UNIVERSITÉ DU QUÉBEC À MONTRÉAL

HÉTÉROGÉNÉITÉ ENVIRONNEMENTALE ET ÉVOLUTION DES DIFFÉRENCES DE TRAITS DE PERSONNALITÉ CHEZ LA MÉSANGE BLEUE (CYANISTES CAERULEUS)

THÈSE

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RÉSUMÉ

Un des objectifs de l'écologie évolutive est de comprendre les causes et conséquences de la diversité biologique. L'étude des facteurs à l'origine de la divergence phénotypique des populations et de la formation d'adaptations locales peut nous donner des indications sur les causes de la diversité intraspécifique et sur la trajectoire évolutive des populations. La divergence phénotypique des populations peut être adaptative ou neutre. L'hétérogénéité spatiale des conditions écologiques, via la variation des pressions de sélection qu'elle engendre, est un des facteurs importants à l'origine de la divergence adaptative des populations. L'hétérogénéité spatiale peut causer une divergence génétique et/ou plastique entre populations. Selon le type de divergence, les populations n'auront pas la même trajectoire évolutive. Traditionnellement, il a été considéré que la divergence génétique et adaptative des populations était peu probable lorsqu'elles sont séparées par des distances que les organismes peuvent franchir lors de leur dispersion parce que les flux géniques homogénéiseraient les génotypes. Par contre, des études récentes suggèrent que ce ne serait pas nécessairement toujours le cas, particulièrement lorsque les pressions de sélection sont fortes et que la dispersion est non aléatoire.

Un nombre croissant d'études rapporte la présence de différences de comportements entre les individus qui sont stables dans le temps et héritables. Ce type de variation intraspécifique a été nommée personnalité. Il a récemment été proposé que les traits de personnalité auraient coévolué avec des traits d'histoire de vie et des traits physiologiques (hypothèse du syndrome de train de vie). Selon cette hypothèse, nous pourrions trouver au niveau de la métapopulation, différentes combinaisons de traits dans l'espace façonnées par le régime local de sélection. Jusqu'à présent peu d'études ont porté sur l'importance relative des effets plastiques et génétiques et des pressions de sélections pour la divergence des populations pour des traits de personnalité et encore moins pour le syndrome de train de vie.

Notre objectif était de déterminer si une forte variation spatiale de conditions écologiques pouvait mener à une divergence phénotypique et génétique adaptative pour des traits de personnalité entre des populations connectées par un flux génique. Nous avons répondu à cet objectif grâce au suivi à long terme de trois populations sauvages de mésanges bleues (*Cyanistes caeruleus*) présentes dans une mosaïque d'habitats très contrastée en Corse (France). Des études réalisées précédemment ont montré que bien qu'elles soient connectées par un flux génique et séparées par de petites distances spatiales (6 à 25 km), ces populations diffèrent au niveau phénotypique et génétique pour plusieurs types de traits, dont des traits d'histoire de vie. Notre étude indique que ces populations divergent également pour des traits de personnalité chez les adultes et chez les jeunes au niveau phénotypique et génétique. De plus, nos résultats suggèrent que ces divergences ne sont pas le fruit de processus neutres, mais pourraient être plutôt causées par la sélection naturelle. Notre étude est une des premières à montrer des divergences génétiques pour des traits de personnalité à une échelle spatiale aussi fine. Par ailleurs, les divergences de moyennes populationnelles observées sont en accord avec les prédictions du syndrome de train de vie. Ainsi, bien que d'autres études plus approfondies soient nécessaires pour le confirmer, nos résultats suggèrent que les divergences observées entre ces populations sont issues de la coévolution d'un ensemble de traits formant un train de vie rapide ou lent façonné par le régime local de sélection.

Cette thèse souligne l'importance de l'hétérogénéité environnementale pour la diversité intraspécifique et montre qu'une divergence phénotypique, génétique et adaptative est possible pour des traits comportementaux souvent considérés comme plus plastiques et moins sujets aux divergences génétiques.

Mots clés : adaptations locales, personnalité, sélection naturelle, hétérogénéité environnementale, *Cyanistes caeruleus*

CHAPITRE 1
INTRODUCTION

Un des objectifs de l'écologie évolutive est de comprendre les causes et les conséquences de la diversité biologique. L'étude des mécanismes à l'origine des variations inter et intraspécifiques actuelles peut nous apporter des informations sur ce qui a créé la diversité biologique. Par exemple, l'étude des mécanismes impliqués dans la divergence des populations actuelles et la formation d'adaptations locales peut nous renseigner sur les facteurs qui sont responsables de la diversité biologique intraspécifique et de la formation des espèces. De plus, la connaissance des mécanismes à l'origine de la divergence des populations actuelles nous renseigne sur leur potentiel évolutif et leur trajectoire évolutive.

1.1 La divergence des populations peut avoir plusieurs origines

La Figure 1.1 illustre les différents types de divergence phénotypique inter populationnelle et les principaux mécanismes qui en sont responsables. La divergence phénotypique des populations peut avoir une origine plastique et génétique, qui peut être adaptative ou neutre. Toutefois, c'est seulement lorsque la divergence des populations a une origine génétique qu'il peut y avoir formation d'adaptations locales. Nous considérons classiquement qu'une population montre des adaptations locales lorsque les individus ont une meilleure valeur adaptative dans leur population d'origine que dans une autre population qui possède des caractéristiques écologiques différentes (Kawecki et Ebert 2004; Hereford 2009).

L'hétérogénéité spatiale des conditions écologiques peut créer des variations de pressions de sélection (Fig. 1.1). Lorsque les traits sous sélection sont héritables, les populations peuvent acquérir avec le temps des caractéristiques phénotypiques et génétiques particulières au contexte écologique dans lequel elles se trouvent (Endler 1986; Wang et Bradburd 2014; Fig. 1.1). Ainsi, l'hétérogénéité spatiale des conditions écologiques est un des facteurs importants à l'origine de la création et du maintien de la divergence génétique adaptative des populations et de la formation d'adaptations locales (Endler 1986; Hereford 2009; Siepielski et al. 2009; Siepielski et al. 2013; Wang et Bradburd 2014; Fig. 1.1).

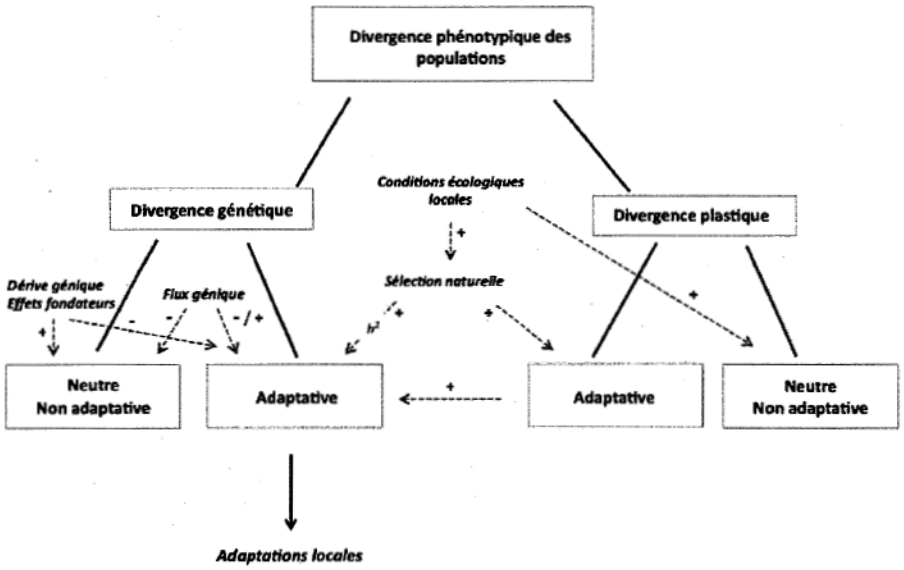

Figure 1.1 Illustration des types de divergences phénotypiques et des principaux processus qui peuvent les causer et qui seront abordés dans cette thèse. La divergence phénotypique des populations peut être d'origine génétique ou plastique adaptative ou neutre et non adaptative. Seule une divergence génétique adaptative peut mener à des adaptations locales. Plusieurs forces (en italique et en pointillé) peuvent favoriser (+) ou défavoriser (-) les différents types de divergences. Une réponse à la sélection est possible seulement si les traits sont héritables (h^2). La diversité génétique, les corrélations génétiques et la variabilité temporelle des pressions de sélection agissent également sur la divergence des populations, mais ne sont pas représentées ici par souci de simplicité.

Lorsque les conditions écologiques varient dans l'espace, les individus peuvent aussi, par plasticité, ajuster leur phénotype selon les conditions écologiques et adopter le phénotype favorisé par le régime de sélection local (Pigliucci 2005). Ainsi, l'hétérogénéité spatiale des conditions écologiques et des pressions de sélection peut également favoriser l'évolution de la plasticité phénotypique et causer une divergence entre populations de type plastique (Sultan et Spencer 2002; Fig. 1.1). La plasticité phénotypique est donc un mécanisme important qui favorise la diversité intraspécifique et peut causer la divergence des populations (Fig. 1.1). Cependant, lorsque la différenciation des populations est produite uniquement par plasticité, elle ne mène pas à des adaptations locales (Fig. 1.1). Néanmoins, la présence de plasticité phénotypique n'implique pas nécessairement aucune adaptation locale. Par exemple, la divergence entre populations peut être influencé simultanément par des effets plastiques et des effets génétiques (Fitzpatrick 2012). De plus, en favorisant notamment la persistance des populations, la plasticité peut sous certaines conditions, favoriser la divergence génétique adaptative et la formation d'adaptations locales (Fitzpatrick 2012; Fig. 1.1).

Les flux géniques homogénéisent les génotypes entre les populations. Ainsi, même en présence d'une hétérogénéité spatiale des conditions écologiques, la dispersion des individus entre les populations engendre des flux géniques qui peuvent défavoriser la différenciation des populations et freiner la formation d'adaptations locales (Slatkin 1987; Garant et al. 2007; Fig. 1.1). Par conséquent, la plupart des études qui ont porté sur la divergence des populations et la formation d'adaptations locales se sont intéressées à des populations séparées par de grandes distances spatiales et peu connectées par un flux génique (Slatkin 1987; Lenormand 2002). Toutefois, des études récentes suggèrent que la différenciation des populations peut être possible même en présence de flux géniques lorsque les pressions de sélection sont fortes et lorsque la dispersion et les flux géniques sont non aléatoires (Garant et al. 2007; Edelaar et Bolnick 2012; Richardson et al. 2014; Wang et Bradburd 2014; Fig. 1.1).

La divergence des populations peut également avoir une origine non adaptative (Fig. 1.1). Par exemple, les contraintes environnementales locales peuvent produire une plasticité non adaptative (Fitzpatrick 2012; Fig. 1.1) et des effets fondateurs ou de la dérive génique peuvent mener à une différentiation génétique et phénotypique neutre et non adaptative (Slatkin 1987; Fig. 1.1). Par contre, ces types de divergences n'engendrent pas d'adaptation locale.

1.2 La variation intraspécifique de comportement

La plupart des études qui ont porté sur la variation intraspécifique et la divergence des populations animales se sont intéressées aux traits morphologiques, physiologiques ou aux traits d'histoire de vie, mais beaucoup moins d'études ont porté sur des traits comportementaux (Siepielski et al. 2009; Siepielski et al. 2013). Cette lacune peut être attribuable au fait que les comportements sont souvent plus difficiles à mesurer. De plus, les traits de comportement ont traditionnellement été perçus comme plastiques et pouvant s'ajuster aux conditions écologiques et donc moins sujets à des différences génétiques entre populations et à former des adaptations locales. Cependant, de plus en plus d'études montrent que les traits de comportement ne sont peut-être pas aussi plastiques qu'on l'aurait cru. En effet, des études ont montré qu'il existe chez plusieurs taxons des différences de comportements entre les individus qui sont répétables et héritables, appelées personnalité (Réale et al. 2007; Bell et al. 2009; van Oers et Sinn 2011). Le phénotype de personnalité est souvent séparé en cinq types de traits (Réale et al. 2007): 1) la témérité, qui est la réaction d'un individu face à une situation risquée; 2) l'exploration, qui est le comportement d'un individu face à une situation nouvelle; 3) l'activité, qui réfère au niveau général d'activité d'un individu dans un environnement connu et non risqué; 4) l'agressivité, qui décrit la réaction d'un individu face à la présence de congénères et 5) la sociabilité, qui indique également la réaction d'un individu face à la présence de congénères, mais on parle ici surtout d'attraction ou d'évitement des congénères.

Depuis une quinzaine d'années, plusieurs études empiriques ont tenté d'expliquer les causes et les conséquences de la variation intraspécifique des traits de personnalité dans les populations naturelles (revue par Réale et al. 2007; Smith et Blumstein 2008; van Oers et Sinn 2011; Réale et al. 2010; Careau et Garland 2012). Ces études ont montré que les traits de personnalité sont souvent corrélés entre eux au niveau phénotypique et génétique (Koolhaas et al. 1999; Sih et al. 2004; Brommer et Kluen 2012; Dochtermann et Dingemanse 2013) et que le phénotype de personnalité peut être associé à la valeur adaptative des individus (Réale et Festa-Bianchet 2003; Smith et Blumstein 2008; Bergeron et al. 2013; Le Galliard et al. 2015). En outre, les différences de personnalité ont souvent été associées à des différences entre les individus pour des traits physiologiques et à des différences de stratégies d'histoire de vie (Réale et al. 2010; Careau et Garland 2012).

1.3 Le phénotype de personnalité pourrait être associé aux compromis d'histoire de vie

Selon plusieurs modèles théoriques et études empiriques, une association entre le phénotype de personnalité et les traits d'histoire de vie peut émerger lorsque les comportements interviennent dans les compromis d'histoire de vie par exemple le compromis entre la reproduction immédiate et future (Clark 1994; Stamps 2007; Wolf et al. 2007; Biro et Stamps 2008; Réale et al. 2010; Nicolaus et al. 2012; Sih et al. 2015). Par exemple, selon le modèle de Wolf et al (2007) les individus pourraient ajuster leur niveau de prise de risque en fonction du nombre de reproductions attendues (valeur reproductrice résiduelle). Ce modèle prédit que les individus qui ont plusieurs reproductions à venir prendraient moins de risques pour défendre leurs jeunes ou pour rechercher de la nourriture, car tout gain en matière de survie se traduirait par un gain en matière de valeur adaptative. Alors que les individus qui ont moins de reproduction à vivre (faible valeur reproductrice résiduelle) seraient plus prompts à prendre des risques, surtout si la prise de risque favorise la reproduction immédiate. Lorsque les phénotypes de personnalité sont associés à des stratégies d'histoire de vie et que leur association maximise la valeur adaptative et que ces traits sont héritables, on peut s'attendre à ce qu'il y ait eu une coévolution entre les différents types de traits dans un habitat donné ou une réponse plastique coordonnée de plusieurs traits (Réale et al. 2010; Nicolaus et al 2012; Sih et al. 2015).

1.4 L'hypothèse du syndrome de train de vie

L'hypothèse du train de vie a originellement été formulée pour expliquer l'association de plusieurs traits physiologiques et de traits d'histoires de vie dans le cadre de la sélection r et K (McArthur et Wilson 1967; Pianka 1970; Reznick et al. 2002). L'hypothèse du syndrome de train de vie se base sur le fait que les individus ont une quantité limitée de ressources disponibles, ils ne peuvent donc pas maximiser tous les traits d'histoire de vie en même temps (par exemple le nombre et la taille et des reproductions et la survie; Stearns 1992). Selon cette hypothèse, les espèces avec un train de vie « rapide » investissent davantage dans la reproduction que dans la survie, elles se reproduisent tôt et massivement, ont une survie limitée, investissent peu dans la qualité des jeunes et ont un métabolisme plus rapide. Alors que les espèces dites « lentes » se reproduisent plus tardivement, elles ont une survie plus longue, investissent davantage dans la qualité des jeunes que dans la quantité et ont un métabolisme plus lent (Lovegrove et al. 2003; Wikelski et al. 2003).

Suite aux modèles théoriques et études empiriques qui suggèrent que les traits de personnalité pourraient intervenir dans les compromis d'histoire de vie, Réale et al. (2010) ont proposé d'élargir l'hypothèse du syndrome de train de vie pour y inclure une dimension comportementale. Ils ont proposé de considérer les traits d'histoire de vie, les traits physiologiques et les traits de personnalité comme étant un ensemble de traits interdépendants qui auraient coévolués selon le contexte écologique des populations et des espèces. Par exemple, les individus qui vivent dans un contexte où la survie est limitée ont une valeur reproductive résiduelle plus faible. Si la prise de risques favorise la reproduction immédiate, nous pouvons alors nous attendre à trouver dans ces habitats des individus qui investissent davantage dans chaque événement reproductif et adoptent des comportements plus risqués si ces comportements permettent de maximiser la reproduction actuelle. Ainsi, selon l'hypothèse du syndrome de train de vie, lorsque les conditions écologiques varient dans l'espace, nous pourrions nous attendre à trouver différentes combinaisons de phénotypes de personnalité, de stratégie d'histoire de vie et de phénotype physiologique dans l'espace, chaque population présentant des combinaisons qui optimisent la valeur adaptative dans leur habitat respectif (Réale et al. 2010).

Plusieurs études ont paru dans les dernières années afin d'examiner les prédictions de l'hypothèse du syndrome de train de vie (notamment Bouwhuis et al. 2013; Le Galliard et al. 2013; Niemelä et al. 2013; Montiglio et al. 2014; Hall et al. 2015). Pour l'instant, il semble qu'il existe souvent des corrélations entre des traits d'histoire de vie, des traits physiologiques et des traits de personnalité, mais que ces corrélations ne sont pas toujours dans le sens attendu par l'hypothèse du syndrome de train de vie (Réale et al. 2010; Careau et Garland 2012; Montiglio et al. in prep). Néanmoins, peu d'études ont été en mesure de déterminer si les traits de personnalité étudiés interviennent réellement dans les compromis d'histoire de vie de l'espèce et de la population étudiée (Nicholaus et al. 2012; Montiglio et al in prep). De plus, peu d'études ont déterminé si les associations de traits varient selon les conditions écologiques locales.

1.5 L'hypothèse du syndrome de train de vie et l'hétérogénéité environnementale

Des études récentes suggèrent que l'hétérogénéité environnementale pourrait être un mécanisme important à l'origine de la création et du maintien de la variation intraspécifique de personnalité au niveau phénotypique et génétique (Dingemanse et al. 2004; Bell 2005; Boon et al. 2007; Quinn et al. 2009; Dingemanse et al. 2010; Atwell et al. 2012; Taylor et al. 2014; Nicolaus et al. 2016; Heinen-Kay et al. 2016). D'abord, il a été démontré que la direction et l'intensité de la sélection sur le phénotype de personnalité peuvent fluctuer dans le temps (Dingemanse et al. 2004; Boon et al. 2007; Quinn et al., 2009; Taylor et al. 2014; Nicolaus et al. 2016) ce qui suggère que la relation entre les phénotypes de personnalité et la valeur adaptative peut varier selon les conditions écologiques. Ensuite, un nombre croissant d'études chez divers taxons ont trouvé différents phénotypes moyens de personnalité entre des populations localisées dans différents contextes écologiques (Bell 2005; Quinn et al. 2009; Dingemanse et al. 2010; Atwell et al. 2012; Herczeg et al. 2013; Maes et al. 2013; Miranda et al. 2013; Heinen-Kay et al. 2016; Karlsson Green et al. 2016). Néanmoins, peu de ces études ont été en mesure de déterminer l'importance de la plasticité et des effets génétiques pour la différenciation des populations et la plupart qui l'ont fait ont été réalisées chez des espèces aquatiques et concernent des populations séparées par de grandes distances spatiales (Bell 2005; Herczeg et al. 2013; Jacquin et al. 2016; Karlsson Green et al. 2016, mais voir Atwell et al. 2012 et Miranda et al. 2013). Ainsi, nous connaissons encore mal les causes de la divergence des populations naturelles pour des traits de personnalité et encore moins pour des espèces terrestres séparées par de petites distances spatiales. De plus, très peu d'études ont considéré simultanément des traits comportementaux, des traits physiologiques et des traits d'histoire de vie en plus du contexte écologique des populations et des flux géniques qui les unissent.

1.6 Objectifs et structure de la thèse

L'objectif général de ce projet était d'améliorer nos connaissances sur les causes de la variation intraspécifique des traits de personalité. Plus spécifiquement, notre objectif était de déterminer si une forte variation spatiale de conditions écologiques pouvait mener à une divergence phénotypique et génétique adaptative pour des traits de personnalité entre des populations connectées par un flux génique. Nous avons répondu à cet objectif grâce au suivi à long terme de trois populations sauvages de mésanges bleues (*Cyanistes caeruleus*) présentent dans une mosaïque d'habitats en Corse (France). Ces populations présentent des différences importantes de conditions écologiques. De plus, des études réalisées précédemment ont montré que bien qu'elles soient connectées par un flux génique et séparées par de petites distances spatiales (6 à 25 km), ces populations diffèrent au niveau phénotypique et génétique pour plusieurs types de traits, dont des traits d'histoire de vie (Charmantier et al. 2016). Ce projet a quatre objectifs principaux (Chapitre 2 à 5) qui forment les quatre prochains chapitres de cette thèse et qui feront chacun l'objet d'un article dans une revue scientifique.

D'abord, au Chapitre 2, nous avons déterminé s'il y avait des différences de phénotype moyen entre les populations, si ces différences étaient reliées aux différences de traits d'histoire de vie qui ont déjà été observées et pourraient être en accord avec l'hypothèse du syndrome de train de vie. Ensuite, au Chapitre 3, nous avons utilisé une expérience de jardin commun afin de déterminer si les différences phénotypiques observées au Chapitre 2 avaient des bases génétiques et si elles étaient le fruit de processus neutres comme de la dérive génique. Au Chapitre 4, nous avons comparé le phénotype moyen de personnalité de mésanges âgées de 12 et 15 jours et, grâce à une expérience de transfert réciproque de nids et d'habitats, nous avons déterminé si ces différences étaient génétiques et héritables. Enfin, au Chapitre 5, pour vérifier si les divergences observées aux chapitres précédents pourraient être adaptatives, nous avons déterminé les pressions de sélection sur les traits de personnalité des individus reproducteurs et des jeunes dans chacune des populations.

1.7 Espèce modèle et populations d'études

La mésange bleue est un petit passereau (9 à 10 grammes environ) de la famille des paridés, elle est commune dans toute l'Europe du Nord et niche dans des cavités naturelles et artificielles. C'est une espèce monogame socialement et les deux partenaires participent aux soins parentaux. En milieu méditerranéen, la mésange bleue est sédentaire. Elle se nourrit d'insectes en tous genres, mais elle se nourrit préférentiellement de chenilles folivores qui se trouvent sur les jeunes pousses des chênes lors de leur saison de reproduction dans notre aire d'étude (Banbura et al. 1999).

Ce projet s'insère dans un suivi populationnel de mésanges bleues initié en 1976 par une équipe de chercheurs du CEFE (Centre d'Écologie et Fonctionnelle et Évolutive) de Montpellier. Chaque année, tous les nichoirs occupés (environ 200) sont visités pendant la reproduction des oiseaux (avril à juin), les nids sont suivis de la construction jusqu'à l'envol des jeunes et les couples reproducteurs sont capturés, bagués et mesurés. Ainsi, nous connaissons la date de ponte, le nombre d'œufs éclos et le nombre de jeunes à l'envol de tous les individus qui se sont reproduits sur les sites d'études. Dans le cadre de cette thèse, nous avons aussi effectué plusieurs mesures de phénotype de personnalité. Les protocoles utilisés pour chacun des traits de personnalité étudiés sont détaillés aux Chapitres 2 à 5.

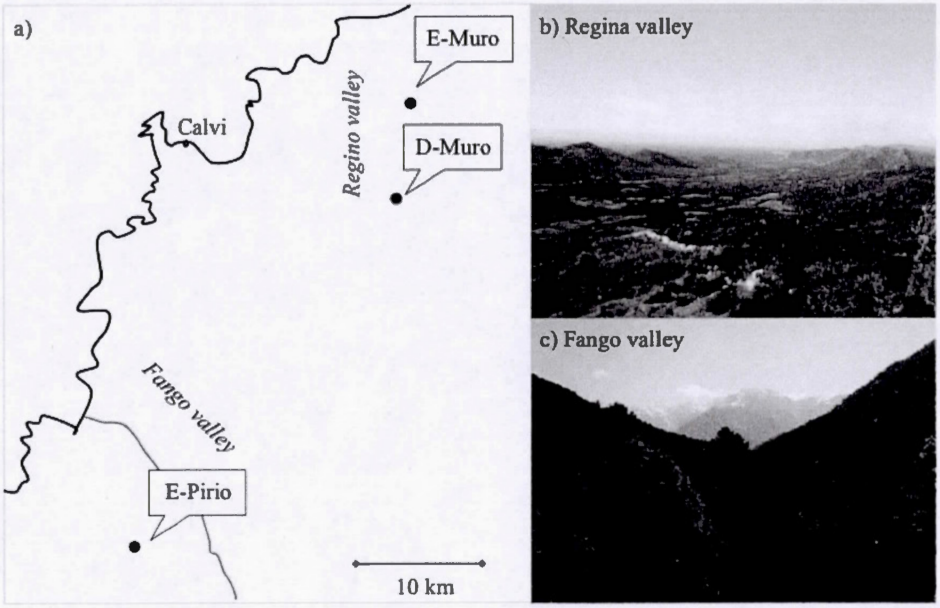

Figure 1.2 a) Représentation schématique des trois populations étudiées. Ces populations sont situées dans deux vallées: la vallée du Fango (*Fango valley*; E-Pirio) et la vallée de Régina (*Regino valley*; D-Muro et E-Muro). E-Muro est situé dans un habitat dominé localement par le chêne vert alors de D-Muro dans un habitat dominé localement par le chêne blanc. La population de E-Pirio est située dans un habitat dominé par le chêne vert à l'échelle de la vallée; b) photo de la vallée de Régina et c) de la vallée du Fango.

Les populations étudiées sont situées dans une mosaïque de chênes verts (*Quercus ilex*) caducifoliés et de chêne blancs (*Quercus humilis*) sempervirents (Fig. 1.2). Deux populations sont situées dans un habitat dominé par le chêne vert (Evergreen-Pirio, E-Pirio dans la suite du texte et Evergreen-Muro, E-

Muro) et une population dans un habitat dominé par le chêne blanc (Deciduous-Muro, D-Muro; Fig. 1.2). Le chêne blanc renouvèle la totalité de son feuillage chaque printemps alors que le chêne vert en renouvèle qu'une partie. Le chêne blanc débourre environ trois semaines plus tôt que le chêne vert. À cause des différences de renouvellement des feuilles, les chenilles sont beaucoup plus abondantes dans les habitats de chênes blancs que dans les habitats de chêne verts. Ainsi, l'espèce d'arbre dominante dans chacune des populations génère des différences de quantité de nourriture entre les habitats et des différences dans la phénologie d'abondance des chenilles. Les milieux de chênes verts sont classiquement considérés comme moins favorables pour la reproduction des mésanges bleues (Blondel et al. 2006). Les populations de E-Muro et de D-Muro sont séparées par environ 6 km et situées dans la même vallée (Regina) alors que la population de E-Pirio est située dans la vallée du Fango, 25 km plus loin (Fig. 1.2). Le contexte écologique de chacune des vallées notamment le degré d'urbanisation et la fragmentation du paysage engendrent une différence de contexte écologique entre E-Muro et E-Pirio, bien que les deux populations aient la même espèce d'arbre dominante (Fig. 1.2).

Le Tableau 1.1 montre les principales caractéristiques écologiques des habitats et les traits phénotypiques des individus qui s'y trouvent. Les mésanges de D-Muro et de E-Pirio montrent des différences phénotypiques marquées. D'abord, les mésanges synchronisent leur date de ponte avec le moment où l'abondance des chenilles est maximale dans leur habitat respectif ce qui cause une différence de date de ponte qui peut aller jusqu'à un mois entre ces deux populations. De plus, les mésanges de D-Muro font plus de jeunes qu'à E-Pirio et leurs jeunes sont plus lourds (Blondel et al. 2006; Charmantier et al. 2016). Les mésanges de E-Muro présentent globalement des phénotypes intermédiaires entre D-Muro et E-Pirio. Basé sur les différences de traits d'histoires de vie connues (Tableau 1.1), il semble que les mésanges de la population de chênes blancs (D-Muro) présentent un train de vie comparativement plus rapide que les mésanges qui habitent les habitats de chênes verts (E-Muro et E-Pirio).

Des analyses génétiques ont révélé que ces populations sont différenciées au niveau génétique malgré le fait qu'elles sont séparées par une distance spatiale que des mésanges peuvent facilement parcourir lors de leur dispersion (Porlier et al. 2012a; Szulkin et al. 2016; Charmantier et al. 2016). Néanmoins, leur F_{st} demeure plutôt faible (entre 0.01 and 0.009; Szulkin et al. 2016), ce qui indique qu'elles sont tout de même connectées par un flux de gènes. Les résultats des études réalisées jusqu'à présent sur ce système suggèrent que les différences observées au Tableau 1.1 pourraient être adaptatives et avoir évolué (Blondel et al. 2006; Charmantier et al. 2016). En effet, il a été démontré que plusieurs des traits présentés au Tableau 1.1 sont héritables, que les différences phénotypiques observées entre les populations pour plusieurs de ces traits pourraient avoir une base génétique (Lambrechts et al. 1999; Braillet et al. 2002; Charmantier et al. 2004a; Teplitsky et al. 2014) et qu'il y a des différences de pressions de sélection entre les habitats (Blondel et al. 2002; Teplisky et al. 2014).

Tableau 1.1 Traits d'histoire de vie et morphologiques (moyenne (*n*)) et abondance de chenilles dans les trois populations de mésanges bleues corses étudiées (France); il est indiqué au bas du tableau le syndrome de train de vie qui caractérise chacune des populations basé sur leurs phénotypes moyens de traits d'histoire de vie.

