstly done with every offspring pooled, then re-run with a subset of the data using only the male offspring and lastly re-run using only the female offspring.

Finally, we measured the heritability of attractiveness (sons only), body mass, pronotum length, SMI, development time and disease resistance by performing sire-offspring and mid-parent regressions using linear mixed-effects models. In our regression models, we entered the offspring trait value as the response variable, the sire (or mid-parent) trait value as the independent variable, and family ID as the random effect (because there were multiple offspring per family). Midparent values were the average value of the mother and father trait value. All models satisfied the assumption of a gaussian distribution except development time (Poisson distribution) and disease resistance (binomial distribution). Sire-offspring regressions permitted the partitioning of the maternal and paternal contributions to offspring phenotype. If sire traits are heritable and correlate with offspring traits, we assume that paternal contributions have an effect on offspring phenotype. Finally, h^2 is calculated as twice the slope of a regression of the same trait of sire (independent variable) and offspring (response variable).

All statistical analyses were completed using the statistical environment R, Version 1.1.453 (R Core Team, 2017). Values are statistically significant at $\alpha = 0.05$. The attractiveness of males was accessed for 259 crickets. A total of 205 offspring (102 daughters and 103 sons) from 54 different families were used to calculate the effects of sire's traits on progeny (see Annexe A).

1.3 Results

1.3.1 Correlations amongst fitness-related traits

Males that eclosed to adulthood more quickly were in better body condition (SMI; z=-2.327, n=274, p=0.02). In contrast, we did not observe significant relationships between development time and any other fitness-related trait (body mass z=-1.87, n=402, p=0.062; pronotum length z=1.516, n=274, p=0.129; attractiveness (z=0.98, n=258, p=0.327; disease resistance z=1.112, n=178, p=0.266; longevity z=-1.82, n=89, p=0.069).

Contrary to prediction, male sexual attractiveness was not correlated with disease resistance (binomial regression: z=0.090, n=167, p=0.929) or longevity (negative binomial regression: z=0.876, n=89, p=0.381) (Figure 1). The results were not qualitatively affected when attractiveness data above 15 min (n=5) were excluded. However, male sexual attractiveness (faster time to mount equals more sexually attractive) positively covaried with adult condition (SMI) because time to mount negatively covaried with SMI (linear mixed-effects: t=-2.039, n=257, p=0.042) and negatively covaried with pronotum length (linear mixed-effects: t=2.313, n=257, p=0.022). Male attractiveness did not covary with development time (generalized Poisson linear mixed-effects: z=0.98, n=258, p=0.327). The large variation between time to mount (i.e. 0.1 min to 60 min) causes some great variation between attractive and unattractive males in the data analysis.

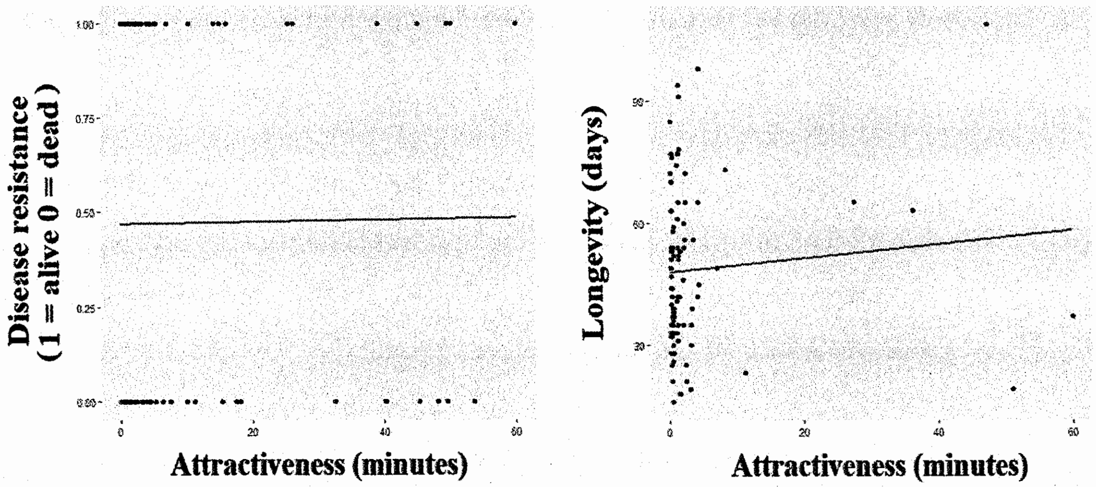

Figure 1.1 Relations of males *G. firmus* disease resistance capacity (n=167) and longevity (n=89) in function of their attractiveness. The left panel is a generalized binominal linear mixed-effects model of disease resistance and the right panel is a negative generalized linear mixed-effects model of longevity in relation to the latency for a female to mount the male.

We also found that neither pronotum length [disease resistance (binomial regression): z=-1.836, n=177, p=0.063; longevity (negative binomial regression): z=1.262, n=89, p=0.207)] nor SMI [disease resistance: z=-1.799, n=177, p=0.072; longevity: z=-0.919, n=89, p=0.376] covaried with disease resistance or longevity.

1.3.2 Direct benefits of male and female morphology on female reproduction

We did not find any effects of female morphology (pronotum width, pronotum length and body condition) or mate morphology (pronotum length and body condition) on female reproductive output (Tables 1.1 & 1.2). Male attractiveness did not have a significant effect on female reproductive traits (i.e. fecundity, fertility, or egg size) (Table 1.2). We also ran three different models to investigate the potential differences between reduced and full models. We included female and male traits in the same model as independent variables and fertility, fecundity or egg size as response variables. The only significant difference we observed was that female pronotum length positively correlated with fecundity in our full model ($z=2.038$, $n=49$ families $p=0.042$). This Poisson generalized linear mixed-effects model used fecundity (response variable), egg size, male attractiveness, male pronotum length, male SMI, female pronotum length and female SMI (independent variables) as fixed effects and family as a random effect.

Table 1.1 Generalized linear mixed-effects models of female *G. firmus* morphology (pronotum width, pronotum length, SMI) on female reproduction (fecundity, fertility, egg width, egg length)

Predictors	N	Estimate	SE	z/t	p
(a) Fecundity (total eggs)					
Female pronotum width	54	0.052	0.219	0.237	0.813
Female pronotum length	54	-0.062	0.204	-0.302	0.763
Female SMI	54	0.235	0.188	1.251	0.211
(a) Fertility (total offspring)					
Female pronotum width	54	-0.090	0.277	-0.324	0.746
Female pronotum length	54	-0.328	0.257	-1.277	0.202
Female SMI	54	0.286	0.279	1.023	0.306
(a) Egg size (PC1)					
Female pronotum width	49	0.030	0.131	0.228	0.821
Female pronotum length	49	-0.851	0.124	-0.687	0.496
Female SMI	49	-0.159	0.108	-1.470	0.148

A separate generalized linear mixed-effects model was fit for fecundity and fertility (a, b). A linear mixed-effect model was run for egg size after reducing egg width and egg length using the PC1 as an estimate of egg size (c). The models a and b have z-values and the model c has a t value. Here fecundity is referring to the total of eggs the female laid in 5 days after one copulation with a virgin male. The fertility is the total of offspring hatched from the 40 eggs that were replaced into wet sand after the 5 days laying period. N= the number of females. SMI=Scaled mass index. * p=<0.05

Table1.2 Generalized linear mixed-effects models of male (mate) *G. firmus* traits (attractiveness, pronotum length, SMI) on female reproduction (fecundity, fertility, egg width, egg length)

Predictors	N	Estimate	SE	z/t	p
(a) Fecundity (total eggs)					
Mate attractiveness	54	0.154	0.170	0.904	0.366
Mate pronotum length	54	-0.038	0.207	-0.182	0.855
Mate SMI	54	0.139	0.210	0.660	0.509
(a) Fertility (total offspring)					
Mate attractiveness	54	0.173	0.256	0.677	0.498
Mate pronotum length	54	-0.529	0.321	-1.647	0.099
Mate SMI	54	-0.027	0.322	-0.084	0.938
(a) Egg size (PC1)					
Mate attractiveness	49	-0.058	0.098	-0.592	0.557
Mate pronotum length	49	-0.039	0.123	-0.317	0.752
Mate SMI	49	-0.165	0.122	-1.351	0.184

A separate generalized linear mixed-effects model was fit for fecundity and fertility (a, b). A linear mixed-effect model was run for egg size after reducing egg width and egg length using the PC1 as an estimate of egg size (c). The models a and b have z-values and the model c has a t value. Here fecundity is referring to the total of eggs the female laid in 5 days after one copulation with a virgin male. The fertility is the total of offspring hatched from the 40 eggs that were replaced into wet sand after the 5 days laying period. N= the number of females. SMI=Scaled mass index. * p=<0.05

1.3.3 Indirect benefits

If females mate with attractive males to acquire indirect genetic benefits for their offspring then there should be positive covariance between male (sire) attractiveness and offspring quality observed from a negative covariance with time to mount. In line with prediction, more-attractive males sired larger offspring (both sexes pooled) (t= -0.105, n=39, p=0.012). It is important to remember that our value for attractiveness is the time for a female to mount the male and a higher number is an estimation of a less attractive male. However, contrary to prediction, the offspring of more-attractive males did not have superior disease resistance, body condition, attractiveness (sons only), or faster development (Tables 1.3, 1.4, 1.5). Interestingly, sire having longer development times produced offspring that were larger (pronotum length: t= 0.217, n=39, p=0.027), heavier (adult body mass: t= 0.293, n=39, p=0.002), and in better body condition (SMI: t= 0.142, n=39, p=0.03) as adults than sires who required less time to eclose to adulthood (Table 1.3). Also, bigger males (mass and pronotum length) had offspring with smaller development time (adult body mass: t= -0.032, n=39, p=0.004, pronotum length: t= -0.06, n=39, p=0.005).

Table 1.3 The effects of sire phenotype and life-history traits on six fitness components in offspring (both sexes pooled)

	Sire trait																	
	Mass			Pronotum length			SMI			Development time			Attractiveness			Disease resistance		
Offspring trait	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p
Mass				-0.261 ± 0.13	39	0.058	0.090 ± 0.14	39	0.533	0.293 ± 0.09	39	0.002*	-0.194 ± 0.11	39	0.098	-0.010 ± 0.13	17	0.448
Pronotum length	-0.089 ± 0.10	39	0.372				0.070 ± 0.14	39	0.635	0.217 ± 0.09	39	0.027*	-0.105 ± 0.04	39	0.012*	-0.118 ± 0.13	17	0.371
SMI	-0.053 ± 0.07	39	0.439	-0.114 ± 0.10	39	0.252				0.142 ± 0.06	39	0.03*	0.473 ± 0.86	39	0.584	0.024 ± 0.11	17	0.828
Development time	-0.032 ± 0.02	39	0.004*	-0.06 ± 0.02	39	0.005*	0.017 ± 0.02	39	0.483				-0.008 ± 0.02	39	0.679	-0.025 ± 0.02	17	0.296
Attractiveness	0.075 ± 0.11	33	0.504	0.092 ± 0.16	33	0.566	0.011 ± 0.16	33	0.944	0.046 ± 0.10	33	0.659				0.098 ± 0.20	17	0.627
Disease resistance	-0.213 ± 0.17	36	0.2	-0.244 ± 0.25	36	0.321	-0.140 ± 0.24	36	0.566	-0.016 ± 0.16	36	0.918	-0.175 ± 0.20	36	0.392			

A separate linear mixed-effects model was fitted for each relationship (family ID was entered as the random factor) when the response variable was mass, pronotum length, SMI or attractiveness. For models with development time as the response variable, a Poisson generalized models were run for each relationships and binomial generalized models for disease resistance. The first value is the estimate (slope) ± SE. n = the number of families. Grayed cells show significant correlations. All the correlations were made using sires traits (horizontal) as the independent variable and offspring's (vertical) traits as the dependable variable. SMI=Scaled mass index. * p=<0.05.