Habitats / populations	Chêne blanc D-Muro	Chêne vert E-Muro	Chêne vert E-Pirio
Première année d'échantilonnage	1993	1998	1976
Probabilité annuelle de survie adulte [1]	0.40 (*15*)	0.58 (*15*)	0.49 (*15*)
Date de ponte (1^{er} oeuf) [2] 1= 1^{st} Mars	38.56 (*1233*)	48.21 (*640*)	70.08 (*1920*)
Masse, mâles (g) [2]	9.82 (*1032*)	9.66 (*1032*)	9.37 (*1607*)
Masse, femelles (g) [2]	9.66 (*1153*)	9.47 (*480*)	9.23 (*1616*)
Taille du tarse, mâles (mm) [2]	16.52 (*578*)	16.42 (*198*)	16.27 (*789*)
Taille du tarse, femelles (mm) [2]	16.05 (*614*)	15.99 (*224*)	15.84 (*798*)
Taille de ponte [2]	8.50 (*1235*)	7.12 (*638*)	6.61 (*1913*)
Nombre de jeunes (15jours) [2]	6.60 (*1092*)	4.14 (*557*)	4.15 (*1273*)
Abondance des chenilles [3]	762.87	689.32	87.10
Train de vie	*Rapide*	*Lent / intermédiaire*	*Lent*

1. Dubuc-Messier et al Chapitre 5; 2. Charmantier et al. 2016 (ces données ont été récoltées entre la première année du suivi populationnel et 2014); 3. Moyenne du nombre maximal de fèces de chenilles mg/m^2 par jour (échantillonné dans chacune des populations entre 2011 et 2015), voir Zandt et al. 1990 pour avoir des détails sur la procédure d'échantillonnage.

CHAPITRE 2
ENVIRONMENTAL HETEROGENEITY AND POPULATION DIFFERENCES IN BLUE TITS PERSONALITY TRAITS.

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2.1 Abstract

Environmental heterogeneity can result in spatial variation in selection pressures that can produce local adaptations. The pace-of-life syndrome hypothesis predicts that habitat-specific selective pressures will favor the co-evolution of personality, physiological and life-history phenotypes. Few studies so far have compared these traits simultaneously across different ecological conditions. In this study, we compared three personality traits (handling aggression, exploration speed in a novel environment and nest defense behavior) and one physiological trait (heart rate during manual restraint) across three Corsican blue tit (*Cyanistes caeruleus*) populations. These populations are located in contrasting habitats (evergreen *vs.* deciduous) and are situated in two different valleys 25 km apart. Birds from these populations are known to differ in life-history characteristics, with birds from the evergreen habitat displaying a slow pace-of-life, and birds from the deciduous habitat a comparatively faster pace-of-life. We expected personality to differ across populations in line with the differences in pace-of-life documented for life-history traits. As expected, we found behavioral differences among populations. Despite considerable temporal variation, birds exhibited lower handling aggression in the evergreen populations. Exploration speed and male heart rate also differed across populations, although our results for exploration speed were more consistent with a phenotypic difference between the two valleys than between habitats. There were no clear differences in nest defense intensity among populations. Our study emphasizes the role of environmental heterogeneity in shaping population divergence in personality traits at a small spatial scale.

2.2 Introduction

Environmental heterogeneity can have a fundamental impact on phenotypic diversity. In particular, heterogeneous environments can result in spatially variable selection pressures, thereby contributing to phenotypic divergence among populations via phenotypic plasticity or via local adaptations (Endler 1986; Kawecki and Ebert, 2004; Nosil et al. 2005; Wang and Bradburd 2014). Gene flow among different habitat patches can limit the action of environmental heterogeneity on the evolution of local adaptations, but its impact varies depending on the distances among habitat patches and on the ecology of the species (Lenormand 2002; Kawecki and Ebert 2004; Wang and Bradburd 2014). The evolutionary importance of environmental heterogeneity and gene flow has been highlighted in multiple studies of morphological or life-history traits (Reznick et al. 2001; Garant, Forde and Hendry, 2007; Garant et al. 2007; Siepielski et al. 2013). In contrast, their roles in the evolution of behavioral adaptations have seldom been studied (Bell 2005; Quinn et al. 2009; Dingemanse et al. 2010; Dingemanse and Réale 2013) maybe because behavioral traits have often been described as highly plastic. However, we now know that repeatable and heritable behavioral differences among individuals, *i.e.* animal personality, can be found in numerous species (van Oers et al. 2005; Réale et al. 2007; Bell et al. 2009; Dingemanse and Dochtermann 2014). In addition, recent studies in various taxa have shown that personality phenotypes can be under strong selection and their selection regime can fluctuate depending on environmental conditions (Réale and Festa-Bianchet 2003; Dingemanse et al. 2004; Boon et al. 2007; Smith and Blumstein 2008; Quinn et al. 2009; Conrad et al. 2011; Montiglio et al. 2014; Nicolaus et al. 2016). For example, in great tits (*Parus major*) the strength of selection on exploratory behavior varies spatially and temporally according to local density and resource availability (Quinn et al. 2009; Nicolaus et al. 2016). In the common lizard (*Zootoca vivipara*) when population density is low, individuals that are more sociable and less active grow faster and survive longer than less sociable, active individuals, but these differences disappear at higher density (Le Gaillard et al. 2015).

An increasing number of studies show that personality traits covary with life-history and physiological traits (Réale et al. 2000; Boon et al. 2007; Dammhahn 2012; Korsten et al. 2013; Montiglio et al. 2014; Careau et al. 2015). Réale et al. (2010) developed the pace-of-life syndrome hypothesis, where they postulated that personality and physiological traits might have (co)evolved with life-history strategies (see also Ricklefs and Wikelski 2002; Wikelski et al. 2003; Wiersma et al. 2007). According to this hypothesis, individuals, populations, or species are positioned along a slow-fast pace-of-life continuum. For example, individuals showing risky behaviors resulting in increased predation probability (e.g. faster exploration patterns, higher aggressiveness and higher boldness) are positioned on the fast end of the pace-of-life continuum, and should therefore reproduce at an earlier age, produce more offspring per reproductive event, and have lower adult survival, while those showing safer behaviors (slower exploration, less aggressiveness and lower boldness) should be at the slow end of the pace-of-life continuum (Réale et al. 2010). Based on the asset-protection principle (Clark 1994), theoretical studies predict that the association between personality traits related to risk-taking and life-history traits might emerge when behavior mediates life-history trade-offs, such as the trade-off between current and future reproduction (Stamps 2007; Wolf et al. 2007). Such an association has been recently observed in a number of empirical studies (Biro and Stamps 2008; Réale et al. 2010; Nicolaus et al. 2012).

The association between personality/life-history traits and fitness may vary in time or in space, depending on the environmental conditions and fitness expectations (Réale et al. 2010; Montiglio et al. 2014). For example, according to the pace-of-life syndrome hypothesis, environmental conditions that reduce residual reproductive value (*i.e.* low adult survival) should favor a fast life-history strategy (*i.e.* strong reproductive investment early in life and reduced longevity), and a fast personality (*i.e.* risky behavior such as fast exploration pattern and high aggressiveness) if the fast personality phenotype favors current reproduction at the expense of future survival. Conversely, environmental conditions that increase residual reproductive value (*i.e.* high adult survival) but provide limited resources for reproduction should favor the evolution of both a slow pace-of-life (*i.e.* prolonged longevity and reproductive investment spread over a long lifetime) and a slow personality (*i.e.* safer behavior such as slow exploration pattern and low aggressiveness). Hence spatial and temporal variation in environmental conditions has the potential to create a geographical mosaic of a combined set of personality and life-history phenotypes or to promote the evolution of a coordinated phenotypic plasticity for a body of traits (Montiglio et al. 2014). To date only a few empirical studies have shown that populations inhabiting different habitats differ in suites of traits involved in the pace-of-life syndrome (but see Atwell et al. 2014).

In this study, we compared the distribution of personality phenotypes across three blue tit (*Cyanistes caeruleus*) populations living in contrasting habitats (Fig. 2.1). Long-term monitoring of these populations has previously revealed strong phenotypic differences for numerous life-history, morphological, and ornamental traits despite their spatial proximity (from 5.6 to 25.0 km between each population; Table 2.2.1; Charmantier et al. 2016). These populations live in two different valleys on the island of Corsica (France) dominated by different tree species, the deciduous downy oak (*Quercus pubescens*) and the evergreen holm oak (*Quercus ilex*). One population is located in a deciduous habitat (Deciduous-Muro, hereafter D-Muro) while the other two populations are located in a habitat dominated locally by evergreen oaks (Evergreen-Muro and Evergreen-Pirio, hereafter E-Muro and E-Pirio; Fig. 2.1). The deciduous *versus* evergreen nature of the locally dominant tree species in each population and valley has a cascading influence on several ecological features, which in turn affect the birds' life-history characteristics (Blondel et al. 1999). For example, large differences in the timing and abundance of food resources (*i.e.* mainly the leaf-eating *Tortrix viridana* caterpillars) result in differences in clutch size, nestling number and up to a month difference in laying dates between E-Pirio and D-Muro (Table 2.1; Charmantier et al. 2016). Furthermore, individuals in the two evergreen habitats have higher adult survival probabilities than individuals from the deciduous habitat (Table 2.1). Hence, based on their life-history characteristics, individuals from the evergreen habitats could be characterized as displaying a slower pace-of-life than individuals from the deciduous habitat D-Muro, which are displaying a comparatively faster pace-of-life (Table 2.1).

In each population, we repeatedly measured three behavioral traits and one physiological trait traditionally used in personality studies and that are related to risk taking. First, we measured docility as the reaction of birds towards handlers (Réale et al. 2007). Docility is related to life-history traits (Réale et al. 2000; (Réale et al. 2009), and has been shown to be repeatable and heritable in blue tits (Brommer and Kluen 2012; Class et al. 2014). Although our test was slightly different than Brommer and Kluen (2012), we decided to call docility "handling aggression", so that the highest score for this behavior corresponds to the most aggressive response and to facilitate comparisons with other works on blue tits (Brommer and Kluen 2012; Class et al. 2014). Second, we quantified heart rate during manual restraint. This trait has been shown to be repeatable in different species (Koolhaas et al. 1999; Réale et al. 2009; Montiglio et al. 2012; Ferrari et al. 2013) and is also potentially associated with life history characteristics (Réale et al. 2010). Heart rate during stressful events, like manipulation, is often studied in the context of coping styles and is linked to the activity of the sympathetic and parasympathetic nervous systems (Koolhaas et al. 1999; Ferrari et al. 2013). Coping styles correspond to the way individuals cope with a stressful situation (Koolhaas et al. 1999; Groothuis and Carere 2005). Coping style is linked with many of the behaviors typically associated with fast and slow pace-of-life (Réale et al. 2010): at one extreme proactive individuals are highly active, highly aggressive, and fast explorers, whereas at the other extreme reactive individuals are, lowly active, lowly aggressive, and slow explorers (Koolhaas et al. 1999). The sympathetic nervous system is presumed to be the dominant system in proactive individuals, whereas the parasympathetic nervous system is presumed to be dominant in reactive individuals (Koolhaas et al. 1999, 2007). Third, we quantified exploration behavior in a novel environment. Exploration in a novel environment is traditionally used in personality studies (Réale et al. 2007), and is repeatable in blue tits (Mutzel et al. 2013). Finally, we measured nest defense behavior, which is assumed to decrease the probability that a predator will harm the offspring in a nest while increasing the probability of injury for the parents (Trivers 1972; Montgomerie and Weatherhead 1988). Nest defense behavior involves a trade-off between parental survival and offspring protection. An increasing number of studies have shown among-individual variation in nest defense intensity revealing among-individual differences in investment in current reproduction *versus* residual reproductive value (Montgomerie and Weatherhead 1988; Hakkarainen and Korpimäki 1994; Kontiainen et al. 2009; Fresneau et al. 2014).

We expected that the difference in ecological conditions between habitats and populations would produce different selection pressures on personality traits that would result in different mean personality phenotypes among habitats and populations in our study system. As proposed by the pace-of-life syndrome hypothesis, we expected that the differences in personality phenotype between habitats would be linked to their difference in life-history characteristics. More specifically, we predicted that in the evergreen habitats individual blue tits would display personality phenotypes associated with a slow pace-of-life, whereas individuals inhabiting the deciduous habitat would display personality phenotypes associated with a faster pace-of-life. Based on previous studies on personality, we expected that a higher handling aggression (Réale et al. 2010), a faster heart rate during manual restraint (increased activity of the sympathetic system; Koolhaas et al. 1999; Ferrari et al. 2013), a faster exploration pattern (Réale et al. 2010; Nicolaus et al. 2012), and a higher nest defense intensity (Montgomerie and Weatherhead 1988) would be associated with a faster life style and would therefore be found in individuals located in the deciduous population (D-Muro). Because the differences in ecological conditions and life-history characteristics are more salient between E-Pirio and D-Muro than between E-Muro and D-Muro (Table 2.2.1), we expected more substantial differences in personality phenotypes between the two former populations. In addition, because sex differences in personality traits and behavioral syndromes are found in an increasing number of studies (Schuett et al. 2010, Dammhahn 2012; Fresneau et al. 2014) we expected to find sex differences in mean phenotypes and sex-specific differences between populations.

The two valleys (Regino and Fango) have different ecological conditions, which could also be important in shaping the personality phenotype of blue tits in each population. Indeed, in the Regino valley (E-Muro and D-Muro populations; Fig. 2.1), the dominant tree species is the deciduous oak, and the evergreen oak is only present in isolated patches (e.g. E-Muro). In contrast, in the Fango valley (E-Pirio) the deciduous oak is completely absent, and the evergreen oak is the dominant species and forms a homogeneous habitat (Porlier et al. 2012a). The two valleys also differ in their level of anthropogenic activities, precipitation and temperature. Therefore, the two evergreen populations, share the same dominant oak species at a small spatial scale, but differ in their ecological conditions at the scale of the valley. Although E-Muro and D-Muro share the same large-scale ecological conditions that are specific to the valley, they experience different ecological conditions at a small spatial scale (e.g. proportion of deciduous oak). The results from previous studies in this system suggest that morphological and life-history traits are shaped by factors that vary at different spatial scales; some traits are shaped by factors specific to the local dominant oak species and others by factors specific to the valley. For example, E-Muro birds display laying dates and female tarsus lengths similar to D-Muro but their average number of fledglings and adult survival probabilities are more similar to E-

Pirio (Table 2.1). Hence, the comparison of personality phenotypes among these three populations may provide insight into the spatial scale at which environmental conditions affect the phenotype of different personality and physiological traits.

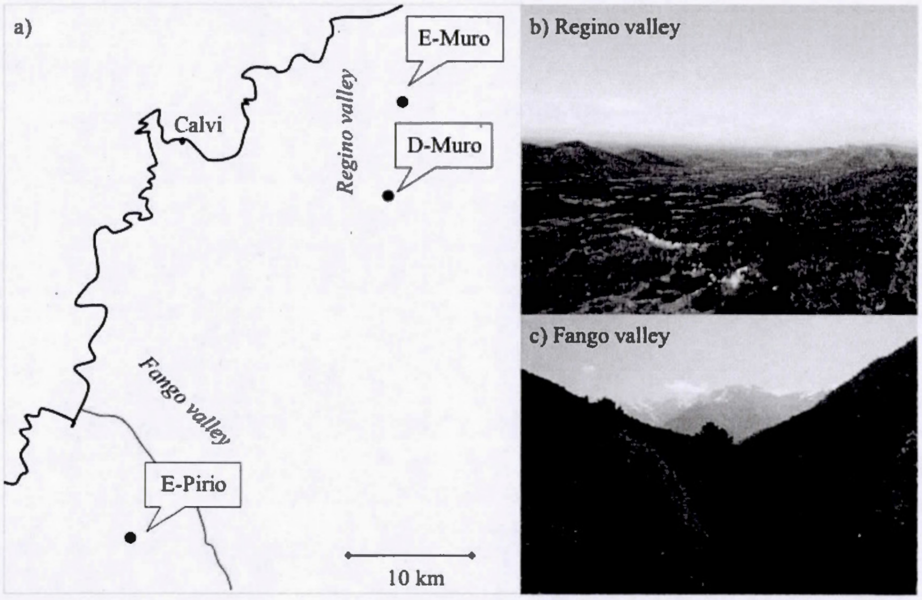


Figure 2.1 a) Schematic representation of our three study populations located in two different valleys: the Fango valley and the Regino valley. The study area in the Regino valley is divided into two study populations: E-Muro and D-Muro. E-Muro is located in a forest dominated locally by evergreen oaks and D-Muro in a forest dominated by deciduous oaks. The E-Pirio population is located in a forest dominated by evergreen oaks in the Fango valley; b) picture of the Regino valley and c) of the Fango valley.

Tableau 2.1 Life-history, morphological characteristics (mean (*n*)) and caterpillar abundance in the three Corsican blue tit populations studied (France). At the bottom of the table we have indicated the pace-of-life syndrome characterizing each population according to their life-history characteristics.

Habitats / populations	Deciduous D-Muro	Evergreen E-Muro	Evergreen E-Pirio
First year of monitoring	1993	1998	1976
Annual adult survival probability ^{1}	0.39 (*15*)	0.58 (*15*)	0.47 (*15*)
Date of first egg laying ^{2} 1= 1st March	38.56 (*1233*)	48.21 (*640*)	70.08 (*1920*)
Male body mass (g) ^{2}	9.82 (*1032*)	9.66 (*1032*)	9.37 (*1607*)
Female body mass (g) ^{2}	9.66 (*1153*)	9.47 (*480*)	9.23 (*1616*)
Male tarsus length (mm) ^{2}	16.52 (*578*)	16.42 (*198*)	16.27 (*789*)
Female tarsus length (mm) ^{2}	16.05 (*614*)	15.99 (*224*)	15.84 (*798*)
Clutch size ^{2}	8.50 (*1235*)	7.12 (*638*)	6.61 (*1913*)
Number of fledglings ^{2}	6.60 (*1092*)	4.14 (*557*)	4.15 (*1273*)
Caterpillar abundance ^{3}	762.87	689.32	87.10
Pace-of-life	*Fast*	*Slow / intermediate*	*Slow*

1. Dubuc-Messier et al in prep.: these survival probabilities were estimated with the software E-SURGE v.1.9 (Choquet et al. 2009; from years 2000 to 2015); they are in line with the survival probability estimations of Grosbois et al. (2006; Pirio : years 1985 to 2000 and D-Muro: 1993 to 2000); the number in parenthesis refers to the number of years considered in the analyses. 2. Charmantier et al. 2016 (collected between the first year of monitoring and 2014); 3. mean maximal frass mg/m^2 per day (sampled in each population between 2011 and 2015 during the breeding period using 0.25m^2 trays placed under the forest canopy and collected twice a week, see Zandt et al. 1990 for details about the sampling procedure).

2.3 Methods

2.3.1 Study species, sites, population characteristics and field protocol

Blue tits are small (9 to 13g) forest cavity-nesting passerine birds, commonly found in wooded habitats of the western Palearctic, ranging from southern Scandinavia to the Canary Islands. Blue tits are socially monogamous with biparental care, and are sedentary in our study populations. This study was conducted in three populations in the region of Calvi, Corsica, France: E-Pirio (42°34'N, 08°44'E; 200 m elevation; 205 nest-boxes distributed in two study plots), E-Muro (42°35'N, 08°57'E; 100 m elevation; 75 nest-boxes distributed in three study plots) and D-Muro (42°32'N. 08°55'E, 350 m elevation; 110 nest-boxes distributed in three study plots). These populations have been studied since 1976, 1998, and 1994, respectively (Blondel et al. 2006; Charmantier et al. 2016).

A weekly to daily monitoring over the course of the breeding season, from early April to the end of June, allowed us to record the exact laying dates and clutch sizes for all broods in nest-boxes. Adult blue tits were captured in nest-boxes, identified or ringed with unique metal rings provided by the CRBPO (France), and weighed to the nearest g using a Pesola® spring. In 2014 and 2015 we used color rings (Ecotone® 2.7mm) placed on the tarsus for further identification during nest defense observations. We determined the sex of each individual by examining the presence/absence of a brood patch during the breeding period or based on feather coloration outside the breeding period (Perrins 1979; Ferns and Hinsley 2010; Fresneau et al. 2014). All nestlings were also weighed, measured, and uniquely identified with metal rings placed on their right tarsus at 9 to 15 days of age.

2.3.2 Behavioral tests

Behavioral tests were run between 2011 and 2015. Tests were performed either during the pre-breeding period when males and females paired up and started defending a territory (from March 17th to 30th for D-Muro and E-Muro, and from April 4th to May 3rd for E-Pirio), or during the breeding period when adults were feeding nestlings. During the pre-breeding period, birds were caught with a mist net or lured into a trap using a live blue tit decoy and playback of territorial calls near a nest-box. Birds were then tested for handling aggression, heart rate during manual restraint, and exploration behavior in a novel environment. During the breeding period we also measured handling aggression on parents caught inside the nest-box when nestlings were 10-14 days old and measured nest defense behavior when nestlings were nine days old. All tests, except handling aggression, were performed only once a year for each individual. Occasionally, a bird was caught twice during the pre-breeding period, but it was immediately released after the second capture, or if a test was done unintentionally this test was discarded from the data set (tests from 22 individuals were discarded). Handling aggression tests were done at most twice per year per individual (once during the pre-breeding and once during the breeding period). For every trait, there were one or two observers that performed most of the observations in every population for at least three years (40 to 70% observations were made by two observers, see Table S2.1 to S2.3 for details).

Handling aggression score

Handling aggression was scored from 2011 to 2014. The test was done within two minutes after capture, directly after removing the bird from the trap and prior to any other manipulations. The handler held the bird in the upright position, head up, with his back facing the handler. He held the bird with one hand and placed the bird's legs between his forefinger, his middle finger and his thumb to let the bird free to move its tails and wings. The handler pointed the forefinger of his other hand at a spot about 2 to 3 cm in front of the bird's beak and noted if the bird struck at his finger, and the position of its wings and tail. After two seconds in this position, the handler moved his forefinger towards the bird's beak two or three times and recorded its reaction. The score ranged from 0 (the bird shows no reaction) to 3 (the bird spontaneously strikes the handler's fingers and spreads its wings and tail). The scoring protocol is reported in detail in Table S2.4. The entire test lasted less than a minute.

Heart rate during manual restraint

Heart rates during manual restraint (HR, hereafter) were collected between 2011 and 2015. Following the handling aggression scoring, the bird was put in a cloth bag and brought to the novel-environment apparatus (approximately 1 to 200 m away) where we recorded heart rate during manual restraint. Prior to recording, the handler placed the bird's head between his forefinger and his middle finger and put the bird's legs between his thumb and forefinger. HR was then recorded for 30 seconds, using a digital recorder with the microphone placed close to the bird's cloaca and directed towards the heart.

Back in the lab, we used the software Avisoft SASLab Pro version 5.1 to extract the mean time interval (sec) between two heart beats using approximately 100 consecutive heart beats per individual. We used the number of heartbeats in a minute (60 / mean time interval) in the analysis. We recorded HR instead of breath rate (BR hereafter), a measure more commonly used in bird studies (Carere and van Oers 2004; Brommer and Kluen 2012; Kluen et al. 2014; Fucikova et al. 2009), because, while the analysis is more time consuming, HR scoring can be automated and is thus less prone to errors or biases than BR. To compare our results with other studies on birds, we examined the correlation between HR and BR on a subsample of 102 birds in 2015. BR was measured right after recording HR, following the protocol described by Brommer and Kluen (2012). In short, we measured the time required for the bird to take 30 breaths and repeated this procedure twice. We transformed the average of the two measures to obtain the number of breaths in a minute (1800 / average of the two measures).

Exploratory behavior in a novel environment

Data on exploration were collected between 2011 and 2014. After a bird's heart rate was measured, it was placed in a novel-environment apparatus built on the model proposed by Mutzel et al. (2013). From 2011 to 2013, the apparatus consisted of a large white cage (120 cm x 50 cm x 50 cm) with six perches and one side composed of small mesh, allowing us to video trials (Fig. S2.1a). The apparatus was placed in the trunk of a car (Kangoo, Renault), and the car side and back windows were covered with a tarp to isolate the tested bird from the external environment (Fig. S2.1a). Natural light was used for the video recording. In 2014, to homogenize light conditions over time and space, we used a slightly smaller novel-environment apparatus (110 x 50 x 50 cm) placed inside a closed trailer and artificial lights for every trial (Fig. S2.1b). Prior to all trials, the bird was placed for two minutes in a closed chamber (15 x 15 x 15 cm) located on the right hand side of the novel-environment apparatus, and connected to the main chamber by a sliding door. We then opened the door, gently pushed the bird inside the main chamber and video recorded its behavior for five minutes. The bird was subsequently retrieved of the novel-environment apparatus, ringed when necessary, weighed, and released. Birds that could not be put in the novel-environment apparatus right after the heart rate measurement were placed in a small cloth bag for a maximum of 30 minutes. When the time interval between the HR recording and the novel-environment trials was more than 30 minutes, the birds were placed in a cage with water and mealworms (n =193 trials).

Back in the lab, we extracted the average speed of the bird (cm/s) during the trial using the software EthoVision XT version 9 and we used this variable in the analyses as a measure of exploratory behavior. Compared to other ways of measuring movements in the novel environment, the computation of average exploration speed can be automated, reducing both errors and biases. Furthermore, the average speed was well correlated to the number of large flights in our novel-environment apparatus ($r = 0.9$, $p < 0.001$, $n = 20$), a measure that has commonly been used to quantify exploratory behavior in other studies (Dingemanse et al. 2002; Mutzel et al. 2013).

Nest defense behavior

Nest defense trials were conducted from 2012 to 2015 in E-Pirio and in 2012, 2014 and 2015 in D-Muro and E-Muro. We measured nest defense behavior with a stuffed Eurasian jay (*Garrulus glandarius)*, a common predator of blue tit nestlings in Corsica. The decoy was placed as close as possible to the nest-box (min = 0.50 m, max = 4.00 m, mean = 1.18 m, standard deviation (s.d.) = 0.67 m). The observer was hidden between 6 and 30 m from the nest-box (mean = 14.14 m, s.d.= 4.33 m). As soon as a parent blue tit approached within 15 meters of the nest-box we estimated its minimal approach distance from the nest-box during the next five minutes. For practical reasons, recording the distance to the nest-box was much easier and more accurate than estimating distance to the predator, but the two distances were highly correlated and parents did not approach nest-boxes with the intention of feeding their nestlings since they systematically dropped or ate their prey once they located the predator, and none entered the nest-box during the test (Dubuc-Messier pers. obs.). We recorded the behavior of the two partners at the same time when they were both present. Tests were done only once per nest-box per year. Birds that did not enter the 15-meter perimeter within fifteen minutes after the beginning of the test (decoy in place) were discarded from the data set. The sex and identity of each parent was determined using individual color rings, the position of the metal ring (adult females are ringed on their left leg), or based on feather coloration. Birds were caught for final identification and/or ringing the day after the test.

2.3.3 Statistical analysis

To test for phenotypic differences among populations, we used univariate linear mixed-models and included population in fixed effect. Models were run separately for each trait. In all models, we also included sex, age (juvenile or adult), year and the two-way interactions between year and population and between sex and population as fixed effects. The time of the day when each test was performed (hour) was also added as a confounding variable for each trait. The random effect structure of each model is detailed at the end of this section.

Relevant confounding, and biological variables were added for each trait. For handling aggression score, because this trait was repeatable within a year and for a given period of captures across years (Table S2.5), we pooled the data from both periods and added 'capture period' as a fixed effect.

For HR, because there was substantial among-individual variation in the time between capture and HR recording (min. time: 0 minutes; max. time: 96 min.), we added the time between capture and recording as a fixed effect in the analyses. We also included body mass as a fixed effect for this trait because HR is related to metabolic rate and both traits are positively correlated with body mass (Green 2011). We investigated the relationship between HR and BR using a univariate linear model. We used HR as a response variable, mean BR as a fixed effect and included in fixed effect all the significant confounding variables for HR identified previously.

For average exploration speed, we also included as confounding variables the time interval between capture and trials (min. = 5 min., max. = 57 min., mean = 21.15 min., s.d. = 11.40 min.) and the confinement system used between heart rate recording and trial (3 classes: no confinement, bag or cage).

For nest defense behavior, we added as confounding variables the distance between the decoy and the nest-box, the distance between the observer and the nest-box, and the identity of the decoy (we used two different stuffed Eurasian jays). To ensure that any difference between populations would not be caused by the availability of perches close to the nest-box, we included the distance from the nest-boxes to the closest branch as a confounding variable in all models. However, this variable was recorded for all years in E-Pirio (2012 to 2015) but only for 2014 and 2015 in D-Muro and E-Muro. The inclusion of this variable in the models thus limited our population comparison to 2014 and 2015. We also tested for a correlation between the nest defense behavior of an individual and its partner's behavior during the test using a univariate linear model. We used female minimal approach distance as a response variable and male minimal approach distance as a fixed effect and included as fixed effect all the significant confounding variables for nest defense. Minimal approach distance was square root transformed prior to analyses.

To control for differences in reproductive status among individuals during trials, we used the time between measurement and laying date as an additional fixed effect for HR and exploration speed. For handling aggression, the 'capture period' fixed effect and the time between measurement and laying date were highly correlated, we thus kept only 'capture period' in models. We did not control for the reproductive status of individuals for nest defense behavior because all trials were performed when nestlings had nine days old.

To control for any effect of habituation of the birds in response to either repeated manipulations by humans or to repeated visits in the novel environment apparatus we used the order of capture (for handling aggression and HR) or order of novel-environment trials as fixed effects in the models. We assumed that there was no habituation during nest defense trials, because this test imitated a real predator attack and trials were done only once a year for a given individual.

The significance of the confounding variables was first tested using likelihood-ratio tests (L-ratio test; Bates et al. 2014) and a backward stepwise procedure starting with a model including all the confounding variables. We then used the same procedure to test for the significance of the biological variables (population, age, sex and year) starting with a model containing all the biological variables and the significant confounding variables. All models were run first on a dataset combining both sexes. When a significant interaction between sex and population was found, we ran separated models for males and females using the fixed effect structure of the models selected with the sexes pooled.

If a significant population effect was revealed for a trait, we tested for a significant difference between two given populations by including two populations in a single model (E-Pirio and D-Muro; E-Pirio and E-Muro; E-Muro and D-Muro) and by running L-ratio tests to test for the presence of a significant population effect. In these models, we did not include the interaction between year and population or between sex and population. This allowed us to test the significance of the population term alone. Comparing a model with the interaction term between population and year or population and sex to a model without the term population would test simultaneously for two effects: the interaction between the two terms and the population. In addition, not including the interaction between population and year or sex allowed us to investigate the difference in phenotype between populations over the entire study period not only for one specific year or sex. We also checked for a significant valley effect (Regino *vs* Fango) rather than a population effect and present these results in Supplementary materials (Table S2.12).

We included individual and observer identity as random effects to decompose the phenotypic variance into among-individual (V_{ID}), among-observer ($V_{OBS,}$ not included for average exploration speed in the novel-environment), and residual (V_R) components and to account for the non-independence of repeated measures on the same individuals. Repeatability of personality traits was estimated using repeated behavioral trials for the same individuals across years. We calculated adjusted repeatability as $r_{ID} = V_{ID}/(V_{ID}+V_R)$ or $V_{ID}/(V_{ID}+V_{OBS}+V_R)$ using the fixed effect structure selected previously and agreement repeatability as $r_{ID} = V_{ID}/(V_{ID}+V_R)$ using no fixed effects (Nakagawa and Schielzeth 2010). We calculated the repeatability of each trait for the metapopulation and for each population and sex, separately. We calculated the observer effect as $V_{OBS}/(V_{ID}+V_{OBS}+V_R)$ using the fixed effect structure selected previously. We assessed the significance of the random terms using L-ratio tests (Pinheiro and Bates 2000).

All analyses were done using the package *lme4* (Bates et al. 2014) in R (version 3.1.3, R core team 2015). Confidence intervals were generated using the *confint.merMod* function of the *lme4* package.

Captures were performed under ringing permits delivered by the CRBPO (Centre de Recherches sur la Biologie des Populations d'Oiseaux, Paris; ringing permit number 1907 to AC, program permit number 369). All experimental protocols described here were approved by the ethics committee for animal experimentation of Languedoc Roussillon (305-CEEA-LR-12066 approved in 2012) as well as by Regional Institutions (bylaw issued by the Prefecture on 15/06/2012 n° 2012167-0003) and by the Comité Institutionnel de Protection des Animaux (UQAM; CIPA-769-2015; 0413-R1-769-0414).

2.4 Results

2.4.1 Repeatability

Significant among-individual differences were observed for each trait, with adjusted repeatability estimates ranging from 0.26 to 0.75 (Table 2.2). Observer identity significantly affected handling aggression (proportion of total variance = 0.03; L-ratio = 21.33; $p < 0.001$; 17 observers) and the minimum approach distance (0.27; L-ratio = 31.60; $p < 0.001$; 7 observers), but not HR (L-ratio = 0; p-value = 0.99; 5 observers). Handling aggression, HR, and average exploration speed were significantly repeatable for all populations except for exploration speed in E-Pirio, where a large proportion of the variance was nevertheless explained by bird identity (Table S6.1). The small number of repeated measures for nest defense behavior prevented us from testing its repeatability in each population separately. All traits were repeatable for both sexes except nest defense behavior, which was repeatable for females only (Table S2.1).

2.4.2 Population difference and variation across sex and time

Handling aggression

Populations differed significantly in average handling aggression score (Table 2.3, Table 2.4, Fig. 2.2a, Table S2.8). Birds in D-Muro (mean = 1.69; s.d. = 0.95) had a significantly higher handling aggression score than those from E-Muro (mean = 1.48; s.d. = 0.96) and than those from E-Pirio (mean = 1.49; s.d. = 0.99), while birds in E-Pirio and E-Muro displayed similar scores (Table 2.4, Fig. 2.2a). Females were less aggressive than males [estimate: -0.34 (95% CI: -0.44; -0.24); Table S2.8]. There was no significant interaction between sex and population for this trait (p-value = 0.31; L-ratio: 2.35) but there was a significant interaction between population and year; with individuals from D-Muro being more aggressive compared to individuals in E-Pirio in 2011, while in 2012 and 2013 individuals in D-Muro were less aggressive (Table 2.3, Fig. S2.2a and Table S2.8).

Heart rate during manual restraint (HR)

Mean HR during manual restraint was positively related to BR [estimate: 0.82 (95% CI: 0.06; 1.66); L-ratio = 4.33; p-value < 0.05]: individuals with a fast heart rate breathed faster during restraint. When we did not control for body mass, birds from E-Pirio had a faster HR (mean = 976.24 beats/min, s.d.= 86.99) than birds from D-Muro (mean: 963.30 beats/min; s.d.= 87.80) and E-Muro (mean = 955.97 beats/min; s.d. = 89.18) but birds from E-Muro and D-Muro had a similar heart rate [E-Pirio vs D-Muro: estimate: 26.64 (95% CI: 1.15; 52.06); L-ratio = 3.90 p-value < 0.05; E-Pirio vs E-Muro: estimate: 30.66 (95% CI: -0.418; 61.71); L-ratio = 3.74, p-value = 0.053; D-Muro vs E-Muro: estimate: -9.09 (95% CI: -36.14; 17.92); L-ratio = 0.44; p-value = 0.53]. There was also a significant interaction between population and year (L-ratio = 21.92; p-value < 0.01; Fig. S2.2b).

Lighter individuals had a faster HR (p-value < 0.001; Table S2.9) and there was a significant difference in body mass between populations: birds from E-Pirio were lighter than birds from D-Muro [estimate: -0.15 (95% CI: -0.27; -0.05); L-ratio = 7.42; p-value < 0.01] and from E-Muro [estimate: -0.11 (95% CI: -0.23; 0.01); L-ratio = 3.11; p-value = 0.078]. Consequently, mean HR did not differ significantly among populations when we controlled for body mass (E-Pirio vs D-Muro: L-ratio = 2.07; p-value = 0.15; E-Pirio vs E-Muro: L-ratio = 2.01; p-value = 0.16; E-Muro vs D-Muro: L-ratio = 0.308; p-value=0.58; Fig. 2.2b). There was also a significant interaction between population and year when we controlled for body mass (Table 2.3; Fig. S2.2b and Table S2.9)..

We found a marginally significant interaction between sex and population (L-ratio = 5.65; p-value = 0.059). When we analyzed both sexes separately and controlled for body mass, males from E-Pirio had a faster HR than males from E-Muro [estimate: 81.03 (95% CI: 35.66; 129.95); L-ratio = 11.62; p-value < 0.001] and males from E-Muro had a marginally significantly slower HR than males from D-Muro [estimate: -32.71 (95% CI: -69.68; 3.90); L-ratio = 3.08; p-value = 0.079; Fig. 2.3]. However, there was no difference in male HR between D-Muro and E-Pirio (L-ratio = 2.36; p-value = 0.12) and no population effect for females (L-ratio = 0.90; p-value = 0.65).

Average exploration speed

We found a significant population effect for average exploration speed (Table 2.3): individuals from E-Pirio (mean = 10.37 cm/s; s.d. = 7.49) were significantly slower in their exploration than individuals from D-Muro (mean = 13.52 cm/s; s.d. = 8.39) and E-Muro (mean = 11.84 cm/s; s.d. = 7.16), while birds from D-Muro and E-Muro did not differ (Table 2.4; Table S2.10 and Fig. 2.2c). Females were slower in the novel-environment than males [estimate: -2.02 (95% CI: -3.49; -0.55); Table S2.10] but there was no significant interaction between sex and population (L-ratio = 0.73; p = 0.69). We also found an interaction between population and year for this trait (Table 2.3). This significant interaction was mainly attributable to 2014, when the difference between D-Muro and E-Pirio was smaller than for the other years (Fig. S2.2c).

Nest defense behavior

There were no significant difference in nest defense between populations (L-ratio = 1.85; p-value = 0.40; Fig. 2.2d) and no interaction between population and year for this trait (L-ratio = 1.92; p-value = 0.38). We found a significant effect of the distance between the closest branch and the nest box on nest defense intensity. The inclusion of the distance from the nest-box to the closest branch as a fixed effect limited our population comparisons to 2014 and 2015. However, this limitation did not hinder our capacity to detect population differences since there was no significant difference between populations even when we did not include the distance to the closest branch in the models and hence included year 2012 in the comparison (L-ratio = 2.89; p-value = 0.24). We also found a significant sex-difference for this trait: females had longer minimal approach distances than males [estimate: 0.20 (95% CI: 0.05; 0.35)]. Partners' nest defense behaviors were significantly correlated [estimate = 0.06 (95% CI: -0.06; 0.19); L-ratio = 122.48; p-value < 0.001].

Tableau 2.2 Among-individual, among-observer and residual variances (confidence intervals 95% (CI)) along with adjusted and agreement repeatability (r_{ID}; Nakagawa and Schielzeth 2010), sample sizes, and statistics for the significance of adjusted repeatability for three personality traits and one physiological trait measured in three Corsican blue tits populations (France).

Trait	V_{ID} (CI)	V_{OBS} (CI)	V_R(CI)	r_{ID} *adjusted; agreement* (N_{ind} 1, 2, 3, 4, +)	L-ratio	p-value
Handling aggression	0.22 (0.16; 0.28)	0.03 (0.01; 0.07)	0.61 (0.55; 0.67)	0.26; 0.30 (458, 242, 114, 66, 33)	82.39	< 0.001
HR (beats / min)	7103 (5396.17; 8972.43)	201.20 (0.00; 458.88)	2326 (1655.02; 3411.38)	0.75; 0.64 (243, 34, 18, 4,1)	41.25	< 0.001
Average exploration speed (cm/s)	22.74 (17.11; 33.83)	N.A.	25.34 (12.20; 32.10)	0.47; 0.40 (385, 89, 19, 1, 0)	17.10	< 0.001
Nest defense (m)	0.15 (0.06; 0.23)	0.14 (0.03; 0.44)	0.22 (0.14; 0.30)	0.30; 0.52 (196, 31, 7, 0, 0)	9.37	< 0.005

(N_{ind}1, 2,3,4, +) indicates how many individuals were included in the models with one, two, three, four or more than four tests. L-ratio and p-values are from the comparison of a full model and a model without the term individual identity as random effect. Data from the three populations and for both sexes are included. V_{ID}, V_{OBS}, V_R and adjusted repeatability were calculated from models with all the significant fixed effects for each trait included; for details on fixed effects structures and effect sizes see Table S2.8 to S2.11.

Tableau 2.3 Population differences and significant biological variables for three personality traits and one physiological trait across three Corsican blue tit populations (France).

Trait	Fixed effect	L-ratio	p-value
Handling aggression	Population	13.84	< 0.001
	Year	22.88	< 0.001
	Population*Year	67.18	< 0.001
	Sex	42.33	< 0.001
HR (beats/min.)	Population	4.15	0.15
	Year	7020.3	< 0.001
	Sex	92.60	< 0.001
	Body mass	398.94	< 0.001
	Population*Year	19.16	< 0.050
Average exploration speed (cm/s)	Population	13.37	< 0.010
	Year	81.91	< 0.001
	Sex	14.74	< 0.050
	Population*Year	8.35	< 0.001
Nest defense (m)	Year	16.34	< 0.001
	Sex	14.35	< 0.001

L-ratio and p-values are from the comparison of a full model and a model without the variable of interest. Confounding variables included in the models are described in Table S2.8 to S2.11. Random effect structures are individual and observer identity. All effect sizes and confidence intervals are describe in Table S2.8 and S2.11.

Tableau 2.4 Differences in handling aggression score and average exploration speed (cm/s) between pairs of blue tit populations in Corsica (France).

Trait	Populations compared	Estimate (95% CI)	L-ratio	p-value
Handling aggression	**E-Pirio *vs* D-Muro**	-0.14 (-0.27; -0.01)	4.268	**< 0.05**
	E-Pirio *vs* E-Muro	0.11 (-0.04; 0.25)	2.110	0.25
	E-Muro *vs* D-Muro	**-0.28** **(-0.41; -0.15)**	**17.752**	**< 0.001**
Average exploration speed	**E-Pirio *vs* D-Muro**	**-3.41** **(-5.33; -1.49)**	**10.444**	**< 0.005**
	E-Pirio *vs* E-Muro	**-2.01** **(-3.97; -0.05)**	**4.324**	**< 0.05**
	E-Muro *vs* D-Muro	-1.27 (-3.30; 0.78)	4.600	0.100

Significant differences between populations are in bold. The second population in the second column is the reference population. Estimates and 95% CI are from a model with the two populations of interest and the same fixed effects structure detailed in Table 2.3, Table S2.8 and S2.10 but without the interaction term between population and year. L-ratio and p-values are from the comparison of a full model and a model without the term population as fixed effect.

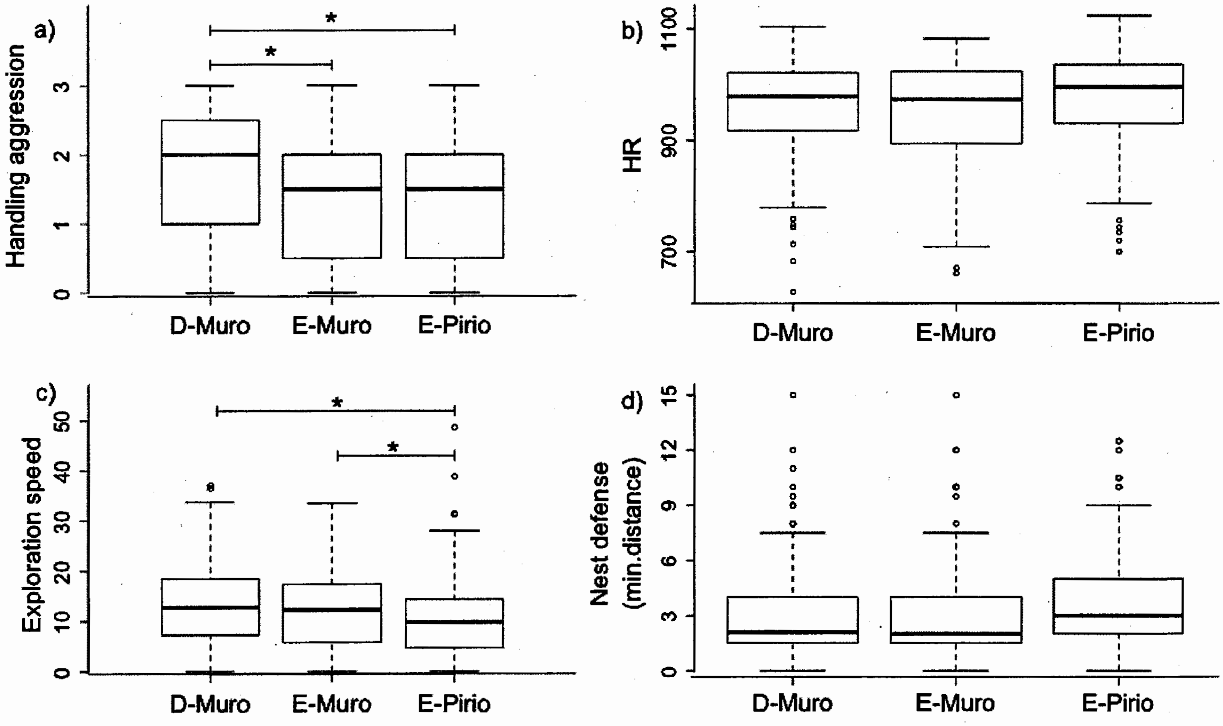


Figure 2.2 Boxplots for a) handling aggression (D-Muro: number of observations (*n*) = 703; E-Muro: *n* = 447; E-Pirio: *n* = 549); b) heart rate during manual restraint (HR in beats/min; D-Muro: *n* = 143; E-Muro: *n* = 116; E-Pirio: *n* = 107); c) average exploration speed (speed in cm/s; D-Muro: *n* = 175; E-Muro: *n* = 100; E-Pirio: *n* = 105); and d) minimal approach distance during nest defense (distance in m; D-Muro: *n* = 75; E-Muro: *n* = 63; E-Pirio: *n* = 147), in three blue tit populations in Corsica (France). Male and female data are pooled. The significance of the between-population differences was assessed with models contrasting two populations at a time with fixed effects structures as detailed in Table 2.2.3, S2.8 to S2.11, but without the interaction term between year and population; "*" indicates a significant difference ($p < 0.05$) between two populations.

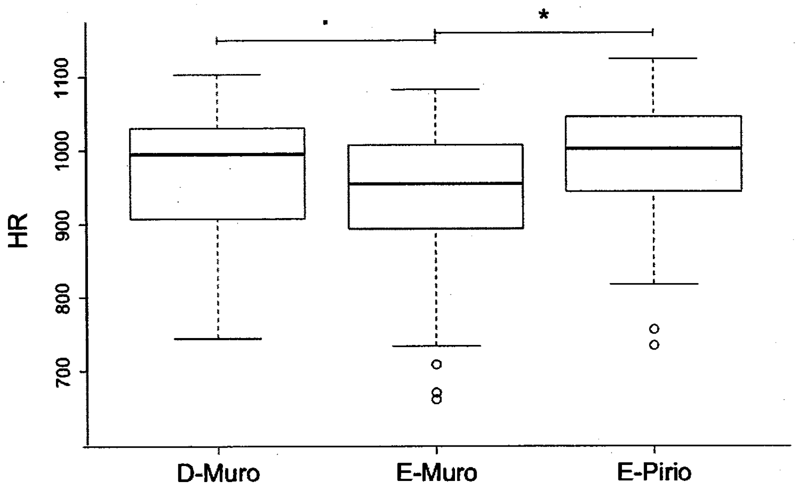


Figure 2.3 Boxplots representing male heart rate during manual restraint (HR; in beats/min) in three Corsican blue tit populations (France; D-Muro: $n = 62$; E-Muro: $n = 57$; E-Pirio: $n = 48$); the significance of the between population difference was assessed with models contrasting two populations at a time with fixed effects structures as detailed in Table S2.9 but without the interaction term between year and population. "." indicates a marginally significant difference ($0.10 > p > 0.05$) and "*" indicates a significant difference ($p < 0.05$) between two populations.

2.5 Discussion

This study reveals that blue tits from contrasting habitats display different mean personality phenotypes. In addition, some of our results are consistent with the pace-of-life syndrome hypothesis, since birds from the deciduous population D-Muro had a faster phenotype on average (faster exploration pattern and higher handling aggression scores), than birds from the evergreen populations E-Muro and E-Pirio (Table 2.4, Fig. 2.2). A small number of studies have compared the personality phenotypes of wild populations that differ in ecological contexts (Fraser and Gilliam 1987; Bell and Stamps 2004; Bell 2005; Quinn et al. 2009; Dingemanse et al. 2010; Korsten et al., 2010; Dingemanse et al 2012). To our knowledge, most of these studies have compared the personality phenotype of a single trait (Fraser and Gilliam 1987; Korsten et al. 2010), the behavioral syndrome structure (Bell and Stamps 2004; Bell 2005; Dingemanse et al. 2010) or the plasticity (Dingemanse et al. 2012) of populations. Very few studies have compared explicitly the personality phenotype of populations that exhibit different life-history characteristics and that differ in ecological conditions and residual reproductive value in the framework of the pace-of-life syndrome hypothesis. The long-term monitoring of these blue tit populations that display pronounced phenotypic variation on many morphological, life-history and behavioral traits at a small spatial scale (Charmantier et al. 2016) was an ideal opportunity to test for personality differences in the context of the pace-of-life syndrome.

According to the pace-of-life syndrome hypothesis, populations experiencing different ecological conditions, in particular differing in adult mortality rates, should show different personality phenotypes. More precisely, in the presence of a trade off between current and future reproduction, theoretical models predict that individuals that have lower residual reproductive value (or asset) should display riskier behavior if it favors current reproduction over future reproduction (Wolf et al. 2007; Sih et al. 2015). In the deciduous population of D-Muro, adult survival is lower than in E-Pirio and E-Muro (Table 2.1; Grosbois et al. 2006). Because of this lower adult survival, birds inhabiting the deciduous habitat have a lower residual reproductive value. We were thus expecting that birds from D-Muro would show a personality phenotype associated with risk-taking and typical of a faster pace-of-life (higher handling aggression score, faster heart rate, faster exploration pattern and higher nest defense intensity; Clark 1994; Groothuis and Carere 2005; Réale et al. 2010; Cole and Quinn 2014; Sih et al. 2015). As predicted, birds from D-Muro had a faster exploration pattern across all years than birds from the evergreen population E-Pirio (Table 2.4, Fig. 2.2c). Our results are also consistent with our predictions for handling aggression scores, as birds from D-Muro had a higher handling aggression score than birds from E-Muro and from E-Pirio (Table 2.4, Fig. 2.2a).

Nevertheless, some of our results are not consistent with our predictions. Indeed, there was no population difference in nest defense intensity and males from E-Pirio had a faster HR than males from E-Muro. In addition, our analyses revealed very strong temporal variation in the differences between populations in handling aggression scores, with patterns that are reversed between years. These results suggest that other factors than the local dominant oak species and the residual reproductive value might be important in shaping the personality phenotype of these blue tit populations.

2.5.1 A matter of scale

Our study design provides insight into the factors and the spatial scales that shape the phenotypes of different personality and physiological traits. For example, exploration behavior differs between birds from the Regino and Fango valleys (Table S2.12) but did not differ between birds with different local ecological conditions in the same valley (D-Muro and E-Muro birds; Fig. 2.2c and Table 2.4). These results suggest that processes occurring at the landscape scale (*i.e.* the valley; proportion of deciduous oak in the surroundings, level of anthropogenic activities, precipitation and temperature) might be more important in shaping exploration patterns than processes resulting from local ecological conditions occurring at a smaller spatial scale. In contrast, we did not find a significant difference in handling aggression score between the two valleys (Table S2.12) but we did find differences between populations with different small-scale ecological conditions (Fig. 2.2a; Table 2.4). These results suggest that small-scale ecological conditions might be more important for shaping handling aggression phenotype than ecological conditions occurring at the landscape level. Our results thus suggest that, depending on the trait under study, personality phenotypes can be influenced by processes happening at different spatial scales (Quinn et al. 2009). More study sites with different degrees of ecological differences at varying spatial scales would be necessary to further explore this interesting phenomenon.

2.5.2 Temporal variation in mean phenotype: selection or plasticity?

The yearly changes in mean phenotypes and the significant interaction between population and year for handling aggression, HR, and exploration speed (Table 2.3 and Table S2.8 to S2.10) suggest two possibilities that are not mutually exclusive. The first possibility is that traits were plastic and their mean varied within a population according to local temporal variation in environmental conditions. Indeed, variation in environmental conditions may affect life-history characteristics, and thus personality traits, either directly through the plasticity of individuals or indirectly through maternal effects (Nicholaus et al. 2012; Montiglio et al. 2014). Second, yearly variation in environmental conditions may have created selection pressures (e.g. through differential mortality) that have led to short-term changes in the mean phenotypes within each population (Réale and Festa-Bianchet 2003; Dingemanse et al. 2004; Boon et al. 2007; Kontiainen et al. 2009; Quinn et al. 2009). In this case, we would expect that traits would not change from year to year within individuals, but that, instead, the populations in different years would be made up of different types of individuals. Exploring the relative importance of these two processes would require testing for within-individual changes in personality traits and personality-dependent demographic changes. These questions were not the goal of this study but we can suggest a few explanations. In great tits, changes in population density and food abundance drive phenotypic changes in personality and selection pressures on behavioral traits (Dingemanse et al. 2004; Nicholaus et al. 2016). These factors may also shape personality in the closely related blue tit. Preliminary analyses in the three Corsican populations suggest that handling aggression was not affected by population density (Fig. S2.3), but depended on the amount of caterpillar frass (an indication of the caterpillar abundance; Fig. S2.4). Testing whether phenotypically plastic changes or personality-dependent survival are responsible for yearly changes in the phenotypes measured would be an exciting follow up, but could only be done on a longer time scale. Whatever the reasons for these changes, these results indicate that among-population comparisons of pace-of-life characteristics should be made with caution if data are not collected over several years and under contrasting environmental conditions.

2.5.3 Heart rate during manual restraint

Heart rate and breath rate reflect the activity of the sympathetic and parasympathetic nervous systems (Koolhaas et al. 1999). The sympathetic nervous system is suspected to be the dominant system in individuals that display fast exploration patterns, high handling aggression, and that exhibit a fast life-history strategy and invest more in current reproduction. The parasympathetic system is suspected to be the dominant system in slow exploring and docile individuals that exhibit a slower life-history strategy and invest more in future reproduction (proactive *versus* reactive coping styles: Koolhaas et al. 1999; Réale et al. 2010; Ferrari et al. 2013). According to the pace-of-life syndrome hypothesis, the birds from the evergreen populations should exhibit a personality typical of a slow pace-of-life and thus a higher activity of the parasympathetic system and a slower heart rate during stressful events (Koolhaas et al. 1999; Ferrari et al. 2013). The tendency for a slower male heart rate in E-Muro than in D-Muro is in accordance with this prediction. However, contrary to our expectations, male heart rate was faster in E-Pirio than in E-Muro. This result contradicts the literature on pace-of-life and coping style (Koolhaas et al. 1999; Réale et al. 2010; Ferrari et al. 2013). However, a fast breath rate has been found to be associated with low activity in the novel-environment apparatus and with low handling aggression in other blue tit studies (Kluen et al. 2014; but see Fucikova et al. 2009). We found a positive relationship between breath rate and heart rate in our populations. Therefore, our results indicate that males in E-Pirio are less active in the novel-environment and have a potentially faster breath rate, which is in line with previous studies on blue tits personality (Kluen et al. 2014) even though it contradicts the general pace-of-life syndrome expectations (Réale et al. 2010). Further studies would be needed to clarify the association between the autonomous nervous system and both personality and life history traits in avian species.

2.5.4 Nest defense behavior

We found a significant repeatability for nest defense behavior (Table 2.2) revealing among-individual differences in nest defense in blue tits. We also found that birds in a pair showed positively correlated nest defense behavior. This correlation between partners could be caused by environmental factors shared by both parents, such as brood size (Montgomerie and Weatherhead 1988), or be the result of individuals matching their behavior to their partner's (Schuett et al. 2010). Alternatively, this relationship could indicate behavioral assortative mating choice in these populations (Schuett et al. 2010; Class et al. 2014).

Nest defense behavior involves a trade-off between parental survival, energy reserve and offspring protection (Trivers 1972; Montgomerie and Weatherhead 1988). Birds that have a lower future reproductive value and invest more in current reproduction should take more risks and invest more in offspring defense (Hakkarainen and Korpimäki 1994; Wolf et al. 2007; Møller and Nielsen 2014). Since they are faced with lower survival probability and larger clutches (Grosbois et al. 2006; Charmantier et al 2016), D-Muro birds were expected to approach the stuffed predator and the nest-box closer than birds from the evergreen populations. Contrary to this prediction, we did not find any difference among populations for nest defense behavior (Fig. 2.2d). It is possible that, contrary to expectations (Wolf et al. 2007; Sih et al. 2015), risk taking during nest defense is not related to other measures of life-history characteristics in these blue tit populations. Alternatively, the correlation between risk taking during nest defense and other life-history traits could exist in our system but be detectable only at the within-population level if we compare individuals instead of populations (between-individual correlation; Dingemanse and Dochtermann 2013)

2.5.5 Sex-specific personality phenotypes

An increasing number of studies show sex differences in personality traits and behavioral syndromes (Schuett et al. 2010; Dammhahn 2012; Fresneau et al. 2014). For example, Fresneau et al. (2014) found different behavioral syndromes between male and female in a Finnish population of blue tits. We also found sex-specific personality phenotypes in this study, with differences between sexes in mean phenotype for all traits and sex-specific difference between populations for heart rate during manual restraint. We also found that nest defense behavior was repeatable for females but not for males. In general, intersexual differences in personality phenotypes are not well understood, but likely arise because of intersexual differences in life-history strategies and selection pressures (Dingemanse et al. 2004; Class et al. 2014; Dammhahn 2012). A detailed investigation of sex-specific selection acting on these traits would help to explain the sexual dimorphism described in this study.

2.5.6 Local adaptation in personality traits

Phenotypic differences between the three blue tit populations could be interpreted as divergent adaptations to habitat-specific ecological conditions, but from the present study we cannot conclude whether these differences are due to behavioral plasticity or due to underlying genetic differences. However, several lines of evidence from recent studies on personality variation and past investigations in these populations suggest that differences in personality traits likely reflect a genetic difference among populations and adaptations to local ecological conditions. First, personality in *Parus* is under selection (Dingemanse et al. 2004; Quinn et al. 2009; Nicholaus et al. 2016) and is heritable (Brommer and Kluen 2012; Class et al. 2014). Second, common-garden experiments have revealed genetic differences in life-history, morphological and other behavioral traits among the three populations (Blondel et al 1999; Braillet et al. 2002; Charmantier et al. 2016). Third, genomic analyses using

RAD sequencing have recently revealed a fine scale genetic differentiation with a significant Fst of 1.8% between D-Muro and E-Muro (Porlier et al. 2012a; Szulkin et al. 2016). Fourth, genetic drift is not likely to have driven such phenotypic difference, considering the very large population size (roughly estimated around 10,000 in the Regino valley alone; Charmantier, pers. com.). Finally, preliminary results from a common-garden experiment suggest a genetic basis for the phenotypic differences between these populations in personality traits (Dubuc-Messier et al. in prep.).

2.5.7 Conclusion and perspective

Our results reveal divergent personality phenotypes among three blue tit populations separated by spatial distances within the dispersal ability of the species and reveals strong temporal variation in mean personality phenotypes within populations. These populations inhabit areas with contrasting ecological conditions and display different life-history characteristics. This study thus emphasizes the role of environmental heterogeneity on behavioral diversity linked to life-history characteristics. An interesting next step would be to determine whether the phenotypic differences described across populations is mainly of genetic or environmental origin, and whether these differences result from habitat-specific selection pressures and represents local adaptations. Different mechanisms could be responsible for fine-scale genetic differentiation for personality traits, among which matching habitat choice (Cote and Clobert 2007; Edelaar and Bolnick 2012), selective barriers against migrants and positive assortative mating (Richardson et al. 2014) would be appealing possibilities for future research. Furthermore, these Corsican blue tit populations are located at the extreme south of the blue tit distribution and, based on their small clutch size, they are located on the slower end of the pace-of-life continuum. An interesting and broader approach to study the pace-of-life syndrome hypothesis would thus be to compare populations at a much larger scale by including populations located further north within the species' range.

2.6 Acknowledments

We thank the landowners for permission to work on their property. We also thank Christophe De Franceschi and the numerous field assistants for their precious work in the field, particularly Virginie Journeau, Marc-Olivier Beausoleil, Catherine Goeffroy, Karine Dubois, Simon Côté-Bougouin and Raphaëlle Mercier-Gauthier. We also thank Carolyn Hall for helpful comments on a previous version of the manuscript and two anonymous reviewers for valuable comments.

2.7 Supplementary materials

Number of observers

Tableau S2.1 Total number of handling aggression observations per observer, year and population for blue tits in Corsica (France); there are an additional 13 observations from an unknown observers.