Table 1.4 The effects of sire phenotype and life-history traits on six fitness components of sons.

Sire trait	Mass			Pronotum length			SMI			Development time			Attractiveness			Disease resistance		
Offspring trait	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p
Mass				-0.080 ± 0.13	34	0.548	0.211 ± 0.14	34	0.138	0.335 ± 0.14	34	0.021*	-0.262 ± 0.11	34	0.017*	-0.098 ± 0.13	14	0.448
Pronotum length	-0.108 ± 0.13	34	0.396				0.079 ± 0.13	34	0.560	0.305 ± 0.13	34	0.027*	-0.107 ± 0.03	34	0.002*	-0.100 ± 0.17	14	0.583
SMI	0.21 ± 0.10	34	0.037*	0.123 ± 0.10	34	0.231				0.060 ± 0.10	34	0.573	0.634 ± 1.04	34	0.543	0.223 ± 0.14	14	0.127
Development time	-0.038 ± 0.02	34	0.032*	-0.048 ± 0.02	34	0.005*	0.011 ± 0.02	34	0.586				-0.019 ± 0.017	34	0.26	-0.035 ± 0.03	14	0.258
Attractiveness	0.075 ± 0.11	33	0.504	0.092 ± 0.16	33	0.566	0.011 ± 0.16	33	0.944	0.046 ± 0.10	33	0.659				0.098 ± 0.20	14	0.627
Disease resistance	-0.221 ± 0.21	33	0.288	-0.378 ± 0.22	33	0.083	0.183 ± 0.21	33	0.375	0.138 ± 0.22	33	0.496	0.068 ± 0.20	33	0.734			

A separate linear mixed-effects model was fitted for each relationship (family ID was entered as the random factor) when the response variable was mass, pronotum length, SMI or attractiveness. For models with development time as the response variable, a Poisson generalized models were run for each relationships and binomial generalized models for disease resistance. The first value is the estimate (slope) ± SE. n = the number of families. Grayed cells show significant correlations. All the correlations were made using sires traits (horizontal) as the independent variable and sons (vertical) traits as the dependable variable. SMI=Scaled mass index. * p=<0.05.

Table 1.5 The effects of sire phenotype and life-history traits on six fitness components of daughters.

Sire trait

	Mass			Pronotum length			SMI			Development time			Attractiveness			Disease resistance		
Offspring trait	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p	Est ±SE	n	p
Mass				-0.324 ± 0.12	33	0.012*	-0.029 ± 0.14	33	0.844	0.422 ± 0.12	33	0.002*	-0.067 ± 0.16	33	0.680	0.123 ± 0.17	16	0.474
Pronotum length	-0.070 ± 0.13	33	0.587				0.070 ± 0.13	33	0.596	0.184 ± 0.13	33	0.166	-0.033 ± 0.04	33	0.447	0.088 ± 0.21	16	0.682
SMI	-0.254 ± 0.10	33	0.025*	-0.227 ± 0.11	33	0.042*				0.269 ± 0.11	33	0.02*	0.208 ± 1.56	33	0.896	0.077 ± 0.15	16	0.618
Development time	-0.027 ± 0.02	33	0.117	-0.040 ± 0.02	33	0.012*	0.019 ± 0.02	33	0.301				0.012 ± 0.02	34	0.26	0.028 ± 0.02	16	0.169
Disease resistance	-0.296 ± 0.36	29	0.407	0.065 ± 0.35	29	0.851	-0.631 ± 0.38	29	0.100	-0.218 ± 0.35	29	0.533	-0.458 ± 0.36	29	0.200			

A separate linear mixed-effects model was fitted for each relationship (family ID was entered as the random factor) when the response variable was mass, pronotum length, SMI or attractiveness. For models with development time as the response variable, a Poisson generalized models were run for each relationships and binomial generalized models for disease resistance. The first value is the estimate (slope) ± SE. n = the number of families. Grayed cells show significant correlations. All the correlations were made using sires traits (horizontal) as the independent variable and daughters (vertical) traits as the dependable variable. SMI=Scaled mass index. * p=<0.05.

The intralocus sexual conflict hypothesis predicts that male attractiveness will have significant effects on offspring traits but that the relationship will trade-off in sons and daughters (i.e. negative correlation). Here, unattractive males (with a higher time to mount) sired sons with a smaller body mass and pronotum length (mass: t=-0.262, n=34, p=0.017; pronotum length: t=-0.107, n=34, p=0.002). The number of descendants we had per sire in this study, did not allow us to test if sire attractiveness is significantly difference between sons and daughters. We did not find any significant effects of sire attractiveness on daughter traits (Table 1.5). Sire attractiveness did not have an impact on offspring SMI regardless of offspring sex (sons: t=0.634, n=34, p=0.543; daughters: t=0.208, n=33, p=0.896). Contrary to our prediction, there was no effect of offspring sex on disease resistance (z=0.100, n=98, p=0.920) and attractive males did not sire daughters with a higher disease resistance (z=-0.458, n=29, p=0.200). Sires with shorter pronotum had daughters with lower body mass (t=-0.324, n=33, p=0.012), poorer condition (t=-0.227, n=33, p=0.042) and shorter development time (t=-0.040, n=33, p=0.012). Sons sired by males with short pronotum also had shorter development times (t=-0.048, n=34, p=0.005).