Observers		D-Muro	E-Muro	E-Pirio	Total
AC	**Total**	68	25	15	108
	2011	25	19	4	48
	2012	35	3	0	38
	2013	1	1	4	6
	2014	7	2	7	16
CD	**Total**	0	0	82	82
	2011	0	0	1	18
	2012	0	0	23	23
	2013	0	0	23	23
	2014	0	0	18	18
CF	**Total**	138	92	99	329
	2011	0	0	0	0
	2012	62	39	40	141
	2013	10	11	30	51
	2014	66	42	29	137
CGE	**Total**	23	18	18	59
	2011	0	0	0	0
	2012	0	0	0	0
	2013	0	0	0	0
	2014	23	18	18	59
DR	**Total**	12	5	0	17
	2011	0	0	0	0
	2012	0	0	0	0
	2013	0	1	0	1
	2014	12	4	0	16
EM	**Total**	19	28	32	79
	2011	19	28	32	79
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	0	0
GDM	**Total**	48	53	62	163
	2011	0	0	0	0
	2012	24	8	25	57
	2013	18	27	19	64
	2014	6	18	18	42
JB	**Total**	43	21	0	64
	2011	0	0	0	0
	2012	18	9	0	27
	2013	25	12	0	37
	2014	0	0	0	0
KD	**Total**	0	0	22	22
	2011	0	0	0	0
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	22	22
MOB	**Total**	51	17	31	99
	2011	0	0	0	0
	2012	0	0	0	0
	2013	30	2	20	52
	2014	21	15	11	47
MP	**Total**	59	21	0	80
	2011	59	21	0	80
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	0	0

Observers		D-Muro	E-Muro	E-Pirio	Total
MS	**Total**	0	0	12	12
	2011	0	0	0	0
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	12	12
OJ	**Total**	0	0	8	8
	2011	0	0	8	8
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	0	0
PAM	**Total**	28	38	30	96
	2011	0	0	0	0
	2012	12	15	0	27
	2013	16	21	17	54
	2014	0	2	13	15
PP	**Total**	188	123	155	466
	2011	56	54	100	210
	2012	46	27	52	125
	2013	31	12	3	46
	2014	55	30	0	85
VJ	**Total**	37	9	23	69
	2011	0	0	0	0
	2012	0	0	0	0
	2013	37	9	23	69
	2014	0	0	0	0
SAC	**Total**	0	0	25	25
	2011	0	0	25	25
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	0	0

Tableau S2.2 Total number of heart rate observations per observer, year and population for blue tits in Corsica (France); there are an additional 17 observations from an unknown observer.

	Observers	D-Muro	E-Muro	E-Pirio	Total
AC	**Total**	51	46	4	101
	2011	22	26	4	52
	2012	29	15	0	44
	2013	0	5	0	5
	2014	0	0	0	0
	2015	0	0	0	0
DR	**Total**	33	10	0	43
	2011	2	3	0	5
	2012	0	0	0	0
	2013	28	4	0	32
	2014	3	3	0	6
	2015	0	0	0	0
GDM	**Total**	43	46	82	171
	2011	0	0	0	0
	2012	10	7	35	52
	2013	6	4	11	21
	2014	6	7	4	17
	2015	21	28	32	81
PP	**Total**	6	9	0	15
	2011	6	9	0	15
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	0	0
	2015	0	0	0	0
SAC	**Total**	0	0	19	19
	2011	0	0	19	19
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	0	0
	2015	0	0	0	0

Tableau S2.3 Total number of nest defense observations per observer, year and population for blue tits in Corsica (France); all observers were identified.

Observers		D-Muro	E-Muro	E-Pirio	Total
CF	**Total**	0	0	4	4
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	0	0
	2015	0	0	4	4
CGE	**Total**	29	26	13	68
	2012	0	0	0	0
	2013	0	0	0	0
	2014	29	26	13	68
	2015	0	0	0	0
GDM	**Total**	31	24	58	113
	2012	0	0	15	15
	2013	0	0	17	17
	2014	27	20	18	65
	2015	4	4	8	16
MOB	**Total**	0	0	33	33
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	33	33
	2015	0	0	0	0
RMG	**Total**	6	5	5	16
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	0	0
	2015	6	5	5	16
SCB	**Total**	7	8	17	32
	2012	0	0	0	0
	2013	0	0	0	0
	2014	0	0	0	0
	2015	7	8	17	32
VJ	**Total**	0	0	15	15
	2012	0	0	0	0
	2013	0	0	15	15
	2014	0	0	0	0
	2015	0	0	0	0

Handling aggression scoring protocol

Tableau S2.4 Blue tit handling aggression scale.

Score	Wings spread	Tail feathers spread	Bird strikes fingers
0	No	No	No
1	No	No	Yes, but only if provoked
2	No	Yes	Yes, spontaneously
3	Yes	Yes	Yes, spontaneously

When the bird displayed one reaction specific to one score and another reaction specific to another score, it received an average score between the two. For example, a bird that struck without any provocation (score 2) but did not have its wings and tail feathers spread (score 1) would be scored as 1.5.

Repeatability estimates for handling aggression scores for the two periods of capture

Tableau S2.5 Adjusted repeatability estimates (r_{ID}) for handling aggression scores for the two periods of capture (among-years for the pre-breeding and breeding period and within-year among periods for every year (2011 to 2014)) for three blue tit populations in Corsica (France).

Period / Year		r_{ID}	L-ratio	p-value	N_{Obs} ; N_{ID}
Among years, within period					
	Pre-breeding	0.21	7.877	< 0.010	615; 491
	Breeding	0.32	41.290	< 0.001	1083; 754
Within year, among periods					
	2011	0.21	4.036	< 0.05	412; 320
	2012	0.33	14.520	< 0.001	431; 331
	2013	0.35	13.930	< 0.001	389; 302
	2014	0.14	2.010	0.16	466; 353

L-ratio and p-values represent the results from the comparison of a full model and a model without individual identity in random effect. N_{Obs} refers to the number of observations, N_{ID} refers to the number of different individuals considered in the models. Data from the three populations and for both sexes were included. All significant fixed effects were included in the models as detailed in Table S2.8 to S2.11.

Repeatability estimates for each population and sex

Tableau S2.6 Variance components (with 95% confidence intervals) and adjusted repeatability estimates (r_{ID}) for three personality traits and one physiological trait for each blue tit population in Corsica (France).

Trait	Population	V_{ID} (CI)	V_{OBS} (CI)	V_{R} (CI)	r_{ID} (N_{Obs}; N_{ID})	L-ratio	p-value
Handling aggression	D-Muro	0.23 (0.15; 0.32)	0.01 (0.000; 0.04)	0.53 (0.45; 0.60)	0.25 (703; 365)	49.398	< 0.001
	E-Muro	0.18 (0.06; 0.31)	0.03 (0.000; 0.11)	0.68 (0.56; 0.82)	0.20 (447; 238)	10.880	< 0.001
	E-Pirio	0.25 (0.14; 0.37)	0.04 (0.006; 0.11)	0.65 (0.55; 0.76)	0.26 (549; 295)	28.093	< 0.001
HR (beats/min.)	D-Muro	5884.50 (2912.90; 8033.22)	524.40 (0.000; 2053.92)	2274.30 (1301.97; 4357.15)	0.68 (143; 114)	15.18	< 0.001
	E-Muro	10620.00 (5183.04; 15434.47)	$1.46\mathrm{x}10^{-10}$ (0.000; 851.09)	3642.00 (1735.36; 6899.64)	0.75 (116; 92)	8.244	< 0.005
	E-Pirio	6389.0 (4297.60; 8508.72)	0.00 (0.000; 381.88)	726.60 (319.28; 1322.37)	0.90 (107; 89)	31.352	< 0.001
Average exploration speed (cm/s)	D-Muro	29.45 (13.78; 45.16)	N.A.	22.12 (13.92; 37.24)	0.57 (175; 143)	12.022	< 0.001
	E-Muro	18.42 (4.93; 32.09)	N.A.	15.63 (8.42; 30.68)	0.54 (100; 86)	4.662	< 0.050
	E-Pirio	12.82 (0.00; 37.24)	N.A.	34.93 (17.43; 61.05)	0.27 (105; 89)	0.844	0.33

L-ratio and p-values represent the results from the comparison of a full model and a model without individual identity as random effect. N_{Obs} refers to the number of observations and N_{ID} to the number of different individuals considered in the models. All significant fixed effects for each trait were included in the models as detailed in Table S2.8 to S2.11.

Tableau S2.7 Sex-specific variance components (with 95% confidence intervals) and adjusted repeatability estimates (r_{ID}) for three personality traits in blue tits from Corsica (France).

Trait	Sex	V_{ID} (CI)	V_{OBS} (CI)	V_R (CI)	r_{ID} (N_{Obs};N_{ID})	L-ratio	p-value
Handling aggression	F	0.24 (0.16; 0.32)	0.02 (0.00; 0.07)	0.62 (0.54; 0.69)	0.27 (886; 457)	51.005	< 0.001
	M	0.21 (0.12; 0.30)	0.04 (0.01; 0.11)	0.59 (0.51; 0.68)	0.25 (813; 449)	30.117	< 0.001
HR (beats/min.)	F	8963.90 (6201.90; 1193.89)	788.80 (0.00; 2190.87)	2157.30 (1014.46; 3296.18)	0.75 (199; 157)	25.498	< 0.001
	M	8108.90 (5726.19; 9949.06)	3643.30 (0.00;10035.68)	479.90 (185.92; 1069.49)	0.66 (167; 140)	33.127	< 0.001
Average exploration speed (cm/s)	F	21.52 (7.34; 34.44)	N.A.	26.78 (15.39; 38.27)	0.45 (208; 173)	7.852	< 0.010
	M	18.66 (2.46; 33.64)	N.A.	30.52 (15.96; 44.70)	0.38 (171; 147)	4.346	< 0.05
Nest defense (m)	F	0.25 (0.09; 0.39)	0.16 (0.02; 0.55)	0.18 (0.07; 0.32)	0.42 (141; 125)	8.4257	< 0.005
	M	0.042 (0.00; 0.14)	0.10 (0.01; 0.33)	0.27 (0.16; 0.37)	0.25 (144; 115)	1.985	0.55

F : female, M: males; L-ratio and p-values represent the results from the comparison of a full model and a model without individual identity in random effect. N_{Obs} refers to the number of observations and N_{ID} to the number of different individuals considered in the models. Data from all years and the three populations were included. All the significant fixed effects for each trait were included in models as detailed in Table S2.8 to S2.11.

Final models describing each personality trait

Tableau S2.8 Final model describing the handling aggression scores measured in three blue tit populations in Corsica (France) between 2011 and 2014; estimates and confidence intervals (95% CI) are presented for each term.

Terms	Estimates	Lower Confidence intervals	Upper Confidence intervals
Intercept	2.29	1.99	2.59
Pop.: E-Muro	-0.77	-0.99	-0.54
Pop.: E-Pirio	-0.88	-1.11	-0.66
Sex: Females	-0.34	-0.44	-0.24
Time of day	0.01	-0.01	0.02
Capture period: Breeding	0.06	-0.02	0.19
Capture rank	0.02	-0.01	0.05
Year: 2012	-0.79	-0.99	-0.59
Year: 2013	-0.90	-1.12	-0.68
Year: 2014	-0.80	-1.01	-0.58
Pop.: E-Muro* Year: 2012	0.73	0.43	1.04
Pop.: E-Muro* Year: 2013	0.68	0.37	1.00
Pop.: E-Muro* Year: 2014	0.69	0.10	0.39
Pop.: E-Pirio* Year: 2012	0.95	0.69	1.26
Pop.: E-Pirio* Year: 2013	1.05	0.77	1.36
Pop.: E-Pirio* Year: 2014	0.88	0.58	1.18

References: Population: D-Muro; Sex: Males; Capture period: Pre-breeding; Year: 2011.

Tableau S2.9 Final model describing mean heart rate during manual restraint (HR; in beats/min.) measured in three blue tit populations in Corsica (France) between 2011 and 2015; estimates and confidence intervals (95% CI) are presented for each term.

Terms	Estimates	Lower Confidence intervals	Upper Confidence intervals
Intercept	936.74	714.10	1157.72
Pop.: E-Muro	26.95	-18.58	72.41
Pop.: E-Pirio	26.05	-28.33	80.48
Year: 2012	4.29	-35.72	43.90
Year: 2013	7.42	-40.82	55.33
Year: 2014	48.89	-14.67	127.90
Year: 2015	51.03	-3.99	105.63
Sex: Females	5.76	-16.92	28.36
Time of day	0.29	-3.54	4.16
Body mass	-3.73	-21.53	24.86
Time between capture and recording	-109.43	-193.39	-25.55
Pop.: E-Muro* Year: 2012	-41.36	-95.24	13.51
Pop.: E-Muro* Year: 2013	-9.27	-78.43	60.80
Pop.: E-Muro* Year: 2014	-53.19	-135.98	31.05
Pop.: E-Muro* Year: 2015	-83.01	-151.39	-14.26
Pop.: E-Pirio* Year: 2012	39.60	-27.67	106.10
Pop.: E-Pirio* Year: 2013	5.09	-78.96	89.26
Pop.: E-Pirio* Year: 2014	-109.06	-216.86	-0.45
Pop.: E-Pirio* Year: 2015	-57.68	-132.34	16.90

Reference: Population: D-Muro ; Sex: Males; Year: 2011.

Tableau S2.10 Final model describing the average exploration speed (cm/s) for blue tits in Corsica (France) between 2011 and 2014; estimates and confidence intervals (95% CI) are presented for each term.

Terms	Estimates	Lower Confidence intervals	Upper Confidence intervals
Intercept	17.62	13.53	21.69
Pop.: E-Muro	-2.90	-6.13	0.33
Pop.: E-Pirio	-5.58	-9.10	-2.04
Sex: Females	-2.02	-3.49	-0.55
Contention method: bag	1.24	-1.11	3.60
Contention method: cage	-2.21	-3.92	-0.50
Time of day	-0.05	-0.31	0.21
Year: 2012	0.69	-2.25	3.63
Year: 2013	0.40	-2.73	3.53
Year: 2014	-8.64	-11.73	-5.57
Pop.: E-Muro*Year: 2012	2.75	-1.56	7.06
Pop.: E-Muro*Year: 2013	-0.17	-5.16	4.82
Pop.: E-Muro*Year: 2014	2.84	-1.69	7.38
Pop.: E-Pirio*Year: 2012	-0.06	-4.65	4.48
Pop.: E-Pirio*Year: 2013	2.66	-2.00	7.29
Pop.: E-Pirio*Year: 2014	6.81	2.03	11.60

Reference for every term: population: D-Muro; Sex: Males; Contention methods: no contention; Year: 2011.

Tableau S2.11 Final model describing the minimal approach distance during nest defense trials for blue tits in Corsica (France) between 2011 and 2015; estimates and confidence intervals (95% CI) are presented for each term.

Terms	Estimates	Lower Confidence intervals	Upper Confidence intervals
Intercept	2.28	1.50	3.05
Year: 2013	-0.75	-1.14	-0.33
Year: 2014	-0.50	-0.82	-0.17
Year: 2015	-0.81	-1.21	-0.39
Sex: Females	0.20	0.05	0.35
Time of day	0.02	-0.05	0.09
Identity of the decoy: no2	0.20	-0.40	0.80
Dist. between decoy and nest-box	0.001	-0.0002	0.002
Dist. to closest branch	-0.001	-0.002	0.0003
Observer dist. from nest-box	0.05	-0.03	0.13

Reference: Year: 2011, Sex: Males, Identity of the decoy: no1

Tableau S2.12 Difference between birds from the Fango and Regino valley in handling aggression score and average exploration speed for blue tits in Corsica (France) between 2011 and 2014; we used the same fixed effect structure as for the models with population as a fixed effect (using valley instead of population; but without the interaction terms between valley and year, see Table S2.8 and S2.10).

Trait	Estimates Fango valley	95% CI	L-ratio	p-value
Handling aggression	-0.054	-0.173; 0.066	0.782	0.37
Average exploration speed (cm/s)	-2.803	-4.493; -1.114	10.479	< 0.001

Reference: Regino valley

The novel-environment apparatus

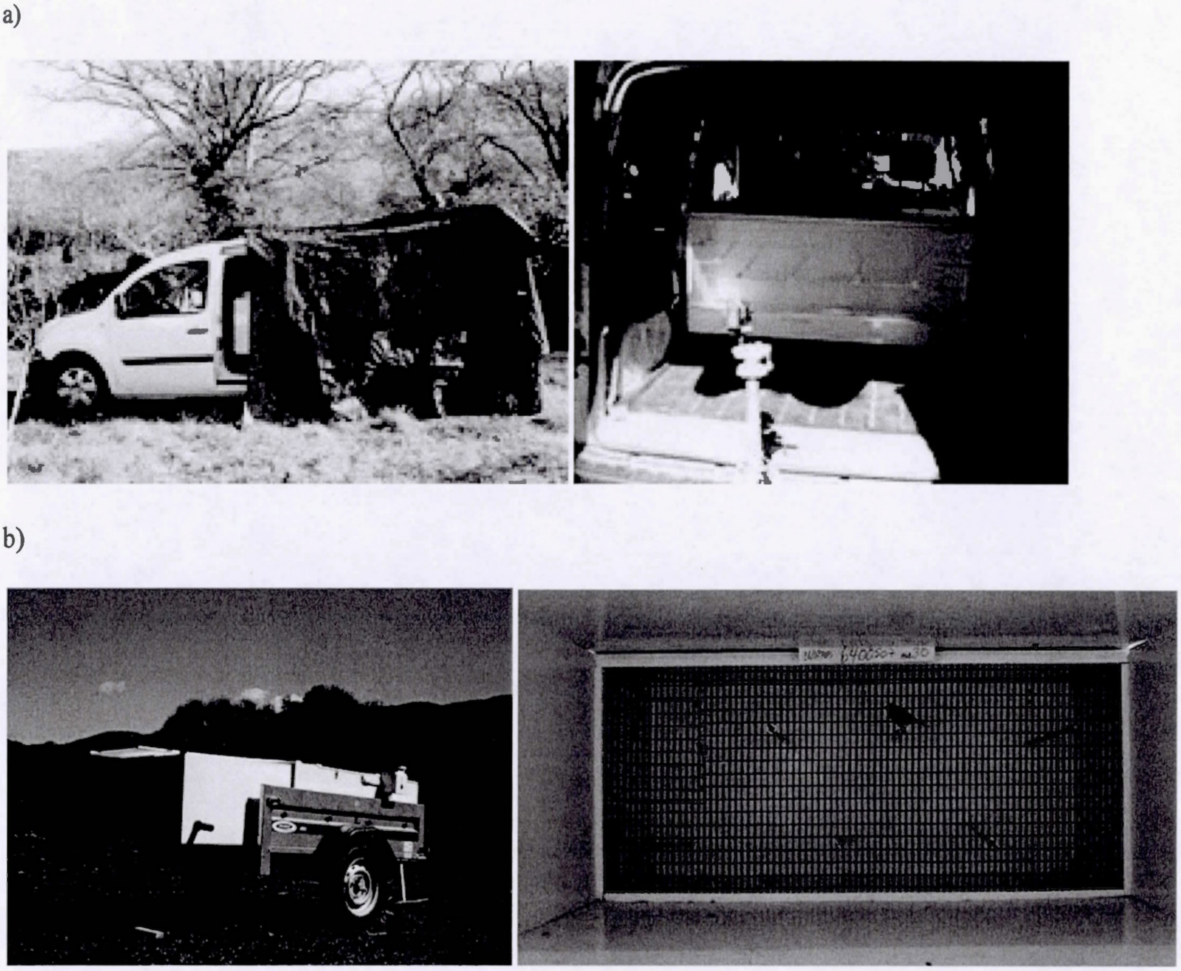
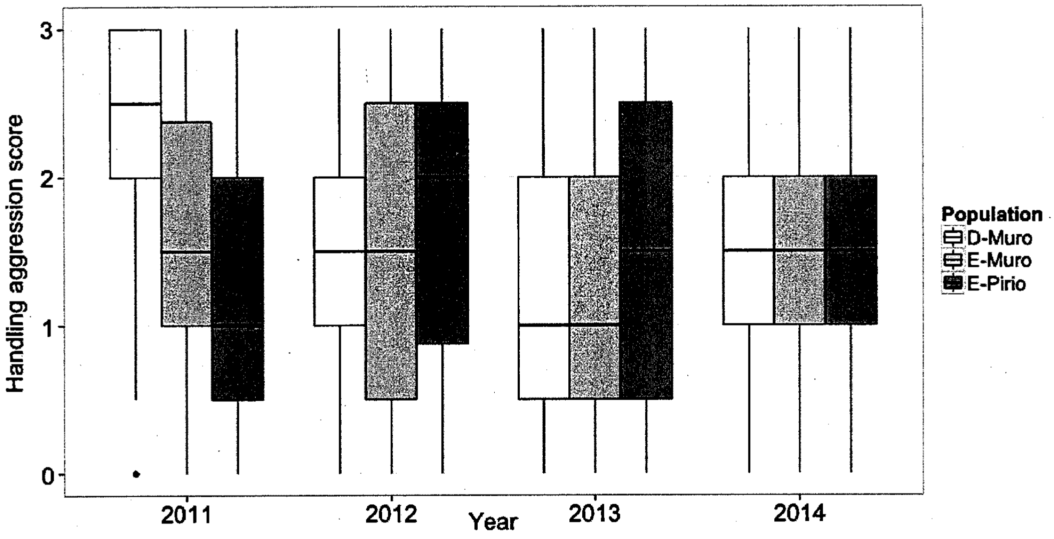


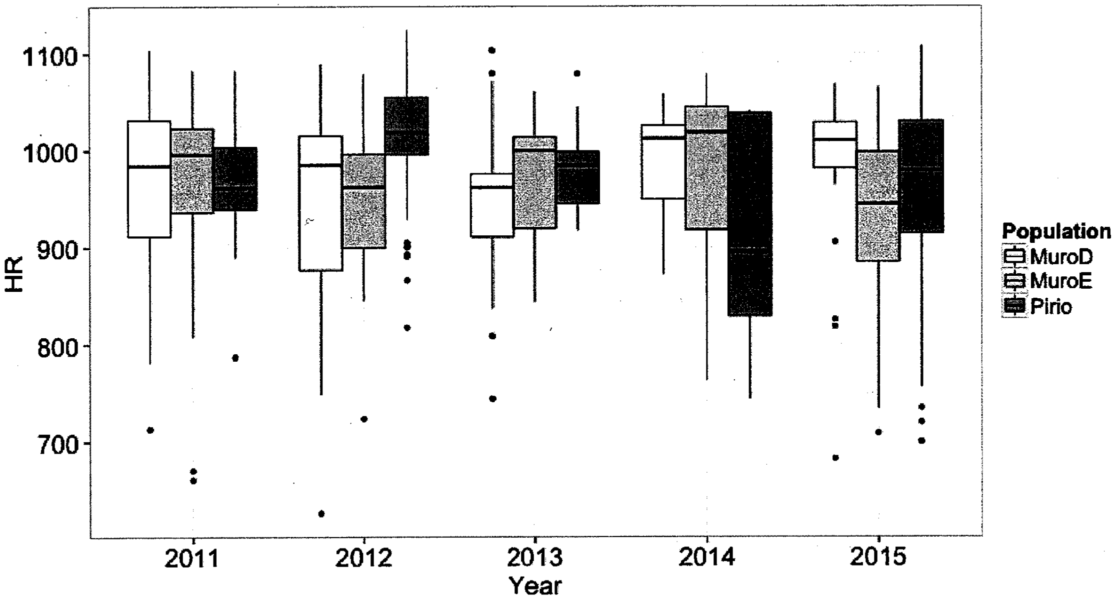
Figure S2.1 Novel-environment apparatus used in a) 2011 to 2013 and b) 2014, view of the entire apparatus and of the cages.

Average personality phenotype for each year and population

a)



b)



c)

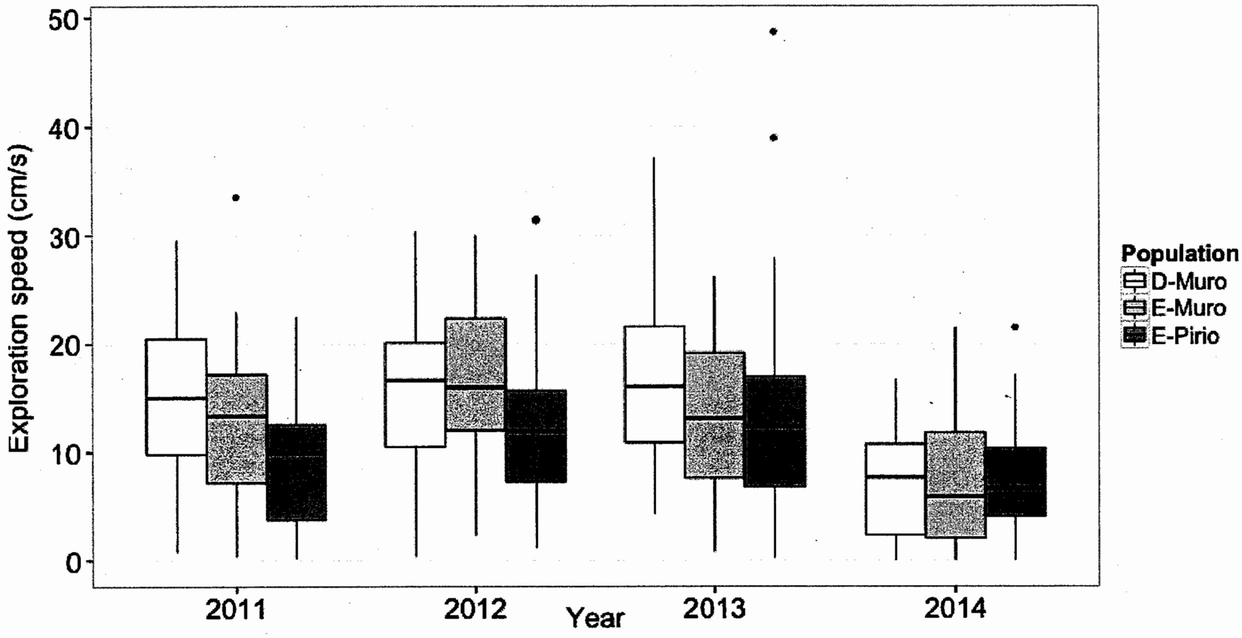


Figure S2.2 Average a) handling aggression score, b) heart rate during manual restraint (beats/min.), c) average exploration speed (cm/s) for each year and population for three Corsican blue tits populations (France).

Variation in mean handling aggression score in function of density and food abundance in each population

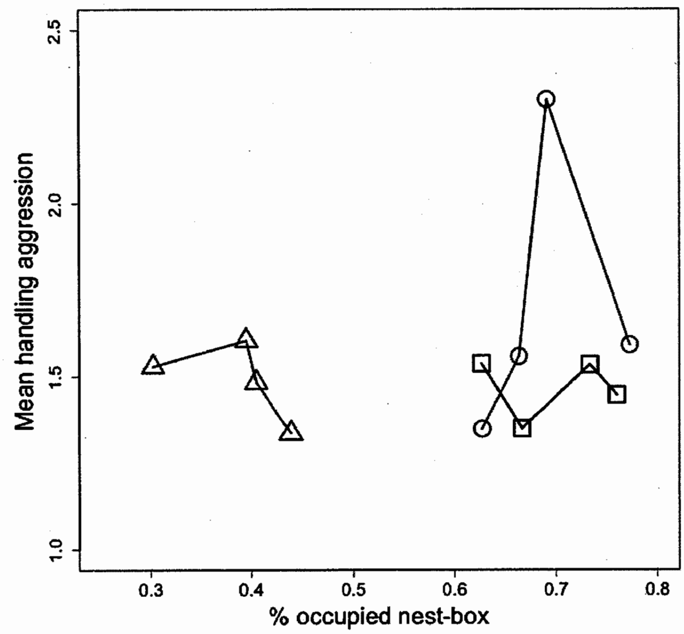


Figure S2.3 Variation across populations in mean handling aggression scores and proportion of occupied nest-boxes (as an indication of density). Blue and circle: D-Muro, black and squares: E-Muro and red and triangle: E-Pirio. A simple model with mean handling aggression for each population as response variable and as fixed effect the % of occupied nest-box, year, population and the interaction between population and % occupied nest-boxes reveals no effect of nest-box occupancy on mean handling aggression score and no interaction between population and % of occupied nest-boxes.

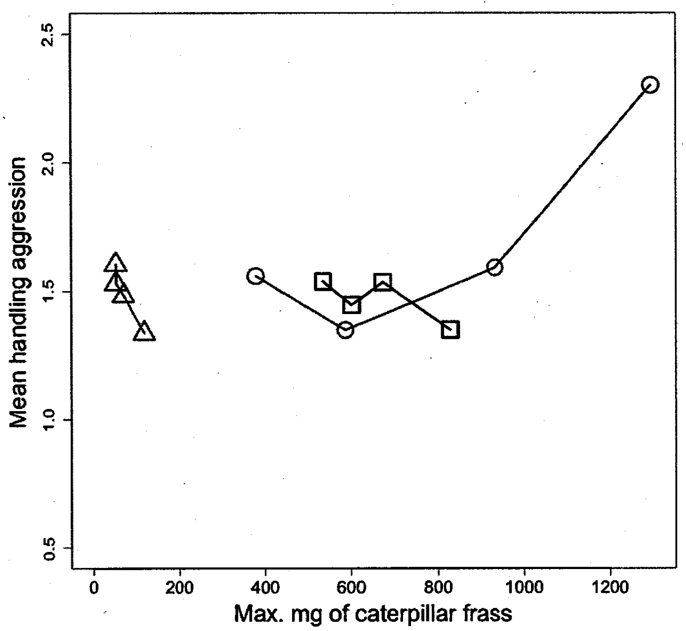


Figure S2.4 Variation across populations in mean handling aggression scores and maximal mg of caterpillar frass per m^2 per day (see Zandt et al. 1990 for details about the caterpillar frass sampling procedure). Blue and circle: D-Muro, black and square: E-Muro and red and triangle: E-Pirio. In D-Muro, caterpillar abundance was positively related with the average population handling aggression (correlation estimate = 0.83). We found the opposite trend in E-Muro and E-Pirio: mean handling aggression scores increase with decreasing frass weight (cor : E-Muro = -0.79; E-Pirio = -0.96). A simple model with mean handling aggression for each population as response variable and as fixed effect the maximum of caterpillar frass, year, population and the interaction between population and max. caterpillar frass reveals a marginally significant interaction between population and caterpillar frass: the relationship between max. frass and mean handling aggression was opposite in E-Pirio and D-Muro (p-value = 0.060). The amount of caterpillar frass and the mean handling aggression scores were both particularly high in 2011 in D-Muro, which might explain the difference in handling aggression phenotypes between E-Pirio and D-Muro for this year in specificaly.