Table 1.6 Sire-offspring heritability of attractiveness, mass, pronotum length, scaled mass index, time to eclose to adulthood and disease resistance in function of offspring sex. A midparent estimation of heritability is assessed by an average of both the sire and mother scores.

Trait	Sex	Sire-offspring				Midparent-offspring			
		h^2	SE	p	n	h^2	SE	p	n
(a) Attractiveness									
	Pooled	-	-	-	-	-	-	-	-
	Sons	-	0.101	0.622	33	-	-	-	-
	Daughters	-	-	-	-	-	-	-	-
(b) Mass									
	Pooled	-	0.097	0.229	39	-	0.105	0.881	39
	Sons	0.112	1.333	0.676	34	0.203	0.135	0.457	34
	Daughters	-	0.126	0.024*	33	-	0.131	0.789	33
(c) Pronotum length									
	Pooled	-	0.141	0.163	39	-	0.128	0.142	39
	Sons	-	0.123	0.153	34	-	0.123	0.128	34
	Daughters	-	0.122	0.341	33	-	0.127	0.617	33
(d) SMI									
	Pooled	0.063	0.100	0.750	39	0.211	0.072	0.144	39
	Sons	0.320	0.100	0.123	34	0.462	0.097	0.019*	34
	Daughters	-	0.115	0.384	33	-	0.119	0.971	33
(e) Development time									
	Pooled	0.096	0.014	<0.001*	39	0.095	0.014	<0.001*	39
	Sons	0.116	0.018	0.001*	34	0.116	0.018	0.001*	34
	Daughters	0.104	0.015	<0.001*	33	0.101	0.015	<0.001*	33
(f) Disease resistance									
	Pooled	0	0.203	0.227	17	-	-	-	-
	Sons	0	0.283	0.910	14	-	-	-	-
	Daughters	0	0.431	0.164	16	-	-	-	-

A separate model was fitted for each relation. N= the number of families. All the correlations were made using sires' traits as the independent variable and offspring's traits as the dependable variable. SMI=Scaled mass index. The family was used as the random factor. Disease resistance does not have a midparent score because mothers were not tested for disease resistance and they were kept alive to lay eggs. When only one parent's data is used, heritability (here h^2) can be estimated with twice the slope value. The rows with a SE, p and n without a h^2 result represent a negative regression. Heritability could not be calculated in these relations, due to the negative regressions. We do not have a pooled, daughters or midparent data for attractiveness because it was only calculated for males.

A key factor of indirect benefits and mate choice is the heritability of traits. If a male's quality-related traits are not heritable, the female will not obtain genetic benefits for her offspring. Testing heritability allows us to see if the parent's quality have an effect on progeny quality. We predicted that males of higher quality would give part of this quality to their offspring. However, in Table 1.6 we can observe that disease resistance is not heritable. Sire's mass correlated with the mass of their daughters ($t=-0.306$, $n=33$, $p=0.024$) but the slope was negative and heritability cannot be calculated with negative slopes (Jansse *et al.*, 1988). Son's scaled mass index correlated with the midparent score obtained from an average of both sire and mother's SMI ($t=0.462$, $n=34$, $p=0.0189$). The time to reach adulthood was heritable ($h^2=0.096$) (Figure 1.2). Therefore, males who took longer to reach adulthood had sons and daughters who also took more time to eclose to maturity. This trait was also correlated with the midparent score (pooled $h^2=0.095$; sons $h^2=0.116$; daughters $h^2=0.101$) (Figure 1.3).

Figure 1.2 Sire-offspring heritability of time to eclose to adulthood in function of offspring's sex. Relations with male offspring is in cyan solid line (n=34), red dashed line for females (n=33) and black dotted line for relationship of both sexes pooled (n=39).

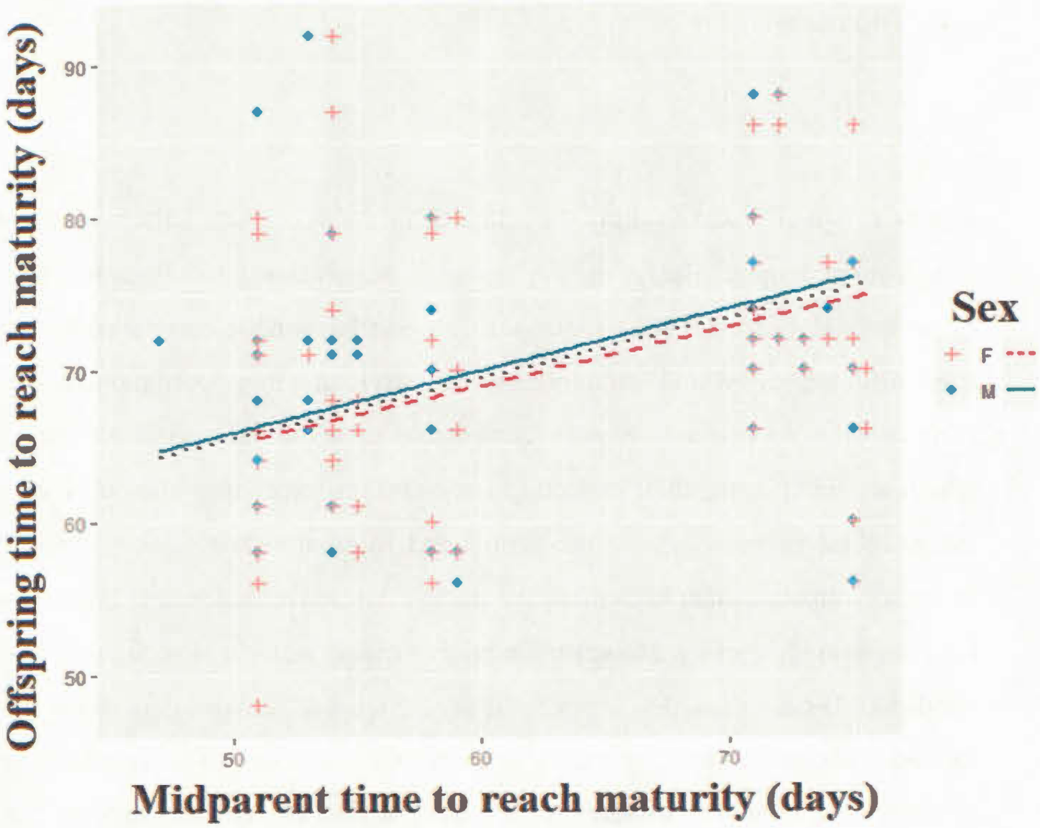

Figure 1.3 Midparent-offspring heritability time to eclose to adulthood in function of offspring's sex. The midparent estimation of heritability is assessed by an average of both the sire and mother's scores. Relations with male offspring is in cyan solid line (n=34), red dashed line for females (n=33) and black dotted line for relationship of both sexes pooled (n=39).

1.4 Discussion

The first objective was to study the relationship between male attractiveness and male fitness-related traits. Based on the resource acquisition and allocation theory (van Noordwijk & de Jong, 1986), we expected a positive genetic correlation between male immunity, longevity, and attractiveness. If individuals in a population mostly vary in their capacity to acquire resources, attractive males should acquire more resources which would enhance their capacity to allocate resources into competitive traits. We did not find support for the prediction that more-attractive males would be more immunocompetent than less-attractive males. Attractive males also did not appear to have superior longevity. However, attractive males were in significantly better body condition. We also failed to support the prediction that females gain direct benefits by mating with more-attractive males as there was no effect of male attractiveness on either female fecundity or fertility. We did not find evidence to support the indirect benefits hypothesis; attractive males did not sire offspring having greater immunocompetence, sexual attractiveness (sons only), faster or larger body size. Finally, our results indicate the possible presence of intralocus sexual conflict since sire body size (i.e. pronotum length and body mass) was negatively correlated with daughter body condition and development time.

1.4.1 Development time and immunity

We found that more-attractive males were smaller-bodied and also in better body condition. It is possible that male crickets maximize their body condition by minimizing their body size (Kelly, Tawes & Worthington, 2014). In our results, male sexual attractiveness positively covaried with body condition. The condition-dependence of the expression of secondary sexual traits could provide a mechanism by which mate choice benefits to females directly and indirectly. If the cost required to express certain sexual traits or sexual behavior is high (e.g. courtship songs), only males in superior condition could be able to withstand the production of such signals (Gray & Eckhardt, 2001). To retain the honesty of sexual signals, sexual selection would favor the evolution of costly signals (Zahavi, 1975; Kodric-Brown and Brown, 1984; Folstad and Karter, 1992). For example, male crickets *Gryllus campestris* who were in better condition had a superior calling rate, thus making them more attractive (Holzer *et al.*, 2003). If male condition and the capacity to allocate resources to sexual-attractiveness-related traits covariates, female would benefit from selecting males with exaggerated traits because of the honest signaling of their genetic quality (Kodric-Brown & Brown, 1984). Attractive males should therefore possess genes related to greater body condition and females would receive indirect benefits for their progeny by selecting these males (Andersson, 1986; Wedell and Tregenza, 1999; Bonduriansky, 2001). Other factors like the different variables of the courtship songs, like chirp rate or amplitude (Holzer *et al.*, 2003; Simmons *et al.*, 2013; Tregenza *et al.*, 2006) or pheromone profile (Tregenza & Wedell, 1997) could also influence female attraction towards a specific male.

Males who took longer to mature sired larger offspring (i.e. heavier body mass, longer pronotum). We observed that development time was heritable independent of whether heritability was calculated using mid-parent values or sire values only. Development time can have important effects on fitness in crickets because individuals that develop faster have an enhanced probability of survival-to-maturity and they can have higher reproductive success (Wedell & Tregenza, 1999). In this study, a positive correlation between SMI and the time to reach adulthood showed that males who matured quicker were in better body condition (i.e. higher SMI). This result is consistent with what Kelly and Tawes (2013) showed in a previous study on field crickets *Gryllus texensis,* where crickets on a low-quality diet required significantly more time to reach adulthood than those on a high-quality diet. A positive correlation between maturation time and body size was also reported in 17 different species in a paper using multiple data sets from the literature (Roff, 2000).