CHAPITRE 3
GENE FLOW DOES NOT PREVENT PERSONALITY AND MORPHOLOGICAL DIFFERENTIATION BETWEEN TWO BLUE TIT POPULATIONS.

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3.1 Abstract

Phenotypic divergence among populations can result from genetic divergence, phenotypic plasticity, or a combination of the two. Few studies have deciphered these mechanisms for populations separated by small spatial scale and connected by gene flow, especially in the case of divergence in personality traits. In this study, we used a common garden experiment to explore the genetic basis of the phenotypic differences observed in two personality traits (exploration speed and handling aggression), one physiological trait (heart rate during restraint) and two morphological traits (tarsus length and body mass) between two blue tit (*Cyanistes caeruleus*) populations inhabiting contrasting habitats yet separated by only 25km. Blue tit nestlings were removed from their population and raised in a common garden for up to five years. We then compared adult phenotypes and **P** (co)variance matrices between the two populations, as well as trait-specific Q_{st} and F_{st}. Our results revealed common garden differences between the two populations similar to those found in the wild, yet no difference in **P** (co)variance matrices. We found that Q_{st} was larger than F_{st} for all traits, suggesting that the divergence is likely the result of dissimilar selection patterns. Our study adds to the growing body of evidence that genetic divergence for potentially adaptive personality traits is possible at a small spatial scale.

3.2 Introduction

Understanding the evolutionary causes of phenotypic divergence among populations is an important aspect of the study of diversity. Environmental heterogeneity can have a major role in creating phenotypic divergence among populations (Wang et Bradburd 2014). Spatial variation in selection pressures resulting from such environmental heterogeneity can lead to genotype by environment interactions for fitness and produce genetic divergence between populations that can lead to local adaptations (Kawecki and Ebert 2004, Wang and Bradburd 2014). Spatial heterogeneity in ecological conditions can also favour the evolution of phenotypic plasticity, allowing organisms to track the local optimal phenotype in changing environments (Réale et al. 2003, Pigliucci 2005; Charmantier et al. 2008; Fitzpatrick 2012). Plasticity can thus cause phenotypic divergence of populations without any genetic divergence (Sultan and Spencer 2002). However, phenotypic divergence of populations does not necessarily involve an adaptive process as phenotypic plasticity can be non-adaptive (Fitzpatrick 2012) and strong founder effects or genetic drift can also lead to phenotypic and genetic divergence of populations (Slatkin 1987). In addition, plasticity and genetic divergence are not mutually exclusive and can occur together, either in the same or in opposite direction (Fitzpatrick 2012). Establishing the relative importance of phenotypic plasticity *versus* genetic changes involved in the phenotypic divergence of populations provides fundamental information about the processes that generate intra-specific diversity in the wild. In addition, determining if this divergence is the result of neutral processes or natural selection is essential because it gives important indications about the eco-evolutionary dynamics of traits and their evolutionary trajectories.

Traditionally, it has been considered that the homogenizing effect of gene flow prevents genetic divergence between populations (Sultan and Spencer 2002). Thus, most research on genetic divergence focused on populations separated by large spatial scales or by important landscape barriers to dispersal (Slatkin 1987; Lenormand 2002). Nevertheless, recent theoretical and empirical studies have revealed that despite gene flow, phenotypic divergence of populations can have a genetic origin when there is strong divergent selection and non-random dispersal (Wang and Bradburd 2014). Despite growing interest on the subject, the mechanisms underlying the phenotypic divergence of populations separated by small geographic distances and connected by gene flow have yet to be discovered.

Behavioural traits have often been considered as highly plastic and thus less prone to genetic divergence. However, several studies are now showing that among-individual differences in behaviour can be repeatable (*personality*; Réale et al. 2007), moderately heritable (van Oers and Sinn 2011), can be subject to selection (Smith and Blumstein, 2008) and could thus evolve in response to local conditions. In this context, an increasing number of studies have compared the personality phenotypes of populations inhabiting contrasted ecological conditions (Bell 2005; Quinn et al. 2009; Atwell et al. 2012; Herczeg et al. 2013; Miranda et al. 2013; Karlsson Green et al. 2016; Jacquin et al. 2016). However, fewer studies have disentangled the role of plasticity from that of genetic effect in shaping small scale phenotypic divergence of population living different habitats for highly mobile organism such as avian species (but see Atwell et al. 2012; Miranda et al. 2013).

Previously, we have revealed phenotypic divergence for personality and morphological traits between two wild populations of blue tits (*Cyanistes caeruleus*) living in contrasting habitats in a Mediterranean landscape (Charmantier et al. 2016, Dubuc-Messier et al. 2016). These two populations occupy contrasted habitats dominated by either evergreen (holm oak, *Quercus ilex*) or deciduous oaks (downy oak, *Quercus pubescens*). The dominant tree species in each habitat is suspected to have an important influence on blue tits' ecological context and on the selection pressures acting on the populations (Charmantier et al. 2016). Blue tits from the evergreen habitat display lower body mass, smaller tarsus length, higher docility, and slower exploration in a novel environment compared to birds from the deciduous habitat (Table S3.1; Charmantier et al. 2016; Dubuc-Messier et al. 2016). These phenotypic differences are surprising considering the species dispersal capacity, the absence of substantial barrier to dispersal, the weak genetic differentiation among them (Porlier et al. 2012a; Szulkin et al. 2016).

In this study, we used a common garden experiment to assess if the personality and morphological divergence between these two blue tit populations has a genetic basis. We collected blue tit nestlings from the evergreen and deciduous habitats and raised them for up to five years in aviaries. First, we compared the personality, physiological and morphological phenotypes of adult birds originating from the two habitats. Previous experiments in aviaries on this system have found a genetic divergence between these populations for life-history traits (Lambrechts er al. 1997). Based on these results, we hypothesized that the phenotypic divergence found previously in the wild for personality and morphological traits would also reflect a genetic divergence. Therefore, we predicted that, following the common garden experiment, individuals originating from the evergreen habitat would show a slower exploration in the novel environment, a higher docility, a smaller tarsus and a lower body mass than individuals from the deciduous habitat. We also compared heart rate during manual restraint (HR hereafter) of birds originating from the two habitats, a physiological measure of stress reaction often used in personality studies (Koolhaas et al. 1999). Although we did not find significant phenotypic differences in HR between these habitats in the wild (Dubuc-Messier et al. 2016), we decided to study this trait in our experiment because a genetic divergence for HR may be masked in the wild by differential plastic responses (countergradient variation, Conover and Schultz 1995).

Second, we compared the phenotypic (co)variance matrices (**P** matrices) between the two habitats. Different environmental conditions experienced by the two populations may have led to different selection regimes for the studied traits that result in different **G** matrices. In the common-garden experiment, birds from the two habitats shared the same rearing environment. As a result, **P** matrix differences between these populations should reflect differences at the genetic level (i.e. good surrogates for **G** matrices). Hence, we expected to find differences in **P** matrix structures between the two populations (Roff and Fairbairn 2012).

Third, we investigated if the potential genetic divergence between these habitats could be attributed to different selection pressures or to genetic drift, using a Q_{st} - F_{st} comparison approach (Leinonen et al. 2013). These two blue tit populations have very large population sizes (roughly estimated around 10,000) and have been found weakly genetically differentiated (Szulkin et al. 2016). Consequently, we considered that it is unlikely that any genetic divergence for these traits would be produced by genetic drift. We thus predicted that the Q_{st} of each trait would significantly exceed the F_{st}. Lastly, in order to better understand the importance of plasticity in shaping the observed phenotypic differentiation in the wild, we compared the genetic differentiation (Q_{st}) from the common garden experiment with the phenotypic differentiation in the wild for the same traits (P_{st}).

3.3 Materials and Methods

The population located in the evergreen habitat (Evergreen-Pirio) is in the Corsican Fango valley (42°34'N, 08°44'E; 200m elevation) and contains 205 nest-boxes distributed in two study plots. The population located in the deciduous habitat (Deciduous-Muro) is in the Corsican Regino valley (42°32'N, 08°55'E, 350 m elevation) and contains 110 nest-boxes distributed in three study plots. A weekly to daily monitoring over the course of the breeding season (from early April to the end of June) allowed the recording of exact laying dates and hatching dates for all broods established in nest boxes.

Nestling were collected for the common garden experiment at 7 to 12 days of age and were brought to the Netherlands Institute of Ecology (NIOO-KNAW, Wageningen, Netherlands) where they were hand raised under standardized conditions. We used 169 blue tits that were collected in 2010 and 2011 in the deciduous habitat (2010: 42 birds, 7 broods; 2011: 39 birds, 6 broods) and in the evergreen habitat (2010: 44 birds, 10 broods; 2011: 44 birds, 8 broods). In 2010, before collecting chicks, broods were cross-fostered between nests containing chick of the same age for another experiment. For this experiment, at 2 to 4 days old, half of the chicks from a given brood were exchanged with half of the chicks of another brood from the same population. Once collected, all birds were transported by car and hand-fed from Corsica to the Netherlands, and were hand reared until independence as described in Reparaz et al (2014). Briefly, all the chicks from a given habitat and year were kept in the same box divided into multiple compartments, each containing one nest of 3 to 5 nestlings, until fledgling. After fledging, birds were housed in cages in groups of 2 to 4 birds, irrespective of their sex and nest of origin. Up to that period, chicks were fed every half-hour, 14 hours per day (7:00 am - 9:00 pm), with a diet consisting of a mixture of curd cheese, ground beef heart, baby cereal, multivitamin solution and calcium carbonate, supplemented with wax moth larvae and bee larvae, until independence. At independence, about 35 days after hatching, birds were relocated to larger individual cages or aviaries. Food and water were provided *ad libitum*. In 2012 and 2015, birds were moved to the Centre d'Écologie Fonctionnelle et Évolutive (CEFE-CNRS; Montpellier, France), where they were kept in outdoor aviaries before being released back into their natal habitat in Corsica. Morphological measurements were taken during the period at the NIOO-KNAW. Tarsus length was measured once, but body mass was measured several times. We were interested in testing for differences in adult body mass, and thus analyzed body mass for birds of one year of age and older.

3.3.1 Behavioural and physiological trials

In total, 169 birds were tested for their exploration behaviour and, among those birds, 137 were tested for handling aggression and 57 for HR. All behavioural traits were measured once for each bird, which prevented us to report their repeatability. However, these behavioural traits have been shown to be repeatable in these two populations in the wild, with repeatability estimates ranging from 0.26 to 0.75 (Dubuc-Messier et al. 2016). In the present study, exploration behaviour was measured using a different protocol (see below) than the one used in the wild (Dubuc-Messier et al. 2016). Nevertheless, we are confident that the exploration behaviour measured here represents repeatable characteristics of the individuals because this trait has been shown to be repeatable in blue tits in several studies using different protocols (Kluen and Brommer 2013; Mutzel et al. 2013; Dubuc-Messier et al. 2016). For details regarding the phenotyping of wild birds used in the P_{st} calculations, please refer to Dubuc-Messier et al (2016).

Exploration behaviour

Exploration behaviour trials were done in fall 2011 in the Netherlands Institute of Ecology as described by Reparaz et al. (2014) and using a novel environment chamber slightly modified from Drent et al (2003). The novel environment chamber consisted of a 4.0 x 2.4 x 2.5m room with five artificial trees. Individuals were placed in cages adjacent to the main chamber 30 to 120 minutes before the trials and introduced in the main chamber through a sliding door. For two minutes, the observer counted the total number of movements between trees and the number small jumps on a given tree / branch. Exploration scores was the sum of both and varied from 10 (a very slow exploration pattern) to 92 (a very fast exploration pattern; Reparaz et al. 2014).

Docility

Docility was measured assessing the bird's aggression towards a manipulator (Dubuc-Messier et al. 2016). We used a score ranging from 0 to 3. A score of 0 was the lowest aggression score (no reaction; high docility) and 3 the highest (see Table S3.2 for detailed protocol). Handling aggression was recorded in 2012 and 2015 at the CEFE-CNRS (France). Birds from the 2010 cohort were tested for handling aggression in 2012 or 2015 (at 2 or 5 years of age), while the entire cohort from 2011 was tested for handling aggression in 2015 (at 4 years of age). Handling aggression score was assessed blindly in 2015 and was assessed by two different observers, one in 2012 and one in 2015.

Heart rate during manual restraint

HR was recorded in 2012 at the CEFE-CNRS (for the 2010 cohort only), as described by Dubuc-Messier et al (2016). Within a few minutes after capture, we recorded HR for 30 seconds using a digital recorder. We used the software Avisoft SASLab Pro version 5.1 to extract the mean time interval (sec) between two heartbeats using approximately 100 consecutive heartbeats per individual.

3.3.2 Molecular markers and F_{st} calculation

For logistical reasons, we were not able to perform a molecular analysis on the birds used in the common garden experiment. As an alternative, we used a dataset, published by Szulkin et al (2016) of wild birds from these two populations (i.e. deciduous, n = 49; evergreen, n = 83 individuals) and genotyped at several thousands SNP using RAD-sequencing. We retained loci genotyped over at least 75% of the individuals. To avoid bias during filtering and in the F_{st} estimates, we pruned highly related individuals from the dataset to keep only individuals linked with values of kinship lower than 0.05 (coefficient of Loiselle; Loiselle et al. 1995; Cheverud 1996) computed in Genodive 2.27 (Meirmans and Van Tienderen, 2004). In order to retain loci more likely to be informative, we applied a 5% MAF threshold (using vcftools 0.1.11; Danecek et al. 2011). We pruned the dataset for SNPs that deviated from Hardy-Weinberg-Equilibrium in at least one of the two populations (p-value > 0.05). To obtain a set of SNPs more likely to be neutral, we filtered out SNPs potentially under divergent selection between the two habitats (p-value ≥ 0.015, Alpha ≥ 0). This was done with a Bayescan 2.0 test (Foll and Gaggiotti 2008, 5 000 pilot iterations, 50 000 burnin, prior odds of 100).

Average F_{st} and 95% confidence intervals were estimated using the R-package hierfstat (Goudet 2005). The final dataset contained 69 individuals (32 and 37 individuals in the deciduous and evergreen habitats, respectively) genotyped at 5407 SNPs.

The behavioural tests run at the NIOO-KNAW were approved by the Animal Experimentation Committee of the Royal Dutch Academy of Sciences (DEC-KNAW; permit number CTE09–04 and NIOO11.09). The work performed in the field was approved by the prefectural office of Corsica and the Regional Direction of Environment (DIREN) committee (permit numbers 2009–0379 and 3467) and the tests run at the CEFE were approved by the Comité Institutionnel de Protection des Animaux (UQAM; CIPA-769-2015; 0413-R1-769-0414) in Canada.

3.3.3 Statistical analysis

Phenotypic divergence between habitats of origin

We tested for a phenotypic difference between the two habitats for each trait with univariate linear mixed-models using habitat of origin, sex, and their interaction as fixed effects. When we found a significant interaction between habitat of origin and sex, we ran a separate model for each sex. Specific confounding variables were added as fixed effects for each particular trait. For exploration score, we included a cohort term as fixed effect to test for any environmental effect early in life or during the hand-rearing period in captivity. However, novel environment tests were done on the two cohorts at the same time 2011. Thus, at the time of the test, individuals born in 2010 were almost 1½ years old, while individuals born in 2011 were 5 months old. Hence, in this model, the cohort term controlled for the combined effect of cohort and age. For handling aggression score, we included cohort, bird age, time of day (hour), and year of test (2012 or 2015) as fixed effects. For HR models we included sex, mean individual body mass as an adult, and time of day (hour) as fixed effects. HR recordings were done on the 2010 cohort only. We thus did not add a fixed effect for bird age, cohort or year to avoid redundancy. For tarsus length, we included cohort only in fixed effect (*i.e.* 2010 and 2011). For body mass, we included age as a continuous variable, cohort, and time of day (hour).

In all the models, we used the random terms “brood of origin” and “rearing brood” to account for the non-independence of birds coming from the same brood or an effect of foster parents for nestlings that have been cross-fostered prior to the captivity period. Because body mass was measured several times for each bird, we also used the bird identity as a random effect for this trait.

All response variables were Z-transform prior to analyses. We tested the significance of the fixed effect by L-ratio using stepwise procedure starting with a model including all variables (Bates et al. 2014). We kept all the random effects in final models. Analyses were done with *R* (Core Team 2015) using the function *lmer* of the package *lme4* (Bates et al. 2014). Confidence intervals were generated with the function *confint.merMod*.

P matrices comparison

To compare **P** matrices, we first constructed a phenotypic (co)variance matrix for each population using the residuals of the model with all the random effects and the significant fixed effects selected previously. We then investigated the similarity of **P** matrices between the two habitats using the random selection skewers method (Cheverud and Marroig 2007) and the *phytools* package in R (Revell 2012) with 10 000 random selection vectors. This method measures the similarity of two observed matrices by comparing their response to random selection vectors (Revell 2007). The correlation between the response vectors of each matrix indicates their degree of similarity (values ranging from 0 (no shared structure) to 1 (identical); Revell 2007). The null hypothesis for this test is that the two matrices have no shared structure (Cheverud and Marroig 2007).

Q_{st}, P_{st} and F_{st} comparison

Because birds where raised in a common garden, we considered that the phenotypic difference among individuals was a realistic approximation of the additive genetic effect. For each trait we thus calculated the Q_{st} between the two habitats based on the phenotypes of birds from the common garden and compared its distribution with the distribution of the mean F_{st} of the two habitats in the wild and of P_{st} of wild birds. We calculated the Q_{st} and P_{st} as (Wright 1949):

$$Q_{st} \text{ or } P_{st} = \sigma_B / (\sigma_B + 2*\sigma_W)$$

Where σ_B is the between-habitat phenotypic variance and σ_W the within-habitat variance extracted from a univariate linear mixed model. We used the phenotype of each individual as a response variable and habitat of origin as a random effect to extract σ_B. For Q_{st} calculation, we also used as random effects the identity of the brood of origin, of the rearing brood, and for body mass we also used the identity of the bird. Fixed effects were the confounding variables selected previously, excluding the term habitat of origin. For P_{st} calculation, we used as random effects the identity of the bird and the observer identity (for handling aggression and HR) along with the significant fixed effects (details in Dubuc-Messier et al. 2016). We calculated σ_W as the sum of the variance attributable to all the random effects except the habitat of origin term. These models were performed in a Bayesian framework with the MCMCglmm package (Hadfield 2010) using slightly uninformative priors (*i.e.* V

$= V_P / n$, $nu = 1$; V_P is the total phenotypic variance of the trait and n the number of random effects), 10 million iterations, a thinning of 200 and a burn-in phase of 500. Q_{st} and P_{st} calculations were performed using the posterior mode of σ_B and σ_W and credible intervals were calculated using the function *HPD interval* of the package *lme4* in R (Bates et al 2014), which computes the 95% posterior density of the distribution. For all traits, we also calculated the ratio Q_{st} / mean F_{st}, and assumed that Q_{st} differed significantly from F_{st} when the credibility intervals around this ratio did not include one.

3.4 Results

3.4.1 Divergence between habitats of origin

Behavioural and physiological traits

For birds in the common garden experiment, habitat of origin had a significant effect on the two behavioural traits: blue tits from the deciduous habitat were faster explorers and were more aggressive to the handler (Table 3.1; Fig. 3.1). Birds from the deciduous habitat had a lower HR than birds from the evergreen habitat (Table 3.1; Fig. 3.1). We found a trend for an interaction between habitat of origin and sex for HR (L-ratio = 3.360, d.f. = 1, p-value = 0.067): evergreen males had a higher HR than deciduous males [estimate = 1.24 (CI: 0.31; 2.17), L-ratio = 6.260, d.f. = 1, p-value = 0.010) but there was no habitat of origin effect for females (L-ratio = 2.150, d.f. = 1, p-value = 0.142). There was no interaction between sex and habitat of origin for the two other behavioural traits, but there was a difference in exploration score between sexes (Table 3.1).

Morphological traits

Habitat of origin also had a significant effect on the two morphological traits: deciduous birds were heavier and had a longer tarsus than evergreen birds (Table 3.1; Fig. 3.1). We did not find any interaction between habitat of origin and sex for these two traits (tarsus length: L-ratio = 0.226, d.f. = 1, p-value = 0.634; body mass: L-ratio = 0.155, d.f. = 1, p-value = 0.694). Among-individual differences in body mass were significant and represented 45% of the total variance of the trait [variance = 0.34 (95% CI: 0.26; 0.46), L-ratio = 421.95, p-value < 0.001].

3.4.2 Brood effects

Differences among broods of origin explained a significant portion (78%) of the total phenotypic variance in body mass, but not the other traits (Table S3.3). Differences among rearing broods explained a significant portion of the total variance in tarsus length (22%) but not for the other traits.

3.4.3 **P** matrices comparison

Random skewers analysis revealed that the responses to random selection vectors of the two observed matrices were more correlated than the responses of two random (co)variance matrices ($r = 0.90$, p-value < 0.001, $n_{\text{evergreen}} = 32$, $n_{\text{deciduous}} = 25$), indicating that the **P** matrices of the two populations were similar. We did not find any significant phenotypic correlations between traits, except between tarsus length and body mass [$r = 0.48$ (0.25; 0.66), p-value < 0.001]. The (co)variance and correlation matrices are reported in Table S3.4.

3.4.4 Q_{st}, P_{st} and F_{st} comparison

We found a significant but small genetic differentiation between the two populations. Mean F_{st} over all loci was 0.004 [(95% CI: 0.003; 0.005), p-value < 0.001]. Q_{st} were higher than F_{st}, with non-overlapping confidence intervals for all traits and the ratio between the Q_{st} and F_{st} was significantly greater than one for all traits but to a lesser extend for body mass (Table 3.2). Credibility intervals for Q_{st} and P_{st} overlapped for all traits (Table 3.2).

Tableau 3.1 Final models describing the phenotype of blue tits originating from two distinct populations and habitats (deciduous or evergreen) in Corsica (France) and reared in a common garden.

	Terms	Estimates	95% CI	L-ratio	d.f.	p-value
Exploration score	Intercept	-0.32	-0.62; -0.03			
	Habitat of origin	-0.48	-0.78; -0.19	9.70	1	0.002
	Sex	0.26	0.004; 0.52	3.97	1	0.046
	Cohort	0.88	0.59; 1.17	23.91	1	< 0.001
Handling aggression	Intercept	0.96	0.09; 1.85			
	Habitat of origin	-0.80	-1.16; -0.44	14.96	1	< 0.001
	Time of day	-0.04	-0.11; 0.03	10.86	1	< 0.001
Heart rate during restraint (HR)	Intercept	1.24	-3.57; 5.80			
	Habitat of origin	1.06	0.38; 1.75	8.39		0.003
	Mean body mass	-0.20	-0.67; 0.31	32.97		< 0.001
Body mass	Intercept	-1.07	-1.40; -0.74			
	Habitat of origin	-0.33	-0.63; -0.03	4.46	1	0.034
	Sex	-0.56	-0.77; -0.35	25.08	1	< 0.001
	Age	0.27	0.21; 0.33	74.23	1	< 0.001
	Time of day	0.09	0.07; 0.11	75.50	1	< 0.001
Tarsus length	Intercept	-0.25	-0.58; 0.08			
	Habitat of origin	-0.60	-1.00; -0.19	7.74	1	0.005
	Sex	1.04	0.81; 1.28	61.46	1	< 0.001

The deciduous habitat, females, and cohort 2010 were set as references in models. Estimates are from a model with 'brood of rearing' and 'brood of origin' identity in random effect (and individuals identity for body mass), variance estimates are shown in Table S2.3. L-ratio and p-values are from the comparison of a full model and a model without the variable of interest.

Tableau 3. 2 Q_{st} and P_{st} values (mode) for each trait, mean F_{st} and Q_{st} / F_{st} ratio [and associated 95% credible interval (CI)] between two blue tits populations originating from distinct populations and habitats (deciduous or evergreen) in Corsica (France) and reared in a common garden.

Traits	Q_{st} (95% CI)	P_{st} (95% CI)	Q_{st} / F_{st} ratio (95% CI)
Exploration score	0.062 (0.011; 0.692)	0.063 (0.018; 0.727)	15.525 (2.795; 173.022)
Handling aggression	0.089 (0.017; 0.752)	0.045 (0.011; 0.692)	22.270 (4.144; 188.028)
Heart rate during manual restraint (HR)	0.061 (0.011; 0.776)	0.032 (0.007; 0.562)	15.298 (2.730; 193.990)
Body mass	0.035 (0.006; 0.553)	0.095 (0.030; 0.773)	8.872 (1.531; 138.164)
Tarsus length	0.084 (0.018; 0.779)	0.212 (0.048; 0.864)	21.081 (4.580; 194.79)
Mean F_{st}	*0.004* *(0.003; 0.005)*		

Q_{st} have been calculated from the phenotypes of birds raised in a common garden and P_{st} from the phenotype of wild birds.

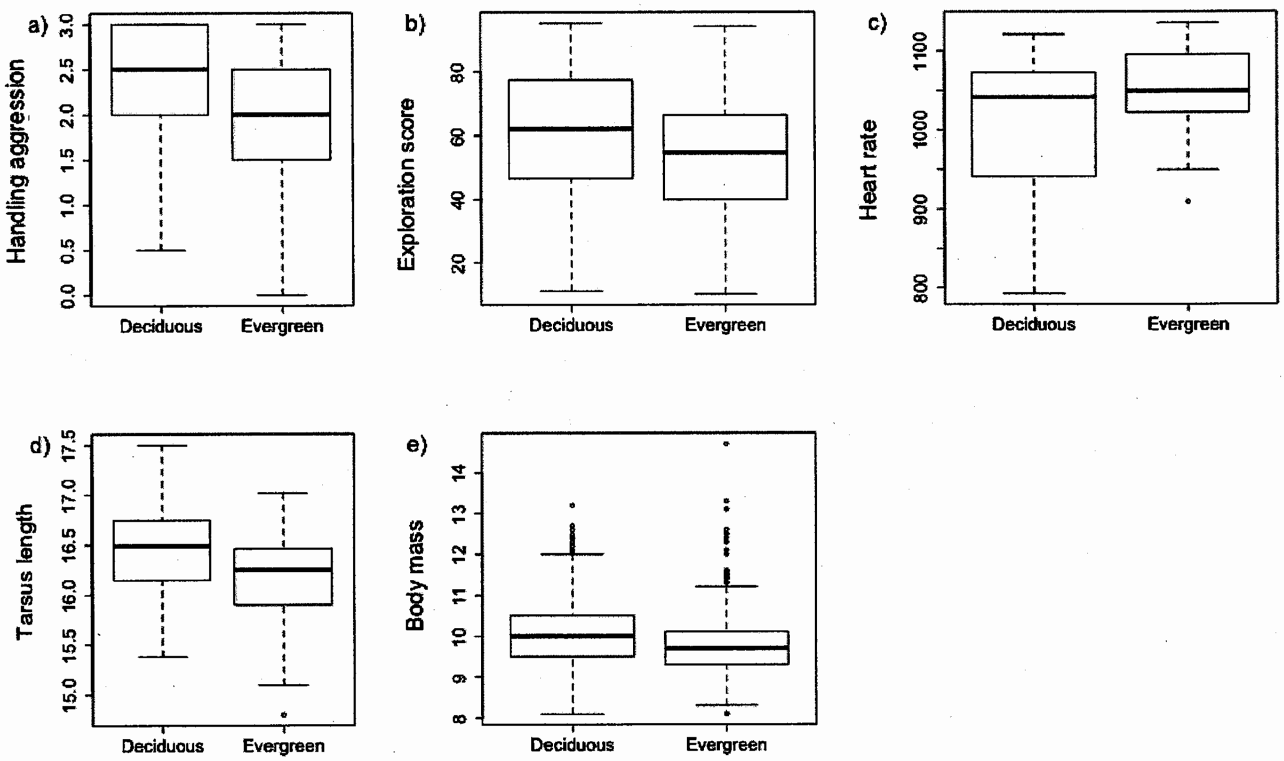

Figure 3.1 a) Exploration score, b) handling aggression score, c) heart rate during manual restraint (heart beats/min.; HR), d) tarsus length (mm) and e) adult body mass (g) of blue tits originating from two distinct populations and habitats (deciduous and evergreen) in Corsica (France) and reared in a common garden. Bloxplots on raw data. All differences are significant (see Table 3.1 for details).

3.5 Discussion

Our common garden experiment revealed genetic divergence for personality, physiological and morphological traits between two blue tit populations that live in contrasted habitats separated by a small spatial distance in regards to the species dispersal capacity. Adult blue tits originating from the evergreen habitat displayed slower exploration behaviour, a lower handling aggression score (higher docility), a faster heart rate, a lower body mass and a shorter tarsus than birds from the deciduous habitat (Table 3.1; Fig. 3.1). These differences are similar to the ones measured in the wild suggesting that phenotypic plasticity alone cannot be responsible for their phenotypic divergence (Charmantier et al. 2016; Dubuc-Messier et al. 2016). We found a significant F_{st} between the two populations, but its low value (0.004) indicated the presence of gene flow. The Q_{st} - F_{st} comparisons revealed that blue tits from these populations are more genetically differentiated for personality, physiological and morphological traits then they are at the genome-wide level (Table 3.2). These results suggest that genetic drift alone cannot explain the observed genetic divergence between the two populations and that differences in selection regimes have been responsible for their divergence.

The divergence we describe in personality, physiological and morphological traits is likely to be mainly of genetic origin, since birds from both habitats were raised in identical conditions for up to five years. In addition, the genetic divergence found in this study for adult body size is consistent with previous studies that have found divergent selection between the two populations (Blondel et al. 2002; Teplitsky et al. 2014) and moderate to high heritability for these traits (Teplitsky et al. 2014). However, we cannot completely exclude that early environmental effects occurring before the chicks were sampled from their nest were at least partly responsible for the observed patterns (Kruuk and Hadfield 2007; Räsänen and Kruuk 2007; Bouwhuis et al. 2010; van Oers et al. 2015). Such strong maternal effects lasting for up to five years for some traits are unlikely since very few studies have reported long-term consequences of early environmental conditions for the studied traits (Taylor et al. 2012; Petelle et al. 2015). In addition, maternal effects are known to decrease during ontogeny (Cheverud et al. 1983; Réale et al. 1999; Wilson et al. 2007). Hence, we are confident that the observed phenotypic divergence reflect primarily genetic effects.