One of the limitations of this study, is that we focused on disease resistance even if it is only one part of the overall immunocompetence of an individual. We did not find correlations between attractiveness and disease resistance, however, theory reveals the presence of trade-offs between different immunocompetence traits in insects (Ahmed *et al.*, 2002; Blount *et al.*, 2003; Gershman *et al.*, 2010; Jacot *et al.*, 2004; McKean & Nunney, 2008; McNamara *et al.*, 2013; Rantala *et al.*, 2003; Rolff & Siva-Jothy, 2002). In addition to disease survival, the number of circulating haemocytes, the levels of phenoloxidase (Gillespie, Kanost, & Trenczek, 1997) and lysozyme-like activity (Adamo, 2004) are important factors of immunity in insects. The number of circulating haemocytes directly affects the rates of encapsulation. Haemocyte recognize a foreign object and cause other haemocytes to aggregate to form a capsule around it (Gillespie *et al.*, 1997). The levels of phenoloxidase are heritable (Cotter & Wilson, 2002) and are part of the humoral immunity (Gillespie & Khachatourians, 1992). It can correlate with resistance to some parasites and pathogens (Nigam *et al*., 1997), melanization of encapsulating hemocytes (Cotter, Kruuk, & Wilson, 2004) and Gram-negative bacteria (Sugumaran, 2001). Lysozyme also appeared to be a major component of cricket (*Gryllus bimaculatus*) immunity against Gram-positive bacteria (Schneider, 1985). In the moth *Spodoptera littoralis* for example, Cotter *et al* (2004) reported a negative correlation between lysozyme-like activity and phenoloxidase. A negative correlation has also been observed between lysozyme-like activity and hemocyte load in crickets (Simmons & Roberts, 2005).

The present experiment does not provide information about these potential trade-offs between immune components. Attractive males did not differ from unattractive ones in term of longevity and disease resistance. We did not observe any correlation between immunity/longevity and body size, attractiveness or body condition. As previously mentioned, it is possible that attractiveness is correlated with other fitness-related traits that were not tested. The genetic quality of an individual and its fitness can be characterized by strong trade-offs between traits (Lailvaux *et al.*, 2010). In this population, individuals seem to mostly differ in their allocation of resources rather than their acquisition. The result of this lower variation in the capacity to acquire resources bring low quality differences among males.

1.4.2 Effects on female reproduction

Mating with attractive males did not significantly affect either female fecundity or fertility. In this situation, we did not detect the presence of direct benefits from mating with attractive males. It is possible that females gain other direct benefits that were not tested in this experimental design. For example, female crickets (*Gryllus texensis)* receive an immune-boost from derived components from a male's ejaculate (Worthington & Kelly, 2016). A boost in disease resistance could be a direct benefit that counterbalances a part of the costs involved in mate choice.

The correlation between female SMI and egg size showed that females in lesser body condition and females with longer pronota produced larger eggs. In *Drosophila melanogaster*, egg size showed positive effects on embryonic viability, development rate, weight at hatching and time to reach maturity (Azevedo, Partridge, & French, 1997). Observations in butterflies revealed that larger eggs tend to develop more slowly, the time to reach maturity was longer for individuals who hatched from larger eggs and adult weight was higher (García-Barros, 2000). Also, our data reveal that females who mated with males who took longer to mature had greater fertility and larger eggs. Thus, females gained direct benefits from mating with males who mature slowly. It could be interesting to investigate if males with longer development time have higher sperm quality or other traits that could lead to a higher number of descendants per reproduction.

1.4.3 Effect of sire traits on the progeny

No correlation was found between offspring disease resistance and sire traits. We predicted that offspring of resistant males should be more resistant to *Serratia marcescens*. This hypothesis was based on the premise that females choose males to gain indirect benefits. Attractive males would consequently have better genes to resist disease or genes conferring a superior longevity. Testing for heritability of traits did not show heritability of disease resistance in this population. Like mentioned above, disease resistance includes multiple factors and these results do not deny that part of the immune system leading to a better disease resistance could be heritable. Disease resistance might imply a vast number of genes too large to be observed in this experimental design. In caterpillars *Spodoptera littoralis*, a strong heritability of haemolymph PO activity and encapsulation response was observed (Cotter & Wilson, 2002). Likewise, haemocyte load has been shown to be heritable in crickets *Acheta domesticus* (Ryder & Siva-Jothy, 2001). However, the overall survival to parasites was heritable in *Drosophila melanogaster* (Kraaijeveld, Limentani, & Godfray, 2001). In a similar way that Fellowes' *et al* studied *Drosophila melanogaster* (Fellowes, Kraaijeveld, & Godfray, 1998), it could be interesting to test immunity on multiple generations to see if there is substantial additive genetic variation from the initial population in crickets. In the wild-derived house mice (*Mus musculus musculus*), offspring sired by preferred males were significantly more likely to resist infection than offspring of non-preferred males (Raveh *et al.*, 2014). Additionally, female crickets *Acheta domesticus* are expected to obtain indirect benefits through mate choice by producing larger offspring with a superior encapsulation response when they choose their mate (Ryder & Siva-Jothy, 2001). We did not see any effects of sire's attractiveness on offspring disease resistance in this study and descendants' survival to infection did not differ significantly between the sexes. Although, attractive males did sire sons with superior mass, there was no correlation between sire's attractiveness and daughters' mass.

It is possible that daughters and sons have differential optima for other fitness traits than disease resistance. Although, based on Bateman's principle — implying that males gain superior fitness by increasing their mating success in contrast to females who enhance their fitness through longevity or survival — males are expected to compromise viability for sexual performance, whereas females would invest more in longevity and immunity (Rolff, 2002). However, we did not see any significant trade-offs in males between viability (here; disease resistance and longevity) and attractiveness (a sexual performance cue).

In this study, the development time of individuals was heritable (h^2=0.096). Like mentioned earlier, individuals that develop faster could have an increased probability of survival to maturity and a potentially higher reproductive success (Wedell & Tregenza, 1999). The time to mature being heritable could have an important effect on offspring fitness. In theory, females who are selecting males that mature faster would gain indirect benefits. However, we did not observe a correlation between development time of males and sexual attractiveness. Thus, development time is not represented or signaled through secondary sexual traits. Female should therefore not be able to detect faster developing males and select them. Moore (1994) detected heritability of development time in the cockroach *Nauphoeta cinerea*. Additionally, male attractiveness and offspring development rate were genetically correlated (Moore, 1994). The heritability of development time we measured in the sand cricket *Gryllus* *firmus* in our experiment is consistent with the literature (Rantala & Roff, 2006; Roff, 1998, 2000; Roff & Sokolovska, 2004). Development time heritabilities have been observed in multiple other species including the Chinook Salmon *Oncorhynchus tshawytscha* (Hankin, Nicholas, & Downey, 1993), the hard clam *Mercenaria mercenaria* (Hadley, Dillon, & Manzi, 1991) and the rainbow trout *Oncorhynchus mykiss* (Crandell & Gall, 1993; Tipping, 1991). If requiring more time to reach maturity reduces fitness (Roff, 1992), but enhances offspring fitness through superior size, males could face fitness trade-offs between maturation time and offspring quality.

Attractive males sired sons with superior mass and longer pronota. Females would, therefore, have heavier sons when mating with attractive males. There is considerable evidence for positive correlations between body size and fitness in insects; superior lifetime mating success (Sokolovska, Rowe, & Johansson, 2000), longevity (Butlin & Day, 1985), ejaculate size (Fox *et al*., 1995), sperm quality (Hatala, Harrington, & Degner, 2018), lytic enzyme activity (Rantala & Roff, 2005), reduced development time (Johansson & Rowe, 1999), enhanced mating rate and attractiveness (Thornhill & Alcock, 1983) to cite a few.

In other words, some rare males had a score (time to mount) almost 600 times superior to other males, which lead to strong standard errors. Developing an attractiveness index for attractive vs unattractive males using the time to mount could be preferable for some analysis and become an important factor for further researches in sexual selection. Attractive males did not have more attractive sons in our study. These results are in contradiction with the sexy son's hypothesis suggesting that females mating with attractive males gain an indirect benefit through the success of their sons (Fisher, 1958). This superior success of their sons should be a result of the inheritance of attractiveness-related genes from the sire. Although our results do not confirm this theory, it supports the idea of multiple trade-offs and a high variation in allocation between individuals.

CONCLUSION

Cette recherche avait pour objectif d'étudier les différents bénéfices associés au choix de partenaire. La première étape de ce projet était d'observer si les mâles attirants étaient différents au niveau de leur masse, taille de pronotum, condition, temps à atteindre maturité, capacité de résistance aux infections et longévité. En second, l'objectif était d'observer s'il y avait présence de bénéfices directs pour la femelle au niveau de sa fécondité, fertilité et qualité d'œufs lorsqu'elle se reproduit avec un mâle attirant. Nous avons aussi observé les effets de trois traits morphologiques de la femelle et de trois traits du partenaire sexuel sur le succès reproducteur de la femelle pour contrôler l'effet de ces traits. Finalement, nous avons testé s'il y avait présence de bénéfices indirects et d'avantages pour la progéniture de mâles attirants. Ceci fut observé en fonction du sexe des descendants, ainsi que l'héritabilité des traits. Les résultats obtenus indiquent que les mâles attirants n'étaient pas significativement différents au niveau de leur résistance à l'infection ou de leur longévité. Par contre, les mâles attirants étaient en meilleure condition et avaient des pronotum significativement plus courts. Néanmoins, l'absence de corrélation entre la masse et l'attirance sexuelle reflète l'importance d'utiliser des indices d'attirances globaux et non seulement des traits individuels.

Les mâles qui ont atteint la maturité plus rapidement étaient eux aussi en meilleure condition corporelle. Le temps de maturation pourrait avoir un impact important sur les aptitudes phénotypiques des individus et la sélection sexuelle. Les femelles ont, en moyenne, atteint la maturité 2 jours plus rapidement que les mâles, ce qui pourrait causer des pressions de sélection sur le temps de développement des mâles. Le temps de maturation était un trait héritable même si les femelles ne semblaient pas être particulièrement attirées par les mâles qui ont atteint la maturité plus rapidement. La vitesse de maturation ne semble pas être reflété par les traits sexuels secondaires des individus et ne ferait pas partis d'un signalement honnête de qualité. Les femelles atteignirent la maturité significativement plus tôt que les mâles. Ceci permet alors aux mâles qui maturent plus rapidement d'avoir un potentiel reproducteur supérieur.

Les femelles qui se sont reproduites avec des mâles attirants n'ont pas semblé obtenir de bénéfices directs sur leur fécondité, fertilité ou qualité des œufs. Lors de l'étude des bénéfices indirects, nous avons observé des différences significatives selon le sexe de la progéniture au niveau de la masse, la condition corporelle et la taille du pronotum. L'attirance du père n'a pas semblé affecter sa progéniture femelle. Néanmoins, les mâles attirants ont eu des fils avec une masse et une longueur de pronotum supérieures. Alors, les femelles qui se reproduiraient avec des mâles attirants bénéficieraient d'avantage indirects pour leur progéniture mâle. Une masse et une taille corporelle supérieures peuvent avoir des avantages importants au niveau des aptitudes phénotypiques des mâles et leur permettre, entre autres, un taux de reproducteur supérieur et assurer un plus grand nombre de descendants. Les mâles qui ont pris plus de temps avant d'atteindre la maturité ont eux aussi eu des descendants avec une masse supérieure.