3.5.1 Environmental heterogeneity, divergent selection and local adaptation

The importance of environmental heterogeneity and gene flow for phenotypic divergence has mainly been studied for life history and morphological traits and much less for behavioural traits. Indeed, few studies have disentangled the role of plasticity from that of genetic differences in shaping the phenotypic divergence of behavioural traits (Bell 2005; Herczeg et al. 2013; Jacquin et al. 2016; Karlsson Green et al. 2016) and fewer for highly mobile avian species (Atwell et al. 2012; Miranda et al. 2013), and none has yet reported Q_{st} - F_{st} comparisons involving personality traits. This shortage of study is probably due to the fact that personality traits are often considered plastic and thus less prone to genetic divergence and local adaptations than morphological traits. However, in this study, we found that the genetic divergence for behavioural traits was as strong as for morphological traits (Table 3.1).

An increasing number of studies are suggesting that life-history and personality traits could have co-evolved to form a pace-of-life syndrome (Réale et al. 2010). For example, empirical and theoretical studies are suggesting that high investment in early reproduction at a cost of reduced residual reproductive value (either via survival or future reproduction) should be associated with boldness, fast exploration, and high aggressiveness (Wolf et al. 2007; Réale et al. 2010; Nicolaus et al. 2012). Our results on this system are consistent with the pace-of-life hypothesis. Indeed, blue tits from the deciduous habitat, which are more aggressive and faster explorers, have a shorter lifespan and a lower residual reproductive value, but larger clutch sizes than birds from the evergreen habitat (Grosbois et al. 2006; Charmantier et al. 2016; Dubuc-Messier et al. 2016; Table S3.1). The present Q_{st} - F_{st} comparison revealed that these differences in personality phenotype are likely the result of different selection pressures. In addition, studies on other blue tit or great tit (*Parus major*) populations have found that the personality phenotypes is heritable and related to fitness (Quinn et al. 2009; van Oers and Sinn 2011; Class et al. 2014). Therefore, taken together, these results suggest that the personality phenotypes in these populations have an evolutionary potential and could be involved in blue tit adaptation to local ecological conditions in deciduous and evergreen habitats.

Some studies have raised concerns regarding biases in Q_{st} and F_{st} estimation and in their comparison (Leinonen et al. 2013). In particular Q_{st} estimation may be imprecise when a small number of populations are compared (O'Hara and Mërila 2005; Leinonen et al. 2013). However, simulations have shown that a small number of populations results in a downward bias in Q_{st} estimation when Q_{st} is high (O'Hara and Mërila 2005). Another important concern is whether genetic markers involved in F_{st} estimation are truly neutral (Leinonen et al. 2013). In this study, we used an F_{st} calculated from markers that included the whole genome. Although we filtered SNPs under potential divergent selection, it is possible that we included potentially non-neutral regions. However, using microsatellites, Porlier et al (2012a) have found a lower F_{st} (0.001) between the same populations during a similar time period (year 2009). Hence, although Q_{st} and F_{st} comparison have some limitations, these limitations should most probably have limited our capacity to detect significant Q_{st} - F_{st} differences rather than reveal false differences.

3.5.2 Genetic divergence and plasticity are not mutually exclusive

The genetic divergence found in this study does not preclude a plastic response to ecological conditions specific to each habitat. Interestingly, in the wild, the phenotypic difference in male HR between habitats was not significant (Dubuc Messier et al. 2016), but using the common garden experiment we found here a significant difference in male HR. It is thus possible that plastic responses of HR to habitat specific ecological conditions in the wild may have hidden the genetic divergence (Conover and Schultz 1995). In addition, the important temporal variation in mean handling aggression in the wild shown by Dubuc-Messier et al (2016) in each population, suggests that individuals can partly adjust their phenotype for this trait depending on the current local conditions. For all focal traits, the P_{st} between the wild populations was however not statistically different from the Q_{st}, revealing that plasticity in the wild does not result in stronger or weaker differentiation compared to genetic differentiation.

3.5.3 **P** matrices and brood effects

Overall the studied traits were not phenotypically correlated apart from a positive correlation between body mass and tarsus length (Table S3.4). The **P** matrices did not differ between birds originating from deciduous or evergreen habitats, suggesting that despite playing a potential role in the divergence of the average values of the traits, ecological conditions specific to each habitat did not produce in differences in trait (co)variation.

We did not find any significant brood-of-origin effect for handling aggression, exploration score, HR, and tarsus length. Since these traits apart from HR have all been shown heritable in previous blue tits studies (van Oers and Sinn 2011; Class et al. 2014; Teplitsky et al. 2014), the absence of heritable variance in our analysis is most probably explained by the relatively small number of broods. Determining the heritability of these traits was not the goal of this study. However, in order to determine the evolutionary potential of these traits, further long-term research in this study system will aim at estimating population-specific heritability for the personality phenotype .

3.5.4 Conclusion

Our study reveals phenotypic and genetic divergence for personality, physiological and morphological traits between two blue tit populations that occupy different habitats but separated by small spatial distances and connected by gene flow. These differences are likely due to different selection pressures and may represent local adaptation. This study thus emphasizes the role of environmental heterogeneity for intra-specific phenotypic diversity and adds to the growing body of evidence that genetic population divergence is possible at small spatial scales even for behavioural traits.

3.6 Acknowledments

We thank the landowners for permission to work on their properties and all the blue tit crew for their work, specifically Marta Szulkin, Christophe de Franceschi, Philippe Perret, Virginie Demeyrier, Samuel Perret and Boris Delahaie. We also thank Marylou Aaldering, Floor Petit, Franca Kropman and Sonja Schaper for taking good care of the birds in captivity.

3.7 Supplementary materials

Tableau S3.1 Caterpillar abundance, life-history, morphological and personality phenotypes (mean (*n*)) of the two Corsican blue tit populations (France) in the wild.

Populations	Deciduous	Evergreen
First year of monitoring	1993	1976
Caterpillar abundance[3]	762.87	87.10
Annual adult survival probability[1]	0.391 (*6*)	0.574 (*14*)
Date of first egg laying[2] (1 = March 1st)	38.56 (*1233*)	70.08 (*1920*)
Male body mass (g)[2]	9.82 (*1032*)	9.37 (*1607*)
Female body mass (g)[2]	9.66 (*1153*)	9.23 (*1616*)
Male tarsus length (mm)[2]	16.52 (*578*)	16.27 (*789*)
Female tarsus length (mm)[2]	16.05 (*614*)	15.84 (*798*)
Clutch size[2]	8.50 (*1235*)	6.61 (*1913*)
Number of fledglings[2]	6.60 (*1092*)	4.15 (*1273*)
Mean exploration speed (cm/s) ± s.d.[4]	13.515 ± 8.385 (*176*)	10.371 ± 7.494 (*117*)
Mean handling aggression score ± s.d.[4]	1.690 ± 0.953 (*703*)	1.486 ± 0.994 (*549*)
Mean heart rate during manual restraint ± s.d.[4]	963.297 ± 87.801 (*159*)	976.240 ± 86.988 (*91*)

[1] Dubuc-Messier et al. Chap. 5; [2] Charmantier et al 2016 (collected between the first year of monitoring and 2014); [3] mean maximal frass mg/m^2 per day in each population (sampled between 2011 and 2015 during the breeding period using 0.25m^2 trays placed under the forest canopy and collected twice a week, see Zandt et al 1990 for details about the sampling procedure); [4] Dubuc Messier et al. (2016).

Handling aggression scores

The test was done within two minutes after capture and prior to any other manipulation. The handler held the bird with one hand and placed the bird's legs between his forefinger and his thumb to let the bird free to move its tails and wings. The handler pointed the forefinger of his other hand at a spot about 2 to 3 cm in front of the bird's beak and noted if the bird struck at his finger, and the position of its wings and tail. After two seconds in this position, the handler moved his forefinger towards the bird's beak two or three times and recorded its reaction.

Tableau S3.2 Blue tit handling aggression scale.

Score	Wings spread	Tail feathers spread	Bird strikes fingers
0	No	No	No
1	No	No	Yes, but only if provoked
2	No	Yes	Yes, spontaneously
3	Yes	Yes	Yes, spontaneously

When the bird displayed one reaction specific to one score and another reaction specific to another score, it received an average score between the two. For example, a bird that struck without any provocation (score 2) but did not have its wings and tail feathers spread (score 1) would be scored as 1.5.

Tableau S3.3 Variance components (brood of origin, brood of rearing, and residual), L-ratio, and p-values for studied traits in two blue tits populations in Corsica (France) raised in a common garden.

	Brood of origin				*Brood of rearing*				*Residuals*
Traits	Variance (95% CI)	L-ratio	d.f.	p-value	Variance (95% CI)	L-ratio	d.f.	p-value	Variance (95% CI)
Exploration scores	0.047 (0.00; 0.15)	0.76	1	0.38	0 (0; 0.001)	0	1	1	0.71 (0.56; 0.89)
Handling aggression	0.01 (0.00; 0.13)	0.002	1	0.97	0.08 (0.00; 0.24)	1.52	1	0.22	0.70 (0.54; 0.94)
HR	0 (0.00; 0.30)	0	1	1.00	0.28 (0.00; 0.70)	3.35	1	0.07	0.66 (0.42; 1.02)
Tarsus length	0.09 (0.00; 0.29)	1.69	1	0.19	**0.14 (0.01; 0.37)**	4.74	1	0.03	0.44 (0.34; 0.57)
Body mass	**0.07 (0.01; 0.14)**	4.10	1	0.04	0 (0; 0.001)	0	1	1.00	0.02 (0.22; 0.26)

L-ratio and p-values are from the comparison of a full model and a model without the variable of interest. Bold indicates significant variance component.

Tableau S3.4 Correlation (below diagonal; with confidence intervals CI) and (co)variance (above diagonal) matrices of two blue tits populations originating from deciduous or evergreen habitat, in Corsica (France) and raised in a common garden. We show the correlations and covariances for the two populations (all data) combined and for each population.

	Exploration score	Handling aggression score	Heart rate	Body mass	Tarsus length
All data					
Exploration score	1.133	0.11	0.11	0.04	-0.14
Handling aggression score	0.10 (-0.17; 0.35)	1.08	-0.13	-0.07	-0.05
Heart rate	0.11 (-0.16; 0.36)	-0.13 (-0.38; 0.14)	0.87	0.05	-0.08
Body mass	0.07 (-0.19; 0.33)	-0.14 (-0.39; 0.12)	0.11 (-0.15; 0.36)	0.25	0.25
Tarsus length	-0.13 (-0.38; 0.13)	-0.04 (-0.3; 0.22)	-0.08 (-0.34; 0.18)	**0.48** **(0.25; 0.66)**	1.05
Evergreen					
Exploration score	0.94	0.12	-0.09	0.05	-0.10
Handling aggression score	0.13 (-0.23; 0.46)	1.10	-0.08	-0.03	0.01
Heart rate	-0.08 (-0.42; 0.28)	-0.12 (-0.45; 0.24)	0.421	0.07	0.01
Body mass	0.04 (-0.32; 0.38)	-0.07 (-0.41; 0.29)	0.28 (-0.08; 0.57)	0.17	0.14
Tarsus length	-0.27 (-0.57; 0.09)	0.01 (-0.34; 0.36)	0.01 (-0.34; 0.36)	0.34 (-0.01; 0.62)	1.03
Deciduous					
Exploration score	1.23	0.092	0.32	0.05	0.01
Handling aggression score	0.18 (-0.072; 0.434)	1.02	-0.19	-0.05	-0.03
Heart rate	0.24 (-0.17; 0.58)	-0.15 (-0.52; 0.26)	1.49	0.03	-0.20
Body mass	0.08 (-0.33; 0.46)	-0.10 (-0.47; 0.31)	0.04 (-0.36; 0.43)	0.29	0.30
Tarsus length	0.01 (-0.39; 0.40)	-0.03 (-0.42; 0.37)	-0.16 (-0.52; 0.25)	**0.55** **(0.20; 0.78)**	1.02

Bold estimates indicate significant correlations ($p < 0.05$); correlation and covariances estimates were taken from a univariate model made for each combination of the traits using one of the traits of interest in response variable (e.g. handling aggression) and the other trait in fixed effect (e.g. exploration score) using the residuals of a model containing the random effects and the significant fixed effects for each trait selected previously (see Table 3.1)

CHAPITRE 4

RECIPROCAL-TRANSPLANT EXPERIMENT REVEALS GENETIC DIFFERENTIATION IN PERSONALITY TRAITS BETWEEN TWO NEIGHBOURING AVIAN POPULATIONS.

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4.1 Abstract

Understanding the causes of population divergence is a central goal in evolutionary biology. An efficient way to disentangle the relative importance of plastic *versus* genetic sources of populations' divergence is to conduct reciprocal transplant experiments. This type of experiment has rarely been conducted for animal populations separated by small spatial scale and for behavioural traits. Here, using a reciprocal transplant cross-fostering experiment, we studied the personality phenotype (handling aggression and activity in a novel environment) of nestling blue tits (*Cyanistes caeruleus*) inhabiting three populations located in two contrasted habitats separated by small spatial distances (6 to 25 km). First, we compared the mean phenotypes of nestlings among the three populations. Second, we estimated whether the phenotypic divergence has a genetic origin and the traits heritabilities by cross-fostering nestlings between two populations located in different habitats. We found a significant phenotypic divergence between habitats for both traits and the reciprocal transplant cross-fostering experiment revealed a significant population of origin effect for handling aggression, which suggests a genetic divergence among habitats. In addition, we found a significant brood of origin effect for both traits suggesting that they are heritable and could evolve in response to the local ecological conditions. Our results indicate the existence of a genetic divergence for nestlings personality traits between habitats at a small spatial scale and despite gene flow, emphasizing the importance of environmental heterogeneity in shaping intra-specific biodiversity for behavioural traits.

4.2 Introduction

Understanding population evolutionary history and their evolutionary potential requires that we evaluate the relative importance of genetic *versus* plastic effects at the origin of intra population phenotypic variation and population divergence and that we determine which mechanisms underlie such diversity (Wang and Bradburd 2014; Merilä and Hendry 2014). Temporal and spatial variation in ecological conditions can have a major role in creating population divergence and intra population phenotypic variation (Siepielski et al. 2009; Kingsolver et al. 2012; Wang and Bradburd 2014). Spatial environmental heterogeneity can create differential selection pressures resulting in between-population phenotypic divergence either by generating different plastic responses to local environmental conditions or by generating genetic divergence between populations leading to local adaptations (Kawecki and Ebert 2004; Wang and Bradburd 2014). However, for populations separated by small geographic distances, gene flow will usually limit their genetic divergence through its homogenizing effect on the genetic composition (Slatkin 1987; Lenormand 2002). Consequently, gene flow may favour the evolution of phenotypic plasticity as the main factor responsible for population divergence (Sultan and Spencer 2002). Yet, recent studies have proposed that strong natural selection and non-random dispersal could lead to genetic divergence between populations despite the presence of gene flow (Richardson et al. 2014; Wang and Bradburd 2014).

The most straightforward way to disentangle the relative importance of plastic *versus* genetic sources of phenotypic divergence is to conduct transplant and common garden experiments (Kawecki and Ebert 2004; Blanquart et al. 2013; Merilä et Hendry 2014). Overall, the majority of transplant experiments have focused on plants species and on populations separated by large spatial scale, with distance between sampled populations beyond the organism's dispersal distance (Hereford 2009 and see for example Ågren and Schemske 2012). For obvious reasons, animal transplants are more challenging. Therefore, cross-fostering experiments have been commonly used to estimate the plasticity and genetic basis of traits in animals. However, these experiments are generally conducted within a given population (Kruuk and Hadfield 2007; Brommer and Kluen 2012).

Recently, several studies have reported intra-specific variation in behaviour and more precisely consistent differences among individuals in behavioural phenotypes a.k.a. personality (review in Réale et al. 2007; Bell et al. 2009; van Oers and Sinn 2011). These studies have suggested that temporal fluctuation in environmental conditions could maintain intra-population variation in personality phenotypes (Dingemanse et al. 2004; Boon et al. 2008; Quinn et al. 2009; Taylor et al. 2014; Nicolaus et al. 2016). An increasing number of studies have investigated the impact of spatial variation in environmental conditions on behavioural variation by comparing the personality phenotype of individuals inhabiting contrasting habitats (Bell 2005; Quinn et al. 2009; Dingemanse et al. 2010; Atwell et al. 2012; Herczeg et al. 2013; Maes et al. 2013; Miranda et al. 2013; Dubuc-Messier et al. 2016; Heinen-Kay et al. 2016; Karlsson Green et al. 2016; Jacquin et al. 2016). However, few studies have investigated the genetic origin of population divergence for personality traits (but see Bell 2005; Herczeg et al. 2013; Jacquin et al. 2016; Karlsson Green et al. 2016) and even fewer for populations separated by small spatial distance and for highly mobile species such as avian species (Atwell et al. 2012; Miranda et al. 2013). Moreover, the majority of studies on personality have focused on mature organisms. Hence, we have much to discover on the personality phenotype of young organisms and in particular on its genetic *versus* plastic origin as well as its stability during development (Stamps and Groothuis 2010; Herczeg et al. 2013; Class and Brommer 2015).

In this study, we combined a reciprocal transplant with a cross-fostering experiment to assess if difference in habitats could lead to a genetic divergence in personality trait in blue tits nestlings (*Cyanistes caeruleus*) and to estimate the heritability of nestling's personality traits. More specifically, we studied three blue tits populations located in two different habitats in a Mediterranean landscape in France (Corsica) separated by small spatial distances (6 to 25 km) and connected with gene flow (F_{st} between 0.01 and 0.009; Porlier et al. 2012a; Szulkin et al. 2016). These populations are known to differ in numerous types of traits at the phenotypic and genetic level (Charmantier et al. 2016). For example, Dubuc-Messier et al. (2016, Chap. 3) found that the mean adult personality phenotypes differ between habitats at the phenotypic and at the genetic level: adult birds in the deciduous habitat had a higher handling aggression and faster exploration pattern than birds in the evergreen habitats. Moreover, Q_{st} - F_{st} comparison and selection analyses revealed that these divergence is likely adaptative (Dubuc-Messier et al. 2016; Dubuc-Messier et al. Chap. 3; Dubuc-Messier et al. Chap. 5). Selection pressures associated with the dominant tree species in each habitat, either evergreen (holm oak, *Quercus ilex*) or deciduous oaks (downy oak, *Quercus pubescens*), and their resulting consequences on the amount of caterpillars in the spring, are suspected to be responsible for the observed divergence in adult personality phenotype and for a variety of other traits (Charmantier et al. 2016; Dubuc-Messier et al. Chap. 3; Dubuc-Messier et al. Chap. 5).

Here, we focused on two nestling personality traits: activity in a novel environment and handling aggression (docility) measured at respectively the age of twelve and fifteen days. We first compared the mean personality phenotype of nestling blue tits between the three studied populations. Second, we investigated the presence of a genetic divergence in personality phenotype between habitats using a reciprocal transplant and a cross-fostering experiment between two of these three populations that are located in two different habitats (deciduous *vs.* evergreen; Fig, 4.1). This experiment also allowed us to study the presence of an interaction between the habitat of origin and the habitat of rearing that could reveal genotype by environment interaction (GxE) on the traits. Third, we investigated the effect of the broods of origin and of rearing for the phenotype of the cross-fostered nestlings to gain insight on the heritability of nestlings' personality phenotype and on the impact of the rearing conditions apart from those related to the habitat. Fourth, we investigated if the personality phenotype was stable during the ontogeny by relating nestling's phenotype to their phenotype as adults for analogous traits in each population.

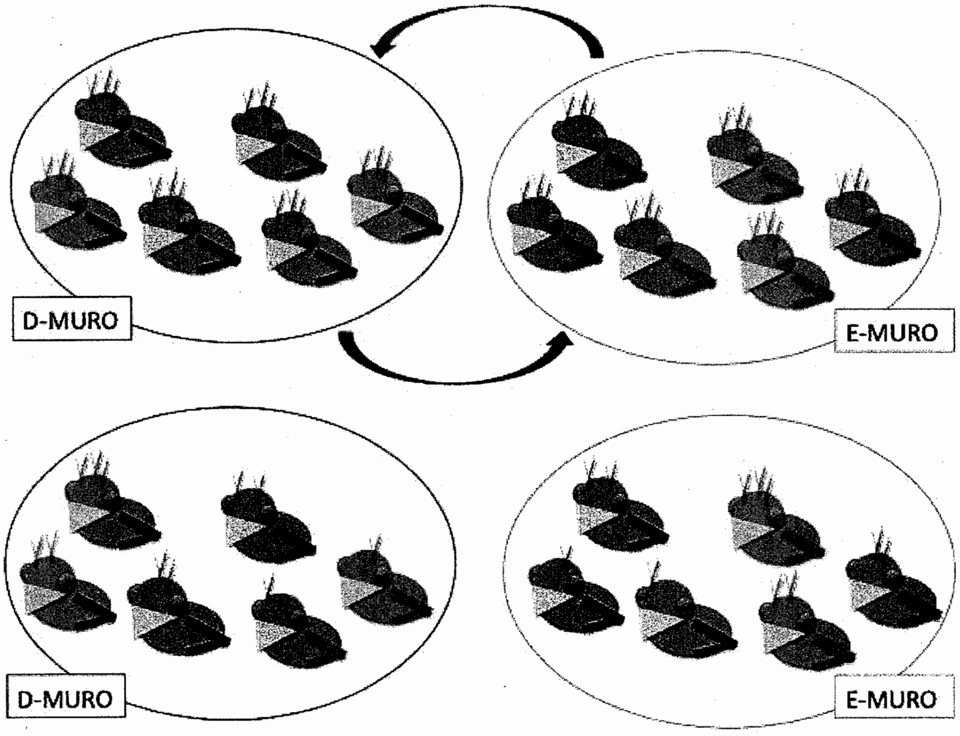

Figure 4.1 Schematic representation of the reciprocal transplant cross-fostering experiment. Broods from two populations located respectively in the deciduous habitat (D-Muro, dark blue) and in the evergreen habitat (E-Muro, light blue) in the same valley 6 km apart were paired based on similar hatching dates and brood sizes. When the oldest nestlings of a brood reached 3 days of age, half the nestlings from each brood were swapped so that each brood was half composed of foster nestlings from the other population and half of native nestlings. Nestlings were individually marked (from 3 to 6 days) by a unique combination of the three feathers bustle on their head (on figure) and with metal rings at 6 days of age. Traits were measured when nestlings were twelve and fifteen days old. A mixed-model was run with habitat of origin (genetic differences), habitat of rearing (environmental differences) and their interaction (genotype by environment interaction) as fixed effects, and with brood of origin (*i.e.* additive genetic effects) and brood of rearing (shared environmental effects) identities as random effects.

Based on the known divergence for adult personality traits and because we predicted that nestling phenotype would be positively related to the adult phenotype (review in Brommer and Class 2015), we expected to find a phenotypic and genetic divergence between habitats in these two nestling traits. More specifically, we predicted that nestlings from the deciduous habitat would have a higher handling aggression phenotype and activity in the novel environment than nestlings from the evergreen habitats and that these differences would be genetic. With our experimental design, a genetic divergence would be shown by a significant effect of habitat of origin: nestlings originating from the deciduous habitat would have a higher handling aggression and a higher activity in the novel environment than nestlings originating from the evergreen habitats. In addition, based on previous studies on handling aggression in a Finnish population of blue tits (Brommer and Kluen 2012; Class and Brommer 2015) and for exploration behaviour in a novel environment (Quinn et al. 2009; review in van Oers and Sinn 2011), we expected significant brood of origin effects suggestive of a significant heritability of these traits in our studied populations. We also expected a significant brood of rearing effect suggestive of an significant effect of the rearing conditions (Brommer and Kluen 2012).

4.3 Materials and Methods

4.3.1 Study species, sites and field protocol

This study was conducted on the island of Corsica (France) between 2013 and 2016 in three populations located in a deciduous (downy oak) or in a evergreen (holm oak) habitat: Deciduous-Muro (D-Muro hereafter; 42°32'N. 08°55'E, 350 m elevation; 110 nest-boxes distributed in three study plots), Evergreen-Muro (E-Muro hereafter; 42°35'N, 08°57'E, 100 m elevation, 75 nest boxes distributed in three study plots), and Evergreen-Pirio (E-Pirio hereafter; 42°34'N, 08°44'E, 200m elevation, 205 nest-boxes distributed in two study plots). These populations have been studied since 1998, 1994 and 1976, respectively (Blondel et al. 2006; Charmantier et al. 2016). D-Muro and E-Muro are located in the Regina valley 6 km apart. E-Pirio is located in the Fango valley, 25 km away from the two other populations. We recorded laying and hatching dates for all the broods with a daily to weekly monitoring routine during the breeding period, from early April to the end of June.

Adults were captured during two different capture periods: during the pre-breeding period, when males and females paired up and started to defend a territory (from March 17th to 30th for D-Muro and E-Muro, and from April 4th to May 3rd for E-Pirio), and during the breeding period, when adults were feeding nestlings. During the pre-breeding period, birds were caught with a mist net or lured into a trap using a live blue tit decoy and playback territorial calls near a nest-box. During the breeding period adults were caught in nest-boxes when nestlings were 9-15 days old. Birds were identified or ringed with unique metal rings provided by the CRBPO (France), and weighed using a Pesola® spring. We determined the sex of each individual by examining the presence/absence of a brood patch during the breeding period or based on feather coloration outside the breeding period (Perrins 1979; Ferns and Hinsley 2010; Fresneau et al. 2014).

Reciprocal-transplant and cross-fostering experiment

The reciprocal transplant cross-fostering experiment was conducted between D-Muro and E-Muro in three consecutive years (2013 to 2015). A one-month difference in blue tit breeding phenology between valleys (see e.g. Charmantier et al. 2016) prevented us from using birds from E-Pirio in this experiment. We used a cross-fostering protocol similar to Brommer and Kluen (2012). We first confirmed a brood hatching date by visiting the nest on the day hatching was predicted based on laying date, clutch size and incubation period. Hatching date corresponded to the day the first egg of a given brood hatched. One day later, we revisited each nest-box to confirm brood sizes. Then, we paired broods from each population with the same hatching date and close brood sizes. An equal number of nestlings were swapped between the two broods of each pair (Fig. 4.1). In case brood sizes differed between the two paired broods we cross-fostered half of the nestlings of the smallest brood. On average paired broods differed by 0.023 ± 1.13 hatched nestlings. Nestlings were cross-fostered three days after the hatching of the oldest nestling. The day of the cross-fostering, we visited the nest with the smallest brood size first. Cross-fostered nestlings were randomly chosen by assigning a number to each nestling and by drawing from a bag the numbers that would be transferred. However, nestlings that just hatched the exact day of the manipulation were replaced immediately in their nest and not cross-fostered (27 nestlings) for fear they would not survive the travelling. We then weighed every nestling and replaced the non cross-fostered nestlings in their nest-box. The cross-fostered nestlings where placed in a small tissue bag and transported by car to the paired brood in the other population (20 min. driving). In the paired brood, we selected for cross-fostering nestlings with similar ranks in the body mass hierarchy of their brood than the incoming nestlings in their own brood, and brought them to the first brood. Because nestlings were too small to be marked with a metal ring, all nestlings were individually marked using the three feather bustles they have on their head. By cutting or not each feather bustle we made a unique combination for every chick in a nest (8 different combinations; Fig. 4.1). At 6 days of age, nestlings were individually marked with unique metal rings.

Behavioural trials

Nestling behavioural trials were conducted in all three populations for manipulated and unmanipulated broods. Activity in a novel environment was assessed on twelve days old nestlings. The novel environment consisted in a 25 x 25 x 11 cm plastic box with a small white cup in the middle (diameter: 4.5 cm, height: 3.0 cm; Fig. S4.1) placed in a shaded but open area close to the nest-box (less than 2 m). Nestlings were randomly taken out of their nest-box one at the time and were therefore visually isolated from their siblings during the trial. The nestling was then placed in a small cup covered by a big mug for 10 seconds. This period of total darkness and isolation allowed us to homogenize the starting conditions for each nestling. The bigger cup was removed at the start of the test. Using an audio recorder, the observer noted when the nestling was moving (head, body or legs) during 30 sec. After each trial, nestlings were weighed. Back in the lab, the time spent moving was extracted from the audio files using The Observer XT 11.0, and used as a measure of activity in a novel environment.

Nestling handling aggression was scored on fifteen days old nestlings using the same protocol as Dubuc-Messier et al. (Chap. 5) and similar to the 'docility' protocol of Brommer and Kluen (2012). Briefly, all nestlings were first taken out of the nest-box and placed in a small tissue bag. Then, nestlings were taken out of the tissue bag, one at the time, and placed with their back towards the observer's hand, their neck between the observer's index and middle finger, and their two legs held by the foot between the observer's thumb and forefinger. The handler held the bird vertically and counted the number of times the fledgling struggled during 10 seconds. The same observer manipulated all nestlings in a given nest-box, yet there were 12 observers across all broods.

A total of 1269 nestlings in 230 unmanipulated broods were assessed for activity in a novel environment (D-Muro: n = 394, E-Muro: n = 243, E-Pirio: n = 632) and 1957 nestlings and 331 broods for handling aggression (D-Muro: n = 877, E-Muro: n = 364, E-Pirio: n = 716). A total of 663 nestlings from 109 broods of origin and 98 broods of rearing were successfully cross-fostered and measured for behavioral traits (the unmatched number of brood of origin and of rearing is due to nest predation).

Adult handling aggression and behaviour in a novel environment were scored according to the protocol described in Dubuc-Messier et al. (2016). The handling aggression trials were performed within two minutes after capture, directly after removing the bird from the trap and prior to any other manipulation. The score ranged from 0 (the bird shows no reaction) to 3 (the bird spontaneously strikes the handler's fingers and spreads its wings and tail). The scoring protocol is reported in detail in Table S4.1. The entire test lasted less than a minute. After the handling aggression trials, the bird was brought to a novel environment apparatus and we video recorded its behaviour for five minutes (see Dubuc-Messier et al. 2016 for details). After the trial, the bird was subsequently retrieved from a novel-environment apparatus, ringed when necessary, weighed, and released. Back in the lab, we extracted the average speed of the bird (cm/s) during the trial using the software EthoVision XT version 9 and we used this variable in the analyses (see Dubuc-Messier et al. 2016 for details).

4.3.2 Statistical analysis

Phenotypic differences between habitats and populations

We tested for a phenotypic difference between the three populations with a univariate mixed-models with a zero-inflated negative binomial distribution for activity in a novel environment and a Gaussian distribution for nestlings handling aggression (square root transformed). For these models, we used data from unmanipulated broods only. Fixed effects included: population, year, ambient temperature (Z-standardized), hour of the test (Z-standardized), and the interaction between year and population. There was some minor hatching asynchrony in our populations, thus even if all the trials were done on the same day for a given brood some nestlings were younger than the rest of their brood. Therefore, we added the nestling age based on feather development as a fixed effect in all models. Brood identity was added as a random effect to estimate the proportion of the total phenotypic variance that could be attributed to brood-specific effects (i.e. additive and dominance genetic, parental, or early environmental effects), and to control for the non-independence of same-brood nestlings. Following recommendations of Schielzeth and Forstmeier (2009), we allowed the variance attributable to brood identity to differ according to the population (random interaction between population and brood identity). Because allowing such population-specific variance component did not change the estimates of fixed effects and were not significant (results not shown), we present models that include only a random intercept for brood identity. We tested for the significance of the fixed and random effects by using L-ratio and stepwise backward procedure starting with a model that included all the variables using ML for fixed effect and REML for the random effect. When we found a significant population effect, we tested specific differences between pairs of populations.

Genetic differences between habitats and heritabilities

We tested for a genetic difference between D-Muro (deciduous habitat) and E-Muro (evergreen habitat) populations with univariate linear mixed models and population of origin as a fixed effect. For this model, we used only broods involve in the reciprocal transplant cross-fostering experiment. Population of rearing was also included as fixed effect to test for population divergence caused by environmental effects specific to the population of rearing. We tested for a genotype x environment interaction on nestling behaviour by adding the interaction between the population of origin and population of rearing in all models. Models also included fixed effects that were significant in the previous models, nestling body mass at three days of age (Brommer and Kluen 2012) and the interaction between year and both population of origin and population of rearing. Random effects were: brood of origin identity to estimate heritability (2x variance of the brood of origin / (brood of origin variance + brood of rearing variance + residual variance); Cheverud et al. 1983; Kruuk and Hadfield 2007), and brood of rearing identity to estimate the proportion of the phenotypic variance that was attributable to parental and early environmental effects. Extra-pair paternity rates estimated in these populations can be high (18.2% to 25.4% of extra-pair nestlings, Charmantier et al. 2004). Since we did not have extra-pair data for nestlings involved in the cross-fostering experiment, our models assumed that nestlings from a single brood were full-sibs. This assumption should result in an underestimation of h^2 although simulations have shown that the bias should be small (Charmantier and Réale 2005). In initial models, we allowed the variance attributable to each type of brood (origin or rearing) to differ according to the population of origin (random interaction between population of origin and brood of rearing), or to the population of rearing (random interaction between population of rearing and brood of origin). Because allowing such population-specific variance component did not change the estimates of fixed effects and were not significant for these models either (results not shown), we present models that include only a random intercept for brood of origin and brood of rearing. We also tested for the significance of the fixed and random effects using L-ratios and stepwise backward procedures starting with a model that included all the variables, using ML for fixed effect and REML for random effects.

All analyses were done in *R* (Core Team 2015). We used the *glmmADMB* package (*glmmadmb* function; Fournier et al. 2012; Skaug et al. 2016) for activity in a novel environment, and the *lme4* package (*lmer* function; Bolker et al. 2009) for handling aggression. Confidence intervals around the fixed effects estimates of the best model were generated using the *confint.merMod* function. For activity in a novel environment, we estimated the proportion of the total phenotypic variance that was attributable to the identity of the broods using the rptR package (Schielzeth et al. 2016) with additive overdispersion, and report results on the logit scale and on the original scale (using equation 35 and 36 of Nakagawa and Schielzeth 2010). For both traits, the proportion of total variance attributable to random effects and heritabilities were estimated using the significant fixed effects selected previously.

Association between traits measured on nestlings and adults

We determined whether handling aggression and activity in a novel environment measured on nestlings were related to the analogous measures in adults taken at the adult stage (breeding individuals). For this analysis, we retained only measures from nestlings of unmanipulated broods and used univariate mixed-models with the adult trait as a response variable. We used as explanatory variable the nestling trait, and the interaction between nestling trait and population. We also added covariables that were previously found to significantly explain variation in adult traits (Dubuc-Messier et al. 2016): sex, year, hour of the day when the measure was taken, and an interaction between population and year. We also included capture period and rank of the test within an individual's lifetime for models on handling aggression and the contention system used before the trials for models on novel environment trials (3 classes: no contention, a tissue bag, a cage; for details see Dubuc-Messier et al. 2016). Adults were scored repeatedly during their lifetime. Hence, we used individual identity as a random effect (and observer identity for handling aggression) in all models. We assessed the significance of fixed effects with an L-ratio test and ML. These analyses were performed in R with the function *lmer* of the *lme4* package using a Gaussian distribution. A total of 94 birds were assessed for their activity in a novel environment both as nestlings and as adults (D-Muro: $n = 23$, E-Muro: $n = 16$, E-Pirio: $n = 55$) and 160 had joint measures for handling aggression (D-Muro: $n = 48$, E-Muro: $n = 38$, E-Pirio: $n = 74$).

4.4 Results

4.4.1 Phenotypic differences between habitats and populations

We found significant phenotypic differences between populations for both traits (Tableau 4.1 and S4.2): nestlings in D-Muro had a higher activity in a novel environment and a higher handling aggression than nestlings in E-Pirio, but there were no significant differences between E-Muro and D-Muro or between E-Pirio and E-Muro for both traits (Tableau 4.1). There was a significant interaction between population and year for both traits (activity in a novel environment: L-ratio = 17.090, p-value = 0.002; handling aggression: L-ratio = 13.817, d.f. = 4, p-value = 0.007; Tableau S4.2). Brood identity explained a significant portion of the total phenotypic variance for both traits: 5.1% (original scale) for activity in a novel environment (among-brood = 0.285, residual variance = 1.535 (log link scale), L-ratio = 43.9, d.f. = 1, p-value < 0.001) and 30.4% for handling aggression (among-brood variance = 0.166, residual variance = 0.38; L-ratio = 173.750, d.f. = 1, p-value < 0.001).

4.4.2 Genetic differences between habitat and heritabilities

Activity in a novel environment was not significantly influenced by population of origin (L-ratio = 0.11, d.f.= 1, p-value = 0.736), population of rearing (L-ratio = 3.624, d.f. = 2, p-value = 0.126), or their interaction (L-ratio = 2.51, d.f. = 1, p-value = 0.112). There were no interaction between year and population of origin (L-ratio = 0.287, d.f. = 2, p-value = 0.866) or population of rearing (L-ratio = 4.480, d.f. = 2, p-value = 0.107). Brood of origin and brood of rearing explained a significant proportion of the total phenotypic variance in activity in a novel environment (brood of origin: L-ratio = 3.360, d.f. = 1, p-value = 0.033; brood of rearing: L-ratio = 10.800, d.f. = 1, p-value < 0.001; Tableau 4.2) suggesting an h^2 of 6 % for this trait.

Population of origin significantly affected handling aggression (L-ratio = 4.923, d.f. = 1, p-value = 0.026): nestlings originating from E-Muro had a lower handling aggression than nestlings originating from D-Muro (Tableau 4.2; Fig. 4.2). We found no significant effect of the population of rearing (L-ratio = 0.669, d.f. = 1, p-value = 0.413) and no interaction between population of origin and population of rearing (L-ratio = 1.053, d.f. = 1, p-value = 0.305), between population of origin and year (L-ratio = 0.505, d.f. = 2, p-value = 0.777), and between population of rearing and year (L-ratio = 1.378, d.f. = 2, p-value = 0.502). Brood of origin was significant (L-ratio = 19.124, d.f. = 1, p-value < 0.001) suggesting an h^2 of 40 % (Tableau 4.2). The identity of the brood of rearing was not significant for this trait (L-ratio = 0.573, d.f. = 1, p-value = 0.449) but was kept in final model.

For both traits, the age effect (based on feathers development) were in the same direction for manipulated or unmanipulated nestlings (Tableau 4.2 and Tableau S4.2) suggesting that the cross-fostering did not influence the effect of age on nestlings phenotype.

4.4.3 Association between traits measured on nestlings and adults

We found no significant correlation between nestlings and adults activity in a novel environment (L-ratio = 0.344, d.f. = 1, p-value = 0.557) and no interaction with population (L-ratio = 4.459, d.f. = 2, p-value = 0.108) but a significant interaction between nestlings handling aggression and population (L-ratio = 8.213, d.f. = 2, p-value = 0.016; Tableau S4.3). Separated analyses for each population revealed a significant negative relationship between handling aggression in nestlings and adults in D-Muro [estimates: -0.220 (95% CI: -0.372; -0.068), L-ratio = 7.666, d.f. = 1, p-value = 0.006; Fig. 4.3a] and a positive but non- significant relationship in the two evergreen populations [E-Muro: 0.080 (-0.060; 0.220), L-ratio = 1.303, d.f. = 1, p-value = 0.254; E-Pirio: 0.027 (-0.114; 0.171), L-ratio = 0.160, d.f. = 1, p-value = 0.689; Fig. 4.3b and c].

Tableau 4.1 Phenotypic differences in nestling activity in a novel environment and in handling aggression between pairs of wild blue tit populations in Corsica (France) from unmanipulated broods.

Traits	Populations compared	Estimates (95% CI)	L-ratio	d.f.	p-value
Activity in a novel environment	E-Muro *vs.* D-Muro	-0.094 (-0.250; 0.061)	1.415	1	0.234
	E-Pirio *vs* D-Muro	**-0.193** **(-0.325; -0.061)**	**8.187**	**1**	**0.004**
	E-Muro *vs* E-Pirio	-0.095 (-0.254; 0.064)	1.367	1	0.242
Handling aggression	E-Muro *vs.* D-Muro	-0.078 (-0.216; 0.060)	1.237	1	0.226
	E-Pirio *vs* D-Muro	**-0.180** **(-0.301; -0.059)**	**8.445**	**1**	**0.003**
	E-Muro *vs* E-Pirio	-0.121 (-0.271; 0.028)	2.531	1	0.111

The second population in the second column is the reference population. Significant differences between populations are in bold; estimates and 95% CI are from a model with the two populations of interest and the fixed effects structure detailed in Tableau S4.2 except the interaction between year and population; L-ratio and p-values are from the comparison of a full model and a model without the term population as fixed effect; significant differences between populations are in bold.

Tableau 4.2 Best models from the reciprocal-transplant cross-fostering experiment between two Corsican populations of wild blue tits populations (France; D-Muro and E-Muro) for nestling activity in a novel environment and handling aggression. We present estimates for each fixed effects (95% CI), variance estimate for random effect, the proportion of total variance explained by each random effect and the estimated heritability (h^2) of each trait.

Traits / Type	Source of variation	Estimate	Proportion
Activity in a novel environment			
Random	Phenotypic	1.827	
	Brood of origin	0.142	0.08; 0.03; $h^2 = 0.06$
	Brood of rearing	0.273	0.15; 0.07
	Residual	1.412	0.773
Fixed	Intercept	2.411 (2.330; 2.491)	
	Body mass (3 days)	-0.114 (-0.205; -0.022)	
	Age	-0.076 (-0.172; 0.020)	
Handling aggression			
Random	Phenotypic	0.579	
	Brood of origin	0.116	0.20; $h^2 = 0.40$
	Brood of rearing	0.014	0.022
	Residual	0.450	0.647
Fixed	Intercept	1.185 (1.002; 1.367)	
	Pop. origin: E-Muro	-0.189 (-0.355; -0.023)	
	Year: 2014	0.193 (-0.040; 0.427)	
	Year: 2015	-0.034 (-0.249; 0.182)	
	Body mass (3 days)	0.085 (0.013; 0.158)	
	Age	0.095 (0.026; 0.163)	

The reference population is D-Muro and year 2013; h^2 was estimated as 2x the brood of origin variance / phenotypic variance; random effects estimates for activity in a novel environment are reported on the log link scale, and proportion of total variance on the log link and original scale for brood of origin and brood of rearing; h^2 for activity in the novel environment was calculated with the variance component on the original scale.

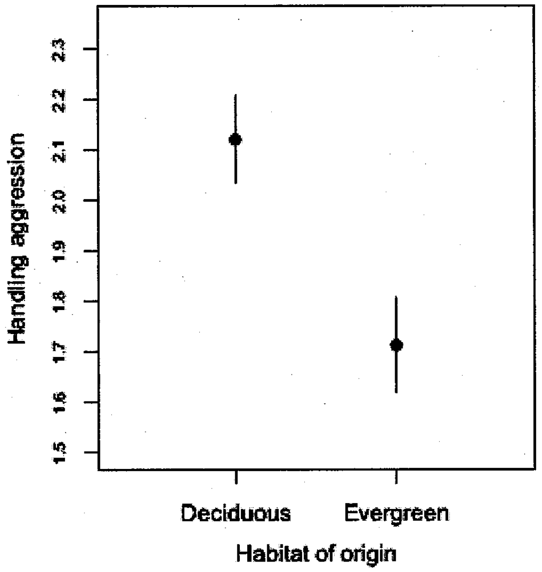

Figure 4.2 Nestlings handling aggression phenotype according to the population of origin for Corsican blue tits (France) fallowing a reciprocal cross-fostering experiment between E-Muro (evergreen habitat) and D-Muro (deciduous habitat). Points and arrows represents mean handling aggression score (raw data) ± SE.

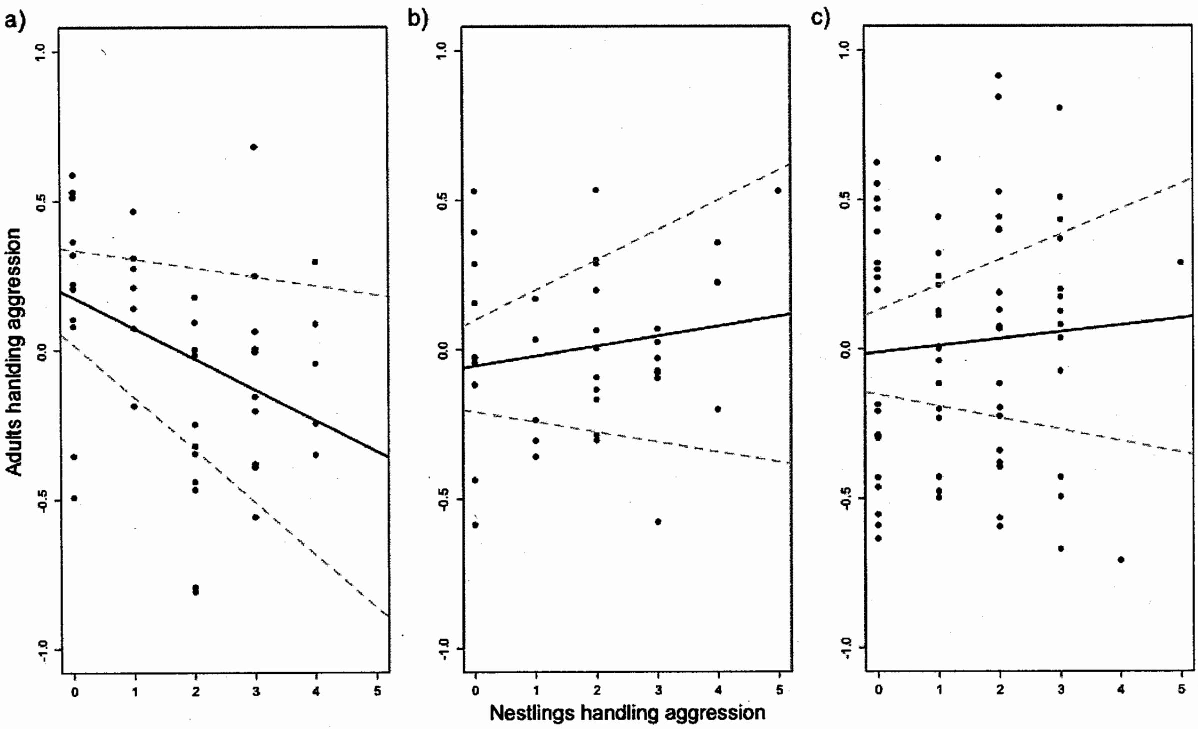

Figure 4.3 Relationship between adults and nestlings handling aggression scores in a) D-Muro (p-value = 0.006), b) E-Muro (p-value = 0.254) and c) E-Pirio (p-value = 0.689); points represents the best linear unbiased predictor (BLUP) of the adult phenotype calculated from a models with all the selected fixed and random effects except nestlings phenotype (see text and Table S4.3); the black lines represents the slope and intercept of a univariate linear model with the BLUP of the adult phenotype as response variable and nestlings phenotype as fixed effect; the dashed gray lines represents the confidence intervals around the slope and intercept.

4.5 Discussion

An increasing number of studies have revealed population divergence for personality traits suggesting that local ecological conditions are important in shaping the personality phenotype (Bell 2005; Quinn et al. 2009; Dingemanse et al. 2010; Atwell et al. 2012; Herczeg et al. 2013; Maes et al. 2013; Miranda et al. 2013; Heinen-Kay et al. 2016; Karlsson Green et al. 2016). In this study, we found, a phenotypic divergence for both activity in the novel environment and handling aggression in nestlings blue tits inhabiting contrasted habitats (D-Muro and E-Pirio). In addition, our reciprocal transplant cross-fostering experiment revealed a genetic divergence between habitats for nestlings handling aggression between two populations separeted only by 6 km, which is within the dispersal range of the species (D-Muro and E-Muro). To our knowledge this is the first study to report a genetic divergence between populations in personality phenotype at such a small scale and with a reciprocal transplant cross-fostering experiment. In addition, our experiment revealed a significant brood of origin effect for both traits suggesting that they are heritable and could thus evolve in response to local selection pressures in each habitat.

4.5.1 Phenotypic and genetic divergence in nestling handling aggression

As expected, we found that nestlings from the deciduous population, D-Muro, had a higher handling aggression phenotype than nestlings from the evergreen population E-Pirio (Tableau 4.1). In addition, the significant population of origin effect for this trait suggests a genetic divergence between D-Muro and E-Muro (evergreen habitat; Fig. 4.2). These results are consistent with the phenotypic and genetic divergence between populations found for the adult handling aggression phenotype (Dubuc-Messier et al. 2016) and with genomic analyses that recently revealed a significant differentiation between D-Muro and E-Muro across the whole genome (Szulkin et al. 2016). The fact that we did not find any significant phenotypic difference in nestlings handling aggression between D-Muro and E-Muro (using unmanipulated brood) but a genetic divergence (using cross-fostered broods; Tableau 4.1) suggests that although the genetic effect is important in shaping nestling phenotype, the trait plasticity might act to diminish the divergence of these populations at the phenotypic level, hence representing a countergradient variation (Conover and Schultz 1995). A common garden experiment involving adult birds from E-Pirio and D-Muro revealed a similar trend for heart rate during manual restraint: there was no phenotypic difference between the two populations in the wild but the common garden revealed a significant genetic difference between the two populations (Dubuc-Messier et al. Chap. 3). Interestingly, we did not find here a significant population of rearing effect for this trait. Therefore, whether the observed genetic variation is really opposed to environmental effects remains to be further investigated. Another possibility is that the smaller number of nestlings considered in the population comparison of the unmanipulated nestlings than in the comparison of cross-fostered nestlings prevented us to find a significant phenotypic difference between populations.

4.5.2 Phenotypic divergence but no genetic divergence in activity in a novel environment

Similarly to handling aggression, we found a phenotypic divergence between populations for the activity in a novel environment: nestlings in D-Muro were more active than in E-Pirio, but there was no phenotypic difference between D-Muro and E-Muro (Tableau 4.1). However, contrarily to handling aggression and to our predictions, there was no population of origin effect for nestling activity in a novel environment, which suggests no genetic divergence between D-Muro and E-Muro for this trait. Overall, our results suggest that variation in ecological conditions within valley (between D-Muro and E-Muro) may induce divergent selection for handling aggression but not for nestling activity. The significant phenotypic difference between nestlings from D-Muro and from the evergreen population of E-Pirio, situated 25 km further in another valley, suggests that the activity in a novel environment might be influenced by conditions that vary at a larger spatial scale (between valley; Tableau 4.1; Dubuc-Messier et al. 2016). Our results are consistent with Dubuc-Messier et al. (2016) who did not find any phenotypic divergence in adult activity in a novel environment between D-Muro and E-Muro, but a significant phenotypic and genetic divergence between valley (Dubuc-Messier et al. 2016; Dubuc-Messier et al. Chap. 3). Nevertheless, in contrast to adult traits, it is not yet possible to conclude that the phenotypic difference in nestling activity in a novel environment between D-Muro and E-Pirio has a genetic basis.

4.5.3 Environmental heterogeneity and local adaptation in blue tit personality phenotypes

Several lines of evidence based on past studies on this system suggest that the observed phenotypic and genetic divergence for nestlings personality traits have an evolutionary origin and may represent local adaptations (Charmantier et al. 2016; Szulkin et al. 2016; Dubuc-Messier et al. Chap. 3; Dubuc-Messier et al. Chap. 5). First, these populations are known to diverge phenotypically and genetically for numerous other types of traits including the adult personality traits (Blondel et al. 1999;

Charmantier et al. 2016; Dubuc-Messier et al. Chap. 3). Second, studies achieved to date suggest that this divergence is the result of contrasting selection pressures (Blondel et al. 2002; Teplisky et al. 2014; Dubuc-Messier et al. Chap. 3; Dubuc-Messier et al. Chap 5.). For example, in the case of personality traits, Q_{st} - F_{st} comparisons based on a common garden experiment revealed that the genetic divergence in adult personality phenotypes is likely the result of different selection regime rather than from genetic drift (Dubuc-Messier et al. Chap. 3). Moreover, Dubuc-Messier et al. (Chap. 5) have shown that adult birds with higher handling aggression phenotype have a fitness advantage in the deciduous population and that nestling handling aggression phenotype is important for their recruitment probability (even though the selection gradients were not very strong). Fourth, several studies have found that personality traits are heritable (review in van Oers and Sinn 2011; Brommer and Kluen 2012) and we found in this study an important heritability estimate (40%) for handling aggression that suggests that this trait could evolve in response to selection pressures.

The ecological factors leading to the evolution of a higher handling aggression and perhaps of a higher nestling activity in the deciduous habitat are unknown yet. Deciduous habitats have been shown to have a particular high food abundance in the spring during blue tit breeding season (Tremblay et al. 2003; Blondel et al. 2006), but other factors differentiate this population from the evergreen populations (and particularly E-Pirio), such as a higher population density, a lower prevalence of nest parasite (*Protocalliphora*) and a higher density and diversity of predators (Hurtrez-Boussès et al. 1999; Blondel et al. 2006; Dubuc-Messier et al. 2016; Dubuc-Messier personal observations). Such factors may have an impact on the selective regime in each habitat and lead to the evolution of faster exploration and more aggressive phenotypes in the deciduous habitat (Both et al. 2005; Smith and Blumstein 2010; Réale et al. 2010; Jacques-Hamilton et al. 2017). Furthermore, previous studies on this system have found that blue tits in the deciduous habitats have a faster life history strategy than birds from the evergreen habitat (Blondel et al. 1999; Charmantier et al. 2016). According to the pace-of-life syndrome hypothesis, fast life history strategies should be linked to boldness, high aggressiveness, and high activity (Wolf et al. 2007; Réale et al. 2010). In particular, individuals or populations that have low residual reproductive value due to reduce survival probability should invest more in current reproduction and display behaviours associated to risk taking such as faster exploration and lower docility (Wolf et al. 2007; Réale et al. 2010; Nicolaus et al. 2012). In agreement with this hypothesis, adult birds from the deciduous habitat D-Muro have lower survival probability, produce larger clutches and are also displaying a higher activity in a novel environment and a higher handling aggression phenotype as adults and as nestlings (Charmantier et al. 2016; Dubuc-Messier et al. 2016; Dubuc-Messier et al. Chap.5). Hence, overall it emerges that the observed divergence in personality between habitats could be the result of selection pressure associated with the local ecological conditions that favours the co-evolution of a variety of traits forming a fast or a slow life style. An interesting next step to test this local adaptation hypothesis would be to compare the fitness of cross-fostered nestlings to the fitness of residents in each population (Kawecki and Ebert 2004).

4.5.4 Brood of origin and brood of rearing effects

Studies using within-population reciprocal cross-fostering in blue tits and great tits revealed that small-scale rearing conditions (i.e. brood of rearing effects) can have important impact on nestling personality phenotype that can be sometimes stronger than the effects of the brood of origin (Brommer and Kluen 2012; Naguib et al. 2011; van Oers et al. 2015). In the present study, we found a significant but weak heritability (6%) and a significant brood of rearing effects (7%) for activity in a novel environment. The non-significant population of rearing effect but the significant brood of rearing effect for this trait suggest that small-scale conditions (breeding territory, parental care, vegetation cover or predation risk around the nest-box) might be more important in shaping this behavioural trait than habitat type (local dominant oak species). In contrast, brood of rearing or population of rearing effects were negligible for handling aggression, but we found significant population of origin and brood of origin effects for this trait translating into a heritability of 40%. This result indicates that the genetic effect might be more important for shaping the handling aggression phenotype than for the activity in a novel environment phenotype. In addition, the variance attributed to brood of origin for the cross-fostered nestlings for both traits suggests that the brood effect found for the unmanipulated nestlings was mainly due to a genetic effect.

An important limitation to keep in mind is that we cannot completely exclude that very early environmental effects that could have occurred prior to the cross-fostering had an impact on the observed patterns. Such effects could have inflated our heritability estimation and could also be partly responsible for the population of origin effect found for handling aggression (Kruuk and Hadfield 2007; Hadfield et al. 2013). Brommer and Kluen (2012) were able to unravel early environment effects attributable to the brood of origin from the additive genetic effect using a cross-fostering experiment in Finnish blue tits. Combining a cross-fostering experiment with an animal model analysis, they found that the brood of origin was responsible for 4% of the phenotypic variance in nestling handling aggression while the additive genetic effect estimated with the population pedigree represented an additional 16% of the total phenotypic variance. Their study also reveals that ignoring early environment effects in cross-fostering experiments leads to overestimation of the heritability of nestling personality traits but not significantly so. Moreover, the fact that we did not find any interaction between year and population of origin for handling aggression suggests that the observed divergence between the two populations does not depend on early environmental effects that could vary from year to year depending on the current ecological conditions.

4.5.5 Ontogeny of the personality phenotype

A growing number of studies are calling for the investigation on personality traits and behavioural syndromes development and on their stability during ontogeny (Groothuis and Trillmich 2011; Brommer and Class 2015). Studies to date have shown a moderate positive correlation (0.3) among personality phenotypes of different age classes, suggesting that the ranking of individuals is relatively constant during development (review in Brommer and Class 2015). Here, we found that the relationship between nestlings and adult phenotypes depends on the habitat and on the trait being studied. We found no relationship between the nestling behaviour in a novel environment and their behaviour once adult. In contrast, we found an interesting pattern for handling aggression. As expected, we found a tendency for a positive relationship between the two age classes in the evergreen populations. However, in D-Muro, we found that nestling handling aggression was negatively related to the analogous phenotype measured on adults (Fig. 4.3). In other words, in D-Muro, the ranking of individuals seems to be inversed between the two age classes: more aggressive nestlings became less aggressive adults (Fig. 4.3). Negative correlations among age classes have seldom been reported for personality traits (Sinn et al. 2001; review in Brommer and Class 2015) and the exact causes of this intriguing phenomenon in this particular population remain to be further investigated. However, we can speculate that the ecological conditions specific to this habitat could have favoured the evolution of plastic change or differential gene expression between life stages that depends on the initial personality phenotype (and/or genotype) of nestlings (Groothuis and Trillmich 2011). Whatever the mechanistic pathway behind such pattern, our results suggest that small-scale ecological conditions might be important for shaping the ontogeny of the personality phenotype.

4.5.6 Conclusion

Our study highlights the impact of environmental heterogeneity on the phenotypic and genetic differentiation of populations and shows that population divergence is possible even at a small spatial scale and despite gene flow for behavioural traits. In addition, our results revealed that the correlation of the personality phenotype between two age classes is habitat- and trait-dependent in our study system. An interesting research avenue on nestling personality evolutionary ecology would be to investigate the relationship between handling aggression phenotype, dispersal patterns and different fitness proxies at the nestling and reproductive stage.

4.6 Acknowledgements

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4.7 Supplementary materials

Adult handling aggression

The adult handling aggression trials were performed within two minutes after capture, directly after removing the bird from the trap and prior to any other manipulations. The handler held the bird in the upright position, head up, with his back facing the handler. He held the bird with one hand and placed the bird's legs between his forefinger, his middle finger and his thumb to let the bird free to move its tails and wings. The handler pointed the forefinger of his other hand at a spot about 2 to 3 cm in front of the bird's beak and noted if the bird struck at his finger, and the position of its wings and tail. After two seconds in this position, the handler moved his forefinger towards the bird's beak two or three times and recorded its reaction. The score ranged from 0 (the bird shows no reaction) to 3 (the bird spontaneously strikes the handler's fingers and spreads its wings and tail). The scoring protocol is reported in detail in Table S1. The entire test lasted less than a minute.

Tableau S4.1 Adult blue tit handling aggression scale.

Score	Wings spread	Tail feathers spread	Bird strikes fingers
0	No	No	No
1	No	No	Yes, but only if provoked
2	No	Yes	Yes, spontaneously
3	Yes	Yes	Yes, spontaneously

When the bird displayed one reaction specific to one score and another reaction specific to another score, it received an average score between the two. For example, a bird that struck without any provocation (score 2) but did not have its wings and tail feathers spread (score 1) would be scored as 1.5.

Tableau S4.2 Best models for nestling activity in a novel environment and handling aggression in three Corsican populations of wild blue tits (France) for unmanipulated broods.