Lors de ce projet, le nombre d'individus et de familles qui furent rejetés des échantillons étudiés pour les résultats limita grandement les tailles d'échantillons finaux et notre puissance statistique. Pour effectuer un test d'attirance sexuelle, le mâle et la femelle se devaient d'être matures sexuellement dans la même période et un grand nombre d'individus ont dû être rejetés par manque de partenaire. De plus, la mortalité aléatoire des individus causa un rétrécissement important du nombre de grillons testés. Finalement, des complications administratives quant à l'utilisation de *S. marcescens* réduisirent de moitié le nombre de familles prévues pour les tests de capacité de résistance aux infections. Des facteurs qui ne furent étudiés lors de cette étude peuvent tout de même avoir une influence sur l'attirance sexuelle et le choix de partenaire. Ces traits non observés font partis des limitations de cette étude. Il est aussi possible, par exemple, que certains traits non-étudiés furent hérités par la progéniture. Une des principales limitations, est l'observation d'un seul aspect de la capacité immunitaire (capacité de survie à l'infection). Plusieurs autres facteurs font partis du système immunitaire chez les insectes, comme le nombre haemocytes et les niveaux de phenoloxidase (Gillespie *et al.*, 1997), et ils auraient pu varier en fonction de l'attirance sexuelle sans que nous les observions.

De plus, nous n'avons utiliser qu'une seule femelle par mâle pour évaluer le niveau d'attirance et la littérature reconnait que certains femelles ont des préférences individuelles (Møller, 1994; Ryan, Perrill, & Wilczynski, 1992; W.E. Wagner, Murray, & Cade, 1995). Utiliser plusieurs femelles par mâles aurait grandement réduit notre échantillon final et il aurait fallu effectuer des tests supplémentaires pour observer si le mâle change ses comportements en fonction du nombre de femelle qu'il a rencontré. Aussi, notre mesure d'attirance sexuelle ne s'est basé que sur les interactions à courte distance entre mâle et femelle. Le chant des grillons peut être un facteur influençant le choix de partenaire sur une longue distance (Simmons *et al.*, 2013) et ceci ne fut pas pris en compte lors de cette étude. Pareillement, les femelles n'ont pas observées de combat entre mâles avant de décider de leur partenaire sexuel, malgré le fait les combats peuvent être un élément important pour le choix de partenaire (Alatalo, Hoglund, & Lundberg, 1991; Berglund & Rosenqvist, 2001; Bisazza & Marin, 1991; Breed, Smith, & Gall, 1980; Savage *et al.*, 2005). Une nouvelle approche pouvant amener des informations supplémentaires testerait différents traits reliés à l'immunité de la progéniture et leurs aptitudes phénotypiques. L'absence de corrélation entre nos traits étudiés et la capacité de survie à l'infection pourrait être causée par des compromis entre les multiples dimensions et mécanismes d'un système immunitaire complet.

L'utilisation d'un indice d'attirance globale comme celui utilisé dans cette étude pourrait être un concept important à instituer dans les futures recherches en sélection sexuelle. Les résultats obtenus suggèrent que les individus d'une même population varient génétiquement principalement dans leur allocation de ressources et qu'il y aurait présence de différents compromis entre les traits.

ANNEXE

STATISTIQUES SOMMAIRES

Table A.1 Statistiques générales pour l'ensemble des grillons

Statistic	N	Mean	St. Dev.	Min	Max	Pctl(25)	Pctl(75)	Median
SMI	419	664.3	119.3	266.9	1,194.0	589.9	717.4	649.1
Mass (mg)	699	657.3	136.6	293.1	1,135.6	568.5	741.8	654.8
Time to mature (days)	699	65.9	10.2	46	92	58	74	64
Pronotum width (mm)	419	6.3	0.4	4.6	7.4	6.0	6.6	6.3
Pronotum lenght (mm)	419	3.9	0.4	2.7	5.4	3.7	4.1	4.0
Attractiveness of males (sec)	259	5.2	11.7	0.1	60.0	0.5	2.8	1.3

Table A.2 Statistiques générales pour l'ensemble des grillons de seconde génération (progéniture)

Statistic	N	Mean	St. Dev.	Min	Max	Pctl(25)	Pctl(75)	Median
SMI	90	687.2	127.6	450.2	1,144.1	599.7	747.0	666.4
Mass (mg)	102	744.1	142.2	328.7	1,135.6	654.8	842.3	735.5
Time to mature (days)	102	69.1	9.1	48	92	61	76.2	69
Pronotum width (mm)	90	6.4	0.4	5.4	7.1	6.2	6.7	6.5
Pronotum lenght (mm)	90	4.1	0.3	3.3	4.8	4.0	4.3	4.1

Table A.3 Statistiques générales pour l'ensemble des grillons mâles de seconde génération (progéniture)

Statistic	N	Mean	St. Dev.	Min	Max	Pctl(25)	Pctl(75)	Median
SMI	98	622.7	92.3	357.9	886.5	566.7	685.7	618.6
Mass (mg)	103	560.5	114.1	294.5	810.6	493.4	640.1	553.8
Time to mature (days)	103	70.4	9.5	56	92	64	75.5	71
Pronotum width (mm)	98	6.1	0.5	4.6	7.0	5.7	6.4	6.1
Pronotum lenght (mm)	98	3.8	0.3	2.7	4.6	3.6	4.0	3.8
Attractiveness of males (sec)	90	5.9	11.9	0.1	53.6	0.6	4.0	1.6

Table A.4 Statistiques générales pour l'ensemble des grillons femelles de seconde génération (progéniture)

Statistic	N	Mean	St. Dev.	Min	Max	Pctl(25)	Pctl(75)	Median
SMI	90	687.2	127.6	450.2	1,144.1	599.7	747.0	666.4
Mass (mg)	102	744.1	142.2	328.7	1,135.6	654.8	842.3	735.5
Time to mature (days)	102	69.1	9.1	48	92	61	76.2	69
Pronotum width (mm)	90	6.4	0.4	5.4	7.1	6.2	6.7	6.5
Pronotum lenght (mm)	90	4.1	0.3	3.3	4.8	4.0	4.3	4.1

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