Trait	Fixed effect	Estimates (95% CI)
Activity in a novel environment	Intercept	1.988 (1.614; 2.361)
	Pop.: E-Muro	0.245 (-0.219; 0.707)
	Pop.: E-Pirio	0.301 (-0.097; 0.698)
	Year: 2014	0.570 (0.178; 0.961)
	Year: 2015	0.646 (0.235; 1.056)
	Age	-0.144 (-0.195; -0.094)
	Pop. E-Muro: 2014	-0.428 (-0.937; 0.082)
	Pop. E-Pirio: 2014	-0.440 (-0.875; -0.005)
	Pop. E-Muro: 2015	-0.290 (-0.837; 0.258)
	Pop. E-Pirio: 2015	-0.700 (-1.151; -0.248)
Handling aggression	Intercept	1.038 (0.895; 1.181)
	Pop.: E-Muro	0.042 (-0.207; 0.291)
	Pop.: E-Pirio	0.105 (-0.094; 0.304)
	Year: 2014	-0.034 (-0.232; 0.164)
	Year: 2015	0.332 (0.124; 0.539)
	Age	0.195 (0.147; 0.242)
	Pop. E-Muro: 2014	-0.251 (-0.587; 0.085)
	Pop. E-Pirio: 2014	-0.515 (-0.798; -0.232)
	Pop. E-Muro: 2015	-0.055 (-0.432; 0.324)
	Pop. E-Pirio: 2015	-0.353 (-0.638; -0.066)

The reference population is D-Muro and year 2013.

Tableau S4.3 Model describing the adults handling aggression phenotype in three populations of Corsican wild blue tits (France), estimates and confidence intervals (95% CI) are presented for each term.

Fixed effects	Estimates (95% CI)
Intercept	2.684 (2.088; 3.281)
Pop.: E-Muro	-0.783 (-1.337; -0.228)
Pop.: E-Pirio	-0.742 (-1.199; -0.284)
Nestling phenotype	-0.224 (-0.389; -0.059)
Sex	-0.267 (-0.539; 0.001)
Hour	-0.035 (-0.072; 0.002)
Nestling phenotype: E-Muro	0.307 (0.060; 0.554)
Nestling phenotype: E-Pirio	0.275 (0.067; 0.483)

D-Muro population is the reference. Data from unmanipulated nestlings.

Figure S4.1 The novel environment apparatus for nestlings.

CHAPITRE 5
ENVIRONMENTAL HETEROGENEITY AND DIFFERENTIAL LOCAL SELECTION PATTERNS ON PERSONALITY TRAITS IN BLUE TIT POPULATIONS

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5.1 Abstract

Environmental heterogeneity, spatial variation in selection pressures and gene flow are known to be important for shaping intra-specific variation and local adaptations. However, their roles as drivers of variation and divergence in behavioural traits have seldom been studied. Here, we compared the pattern of selection acting on handling aggression for breeding and fledgling blue tits (*Cyanistes caeruleus*) across three wild populations situated in contrasted habitats yet connected by gene flow. We used four fitness proxies: survival probability, annual number of fledgling, and mean annual fledging body mass for breeding birds, and recruitment probability for fledglings. We found support for selection on handling aggression in all populations and via all fitness proxies, but selection appeared to act mainly through differential parental survival probability in our system. As expected, our results suggest that selection regimes differ between populations and habitats. In addition, we found disruptive selection patterns in two populations that could explain the maintenance of intra-population variation in behaviour. Our multivariate approaches allowed us to partition the phenotypic covariance between handling aggression and fitness into its underlying among-individual and residual components. These analyses revealed contrasting covariance patterns among levels of variation that could explain the overall small phenotypic selection gradients. As expected, these results suggest that spatial variation in ecological conditions contribute to the maintenance of small-scale among and within-population variation for personality traits in this system and that contrasted local ecological conditions can shape local adaptations despite gene flow.

5.2 Introduction

A central aspect in the study of biological diversity is to identify the factors that generate and maintain intraspecific phenotypic and genetic variations. Heterogeneous selection pressures associated with spatiotemporal environmental heterogeneity have been recognized as an important mechanism responsible for the maintenance of intraspecific diversity by promoting within-population phenotypic and genetic variation and population differentiation (Wang and Bradburd 2014; Siepielski et al. 2009; Kingsolver et al. 2012). Indeed, temporal variation in selection pressures resulting from variation in environmental conditions can lead to genotype by environment interaction for fitness and maintain within-population phenotypic and genetic diversity (Ellner and Hairston 1994). Differential selection pressures related to spatial variation in environmental conditions can lead to phenotypic and genetic divergence of populations and ultimately to local adaptations (Kawecki and Ebert 2004; Wang and Bradburd 2014). However, gene flow between populations can limit the impact of spatial variation in environmental conditions on phenotypic and genetic divergence and thus limit the evolution of local adaptations (Lenormand 2002; Garant et al. 2007; Siepielski et al. 2009; Richardson et al. 2014). Hence, until recently, most research on genetic divergence focused on populations separated by large spatial scales or separated by important barriers to dispersal (Slatkin 1987; Lenormand 2002). Yet, an increasing number of studies have suggested that strong selection pressures related to variation in ecological conditions and biased dispersal could lead to phenotypic and genetic divergence of populations despite gene flow (Richardson et al. 2014; Wang and Bradburd 2014).

Intraspecific variation in behaviour, and more precisely consistent differences among individuals in behavioural phenotypes (*i.e.* personality), has been extensively reported over the last ten years (Réale et al. 2007; van Oers and Sinn 2011) and an increasing number of studies are revealing that personality traits can be the target of selection (Dingemanse et al. 2004; Smith and Blumstein 2008; Quinn et al. 2009; Bergeron et al. 2013). These studies have reported that selection on personality traits often fluctuates temporally (Dingemanse et al. 2004; Boon et al. 2007; Quinn et al. 2009; Taylor et al., 2014; Nicolaus et al. 2016), which suggests that the relationship between personality and fitness can vary depending on the current environmental conditions and that temporal variation in selection pressures could be one of the mechanisms that maintains personality variation within a population. Recent studies have investigated the impact of spatial variation in environmental conditions on behavioural variation by comparing the personality phenotype of individuals inhabiting contrasting habitats (Bell 2005; Quinn et al. 2009; Dingemanse et al. 2010; Dochtermann et al. 2012; Atwell et al. 2012; Heinen-Kay et al. 2016; Jacquin et al. 2016). However, although the importance of spatial heterogeneity in selection pressures has been highlighted in several studies on life-history and morphological traits we still have much to discover on its importance for intraspecific variation in personality traits and on whether or not they could lead to behavioural adaptations to local environmental conditions.

In this study, we compared selection patterns on a personality trait over a five-year period across three wild blue tit (*Cyanistes caeruleus*) populations. These populations are located in contrasted habitats separated by small spatial distances (6 to 25 km) and are connected by gene flow (F_{st} between 0.01 and 0.009; Porlier et al. 2012a; Szulkin et al. 2016). We investigated the selection pressures on handling aggression (HA), a common measure of the animal reaction to stressful situations such as human handling (*docility*; Réale et al. 2007). This personality trait has been related to life-history traits (Réale et al. 2000; Réale et al. 2010), is repeatable (Bell et al. 2009), heritable (Brommer and Kluen 2012; Class et al. 2014) and has been related to fitness in various taxa, including blue tits living in other populations (Réale et al. 2000; Réale et al. 2009; Brommer and Kluen 2012; Bergeron et al. 2013; Class et al. 2014; St-Hilaire et al. 2017).

The populations under study live in two different valleys on the island of Corsica (France), in two different habitats each dominated by a particular tree species, the deciduous downy oak (*Quercus pubescens*) or the evergreen holm oak (*Quercus ilex*). Past studies on these populations have shown that the deciduous *versus* evergreen nature of the locally dominant tree species influences the selection regime acting on life-history and morphological traits, leading to phenotypic and genetic divergence between populations for these traits (Blondel et al. 1999; Blondel et al. 2002; Teplisky et al. 2014; Dubuc-Messier et al. Chap. 3). We found previously that breeding individuals and fledglings inhabiting the deciduous oak habitat have a higher handling aggression phenotype and are faster explorers than those living in the evergreen oak habitats (Dubuc-Messier et al. 2016; Dubuc-Messier et al. Chap. 4). A common garden and a reciprocal cross-fostering experiments revealed a genetic basis to these behavioural differences, and Q_{st} - F_{st} comparisons suggested this population divergence was the result of different selection pressures rather than of a neutral process (Dubuc-Messier et al. Chap. 3). It is thus suspected that, despite gene flow, the observed divergence in personality traits is an evolutionary outcome of adaptation to local environmental conditions. However, evidence for differential selection pressures on personality between these populations has yet to be confirmed.

Here, we first determined the survival probability of breeders for the three populations using capture-mark-recapture data spanning 16 years. Then, we explored selection patterns on handling aggression in each population, using four different fitness proxies during two different life stages over five years (2011 to 2015). Using a capture-mark-recapture framework and the Lande and Arnold (1983) approach, we analyzed the relationship between breeding individual (females and males) handling aggression and their survival probability, their number of fledglings produced annually, and their annual mean fledgling body mass and explored selection on fledglings' handling aggression by estimating its correlation with recruitment probability. In addition, we explored the temporal dynamics of selection patterns for each fitness proxy and each population.

Based on previous studies on personality traits and particularly on docility, we expected selection on handling aggression in each population (Smith and Blumstein 2008; Bergeron et al. 2013; Class et al. 2014; St-Hilaire et al. 2017). However, because we knew that these three populations differ in mean handling aggression and that these differences have a genetic basis (Dubuc-Messier et al. 2016, Dubuc-Messier et al. Chap. 3), we predicted contrasted selection patterns between habitats and populations. More specifically, we predicted that selection would favor lower handling aggression in the evergreen habitats and higher handling aggression in the deciduous habitat.

Phenotypic covariances between traits and fitness can be partitioned between among-individual and within-individual covariances (Price et al. 1988; Lynch and Walsh 1998; Kruuk et al. 2003). Among-individual covariance reveals potential genetic covariance between the trait and fitness and is necessary for a evolutionary changes in response to selection (Price et al. 1988; Lynch and Walsh 1998; Kruuk et al. 2003). In contrast within-individual covariance reflects potential environmental covariance between the trait and fitness that does not translate into evolutionary change (Rausher 1992). Hence, to better understand the relationship between handling aggression and fitness and the evolutionary trajectory of handling aggression in these populations, we partitioned the phenotypic covariances into their underlying among- and within-individual components, using a multivariate mixed-models framework (Brommer et al. 2014; Dingemanse and Doctermann 2014; Araya-Ajoy et al. 2016). Although we did not test for the genetic covariance between handling aggression and fitness, this approach allowed us to determined whether their phenotypic covariance was attributable to plasticity and may be environmentally driven or if it was attributable to repeatable differences in covariance patterns between fitness proxies and handling aggression and may thus represent in part genetic covariances (Stinchcombe et al. 2002; Brommer et al. 2014; Araya-Ajoy et al. 2016).

5.3 Materials and Methods

5.3.1 Study species, sites and field protocol

Blue tits are small socially monogamous passerine birds that nest in tree cavities and are commonly found in forested habitats of the western Palearctic. They are sedentary in our study area. This study was conducted in Corsica (France) between year 1999 and 2015 using nest-box monitoring. One population is located in a deciduous habitat, Deciduous-Muro (D-Muro hereafter; 42°32'N. 08°55'E, 350 m elevation; 110 nest-boxes distributed in three study plots) and two populations are located in evergreen habitats, Evergreen-Muro (E-Muro; 42°35'N, 08°57'E; 100 m elevation; 75 nest boxes distributed in three study plots), and Evergreen-Pirio (E-Pirio; 42°34'N, 08°44'E; 200m elevation; 205 nest-boxes distributed in two study plots). These populations have been studied since 1994, 1998, and 1976, respectively (Blondel et al. 2006; Charmantier et al. 2016). D-Muro and E-Muro are in the same valley (Regino valley) 6 km apart and E-Pirio is in an other valley (Fango valley) 25 km further away.

A daily to weekly monitoring, from early April to the end of June allowed us to record the exact laying dates, clutch sizes and number and body mass of fledglings for all broods occupying nest-boxes. Fledglings were individually ringed at age 9 to 15 days and their tarsus length and body mass were measured at 14-15 days. Breeding blue tits were captured during two different capture sessions: the pre-breeding period when males and females paired up and started defending a territory (from mid-March to April for D-Muro and E-Muro, and from mid-April 4th to May for E-Pirio) and the breeding period (April-May for D-Muro and E-Muro, and May-June for E-Pirio). During the pre-breeding period, birds were caught with a mist net or lured in traps using a live blue tit decoy and playback of territorial calls placed near a nest-box. During the breeding period, birds were caught in nest-boxes when nestlings were nine days or older. Because the capture session occurred right before or during breeding time, we considered all birds to be mostly breeders. All individuals were identified with unique metal rings provided by the CRBPO (France). We determined the sex of each breeding birds by examining the presence/absence of a brood patch during reproduction or based on feather coloration outside of the breeding period (Perrins 1979; Ferns and Hinsley 2010; Fresneau et al. 2014). Age (i.e., juveniles ≤ 1 year old *vs* adults ≥ 2 years old at the onset of the reproductive period) was determined using standard criteria based on feather coloration (Blondel et al. 1993; Blondel et al. 1999b).

5.3.2 Behavioural tests

Adult trials were run over five years (2011 to 2015) following the protocol detailed in Dubuc-Messier et al. (2016) and in Supplementary information (Tableau S5.1). Briefly, as soon as possible after capture, the observer held the birds in the upright position and noted its reaction to the handling. The score ranged from 0 (the bird shows no reaction) to 3 (the bird spontaneously knocks fingers and spreads its wings and tail). Fledglings' HA was assessed during two years (2013 and 2014) on fifteen days old fledglings. All fledglings were first taken out of the nest-box and placed in a small tissue bag and scored for HA one at a time using a protocol similar to the 'docility' protocol of Brommer and Kluen (2012). Briefly, the fledgling was placed with its back towards the observer's hand, its neck between the observer's index and middle finger, and its two legs held by the foot between the observer's thumb and forefinger. The handler held the bird vertically and counted the number of times the fledgling struggled during 10 seconds. The same observer did all the observations for the fledglings in a given nest-box, yet there were seven observers across all broods. The fledgling was weighed, measured and ringed after the trial.

5.3.3 Statistical analysis

Survival probability (1999 to 2015)

Survival probability was estimated using a capture-mark-recapture framework and the software E-surge v.1.9 (Choquet et al. 2009) over the 1999-2015 period. This framework allows accounting for potential biases caused by variation in recapture probabilities (Lebreton et al. 1992). A logit link function was used in order to constrain the survival and recapture estimates between 0 and 1 (Lebreton et al. 1992). We built the capture histories by assigning a score of 1 to an individual if it was captured at least once during a given year and of 0 if it was not captured. We tested whether the models respected Cormack-Jolly-Seber's assumption and assessed the presence of over-dispersion using Goodness-of-fit tests with U-CARE 2.2 (Choquet et al. 2009). We modeled survival and recapture probabilities separately for each population. The survival and recapture probabilities were modeled as functions of year and sex. We anticipated that the survival and recapture probabilities between the first and the second breeding attempt would differ depending on the age of the individuals at their first breeding attempts (juveniles or adults). We therefore included an age parameter in all models, that fitted different survival and recapture probabilities for the time interval between the first and second capture occasion for individuals that were juveniles at their first capture compared to all other time intervals. In all models, the recapture probability of the first capture occasion was fixed to one. We first selected the appropriate model structure for the recapture probabilities according to the lowest quasi Akaike information criteria (QAICc), by sequentially removing each effect from the full model. Once the model with the lowest QAICc for recapture probabilities was selected, we used the same sequential procedure for the survival probabilities.

Selection on breeder HA

For all selection analyses, except the multivariate models, we used one single lifetime value of HA for each individual (HA_i) using Best Linear Unbiased Predictors (BLUPs) from a linear mixed model on repeated measures of HA over the years (Taylor et al. 2014; Bergeron et al. 2013; St-Hilaire et al. 2017). In these models we controlled for important fixed effects affecting variation in HA phenotype including population, sex, year, capture period (pre-breeding *versus* breeding) and an interaction term between population and year (Dubuc Messier et al. 2016). BLUPS were obtained using the *lmer* function of the *lme4* package in R (Bates et al. 2014).

We estimated the strength and shape of viability selection on HA between 2011 and 2015, using the software E-surge v.1.9 (Choquet et al. 2009) as detailed previously. Survival and recapture probabilities were then modeled as functions of year, sex, age, HA_i, and HA_i^2. We also tested for the presence of an interaction between HA_i or HA_i^2, and year, sex, and age. We first selected the appropriate model structure for the recapture probability as described earlier, but the effect of HA_i and HA_i^2 was tested last, after all the other terms were selected or removed.

We also estimated selection on breeder HA using two proxies of annual reproductive success: 1) annual number of fledglings produced (thereafter: annual fledgling number), and 2) brood-specific mean annual fledgling body mass at fifteen days (thereafter: annual fledgling mass) which is positively related to fledgling survival (Tinbergen and Boerlijst 1990). We ran one model for each population. We based the annual reproductive success on data collected only on first broods because second broods were very rare (< 1% of the broods produced each year). Selection analyses were performed by running separate univariate mixed models for each population and each fitness proxy. In these models, we used each fitness proxy as the response variable and HA_i and HA_i^2 as fixed effects. The HA_i values of the two partners in a pair were not correlated (cor: 0.029, p-value = 0.461, $R^2 = 0.001$), indicating that their effect on fitness could be statistically separated. Therefore, we used both partners HA_i in the same models and used the female and male identities as random effects. In addition, because the date of first egg laying (LD hereafter) is known to be under selection in these populations (Porlier et al. 2012b) and could covary with HA (Réale et al. 2010) we added LD, and LD^2 in our models, and reported selection acting on HA_i once the effects of LD were controlled for. For each population, the full model was:

$$w_{mfj} \sim HA_{if} + HA_{im} + HA_{if}^2 + HA_{im}^2 + Year + LD_{mfj} + LD_{mfj}^2$$

Where w_{mfj} is the fitness (annual fledgling number or annual fledgling mass) of a given pair (*mf*) at year *j*, HA_i and HA_i^2 are the BLUP and $BLUP^2$ of female (*f*) and male (*m*) handling aggression extracted from the mixed-model described previously, and LD_{mfj} and $LD_{mfj}{}^2$ are the date of the first egg laying of a given pair (*mf*) at year *j*. In previous models, we also included as fixed effects the interaction between male and female HA_i and an interaction between year and both HA_i, and HA_i^2 of males and females to test respectively for the significance of correlational selection potentially acting on the behaviour of male and female in a pair (Class et al. 2014) and temporal fluctuation in selection patterns. These interactions never provided a better fit and were therefore dropped from the models (results not shown). Because we were interested in controlling for LD, we kept this variable in all models.

In a first step, we selected the fixed effects from the full model presented above using absolute annual fitness as a response variable. For these models, we used a Poisson error distribution and a log-link function for annual fledgling number (Bolker et al. 2009), and a Gaussian distribution for annual fledgling mass. In a second step, we used the relative annual fitness (individual annual fitness / average annual fitness of the population; Lande and Arnold 1983) as response variable in a mixed model to estimate the linear and quadratic selection gradients on HA_i. In these models, we used the fixed effects structure (except year as relative fitness was calculated within each year) kept the model with the lowest QAICc selected in the previous absolute fitness models and female and male identity as random effects. We reported quadratic selection gradients and standard errors after they were doubled (Stinchcombe et al. 2008) and linear selection gradient when the quadratic term was excluded from the model.

We explored the relationship between breeding individuals HA and fitness at both the within- and the among-individual level with a multivariate linear mixed model approach in a Bayesian framework using the MCMCglmm package (Hadfield 2010). We built one separate model for each population. We used four response variable: the repeated measures of females and males HA (Z-standardized; not BLUPs), LD (Z-standardized) at each reproductive attempt and the relative annual fledgling number and annual fledgling mass. Year and the hour of the HA trials were included as fixed effects. We included as random effects female and male identities for all traits, and observer identity for HA. We used non-informative prior (V = phenotypic variances / 3; nu = 0.1), 10 million iterations, a burn-in of 500 iterations, and only one iteration from every 200 in the Markov chain to avoid autocorrelation between successive iterations. For each population, we reported the covariances and correlations between each pair of traits at the among-female and among-male levels, at the within-individuals (residuals) level, and at the phenotypic level. We calculated the correlations between each trait at each hierarchical level as:

$$rF_x,F_y = \frac{\mathrm{Cov}_{Fx,Fy}}{\sqrt{(V_{Fx}\,V_{Fy})}} \qquad rM_x,M_y = \frac{\mathrm{Cov}_{Mx,My}}{\sqrt{(V_{Mx}\,V_{My})}} \qquad rR_x,R_y = \frac{\mathrm{Cov}_{Rx,Ry}}{\sqrt{(V_{Rx}\,V_{Ry})}}$$

$$\begin{aligned} rP_xP_y = {} & rF_x,F_y \ \sqrt{}\,(V_{Fx} / V_{Fx}+V_{Mx} + V_{Rx} + V_{OBSx})\,(V_{Fy} / V_{Fy} + V_{My} + V_{Ry} + V_{OBSy}) \\ & + rM_x,M_y \ \sqrt{}\,(V_{Mx} / V_{Fx}+V_{Mx} + V_{Rx} + V_{OBSx})\,(V_{My} / V_{Fy} + V_{My} + V_{Ry} + V_{OBSy}) \\ & + rR_x,R_y \ \sqrt{}\,(V_{Rx} / V_{Fx}+V_{Mx} + V_{Rx} + V_{OBSx})\,(V_{Ry} / V_{Fy} + V_{My} + V_{Ry} + V_{OBSy}) \end{aligned}$$

where rF_x,F_y, rM_x,M_y, rR_x,R_y and rP_xP_y are the correlations between traits x and y, at the among-female, among-male, within-individual, and phenotypic level, respectively; $COV_{Fx,Fy}$, $COV_{Mx,My}$ and $COV_{Rx,Ry}$ are the covariances at these different hierarchical levels; $V_{Fx,}$ V_{Mx}, V_{Rx} and are the variances of traits x at these different hierarchical levels; V_{OBS} is the variance attributable to the observer for trait *x*, where applicable. We assumed that the covariances and correlations between traits were different from zero when the 95% credibility intervals around the covariances estimates (posterior mode) were not overlapping zero.

Selection on fledglings' HA

We investigated the relationship between fledglings' HA and recruitment probability using a univariate generalized linear mixed model with a binomial distribution (1: recruited fledgling; 0: fledgling not recaptured as breeder). We built one model for each population and used fledglings HA and HA^2 (Z-standardized) as fixed effects. To test for variation between cohorts in selection patterns, we also used 'cohort' (birth year) as a fixed effect and the two-way interactions between cohort and HA and HA^2. We also fitted the fledgling body mass as an additional fixed effect to control for variation in body condition. To control for the non-independence of birds from the same brood, we used brood identity as a random effect. We then proceeded to model selection and extraction of selection gradients as described previously.

All models on breeder reproduction selection and on fledglings' recruitment probability were run in R (R Core Team 2015). Model selection was performed with the function *aictable* of the package *AICcmodavg* (Mazerolle 2016) except for the multivariate analyses. Models on fledglings' recruitment probability and annual fledgling number were performed using the *glmer* function and models on mean annual fledgling mass were performed using the *lmer* function (*lme4* package; Bates et al. 2014). We used *lmer* and *confint.merMod* of the *lme4* package to extract the selection gradients, standard errors and confidence intervals. Sample sizes for each fitness proxy are provided in Tableau 5.1.

5.4 Results

Survival probability (1999 to 2015)

For the long-term data set (1999-2015), the goodness-of-fit test conformed to the Cormack-Jolly-Seber's assumptions in each population (D-Muro: quadratic $chi^2 = 89.122$, d.f. = 129, c-hat = 1.45, p-level = 0.997; E-Muro: quadratic $chi^2 = 74.467$, d.f. = 105, c-hat = 1.42, p-level = 0.989, E-Pirio: quadratic $chi^2 = 88.410$, d.f. = 120, c-hat = 1.36, p-level = 0.986). These c-hat values were included in all models. Model selection for each population is presented in supplementary materials (Tableau

S5.2). Over all years, survival probability was the lowest in D-Muro, intermediate in E-Pirio and the highest in E-Muro and recapture probabilities were high in all populations (ranging between 0.74-0.80; Tableau 5.2).

Viability selection on breeders HA

The goodness-of-fit test conformed to the Cormack-Jolly-Seber's assumption in each population also for this subset of data (2011 to 2015), with non-significant results for the overall test (D-Muro: quadratic chi^2 = 17.108, d.f. = 22, c-hat = 0.773, p-level = 0.757, E-Muro: quadratic chi^2 = 8.429, d.f. = 19, c-hat = 0.421, p-level = 0.982, E-Pirio: quadratic chi^2 = 20.44, d.f. = 20, c-hat = 1.02, p-level = 0.430). The c-hat value was included in the model for E-Pirio, but was kept to one for E-Muro and D-Muro. Recapture probabilities were high in all populations (D-Muro and E-Muro: 0.84; E-Pirio: 0.99-1; Tableau S5.3 and S5.4). Model selection for recapture probabilities is presented in Tableau S5.3.

The model with the lowest QAICc included both linear and quadratic effects of HA_i on survival probability in E-Pirio and D-Muro revealing both directional and disruptive selection on HA_i (Tableau 5.3; Fig. 5.1). In contrast to E-Pirio, in D-Muro, the confidence intervals around the estimates of the linear component of the relationship did not include zero [estimate on the logit scale: 0.807 (95% CI: 0.172; 1.442); Tableau S5.4]. These results suggest that the linear component is more important in D-Muro than in E-Pirio revealing a positive linear and directional selection on HA_i in D-Muro and mainly disruptive selection in E-Pirio (Fig. 5.1). In E-Muro, the model with the lowest QAICc included a positive linear effect of HA on survival probability: individuals with high HA had higher survival probabilities (Fig. 5.1). However, the model with a constant survival probability had similar QAICc values than the model with only the positive linear effect of HA_i (Tableau 5.3) suggesting that selection was not very strong in this population.

Selection on HA via reproductive success

Using annual fledgling number as a fitness proxy, we found selection pressures on HA that varied in direction and intensity depending on sex and population (Fig. 5.2a; Tableau S5.5). In D-Muro, the model with the lowest AICc included both a negative linear and a positive quadratic effect of female HA_i [β_i = -0.015 (-0.056; 0.027); γ_{ii} = 0.078 (0.004; 0.150)], and a linear positive effect of male HA_i [β_i = 0.023 (-0.013; 0.058)]. In E-Muro, the best model included positive linear effect of female and male HA_i [females: β_i = 0.018 (-0.046; 0.082); males: β_i = 0.009 (-0.065; 0.083)]. In E-Pirio, the model with the lowest AICc included a positive linear effect of female HA_i [β_i = 0.028 (-0.043; 0.100)], and a negative linear effect of males HA_i [β_i = -0.008 (-0.077; 0.060)].

Using annual fledgling mass as a fitness proxy we also found selection pressures on HA that depended on sex and population (Fig.5.2b; Tableau S5.6). In D-Muro, the model with the lowest AICc included a positive linear selection on HA_i for females and males [females: $\beta_i = 0.006$ (0.0005; 0.011); males: $\beta_i = 0.001$ (-0.005; 0.008)]. In E-Muro, the best model did not include an effect of female or male HA_i and the best model in E-Pirio included only a positive linear effect of female HA_i [$\beta_i = 0.002$ (-0.009; 0.013)]. It is important to note that for both the annual number of fledglings and for mean annual fledgling mass, the selection gradient on HA_i had 95% CI that did not included zero for D-Muro only (Fig. 5.2), suggesting that although HA_i and HA_i^2 were kept in best models based on AICc, selection might not be very strong in the other populations or that we did not have the power to uncover it.

Covariances between HA and fitness proxies at the different hierarchical levels are shown in Fig. 5.3. All variance components are provided in Suppl. mat. along with the correlation estimates between all pairs of traits (Tableaux S5.7 and S5.8). In D-Muro, we found a positive among-female correlation between HA and fitness: females that had a higher HA had more fledglings in general [mode: 0.686 (95% CI: 0.317; 0.995); Fig. 5.3]. However, we found a negative within-individual (residual) correlation in this population for this pair of traits: when individuals decreased HA, they increased their annual fledgling number [-0.398 (-0.580; -0.171); Fig. 5.3]. As a result, the phenotypic correlation between HA and the annual fledgling number was not different from zero [-0.174 (-0.355; 0.016); Fig. 5.3]. In E-Pirio, we found a small positive among-male correlation between HA and mean fledgling body mass [0.156 (-0.002; 0.607); Fig. 5.3], but a negative within-individual correlation between these traits [-0.040 (-0.072; -0.011); Fig. 5.3] also resulting in low correlation between these two traits at the phenotypic level [0.008 (-0.035; 0.115); Fig. 5.3]. There was no correlations between HA and fitness traits at any level for E-Muro. We also found a positive among-female correlation between HA and LD in E-Pirio [0.965 (0.208; 0.997)] and a negative among-female correlation between LD and both annual fledgling number and annual mean fledgling mass in all populations at different hierarchical levels depending on the population (Tableau S5.7). In all populations, we found a positive correlation between female and male HA phenotype at the within-individual level [D-Muro: 0.337 (0.083; 0.509); E-Muro: 0.399 (0.129; 0.579); E-Pirio: 0.462 (0.196; 0.664)], but not at the among-individual level. These correlations translated in positive correlations between partners' phenotypes at the phenotypic level in E-Muro [0.169 (0.017; 0.360)].

Selection on HA via fledgling recruitment

Models including fledglings' HA and HA^2 had the lowest AICc in all populations [Tableau S5.9; D-Muro: $\beta_i = 0.159$ (-0.272; 0.590), $\gamma_{ii} = -0.308$ (-1.369; 0.489); E-Muro: $\beta_i = -0.048$ (-0.492; 0.402); E-Pirio: $\beta_i = -0.325$ (-0.784; 0.136), $\gamma_{ii} = -0.838$ (-2.933; 1.156)]. A cohort by HA interaction was kept in the best model in D-Muro (Tableau S5.9), indicating different directions of selection on the trait depending on birth year (Tableau S5.10). Confidence intervals around all selection gradients all included zero indicating that although HA and HA^2 were kept in models based on AICc, selection might not be very strong on fledglings' HA or that we did not have the power to uncover it. We found a support for a small effect of brood identity for the relative recruitment probability in D-Muro and to a lower extent in E-Muro (D-Muro: Delta AICc = 7, variance = 2.34, proportion of total variance = 8.6%; E-Muro: Delta AICc = 2, variance = 0.057, proportion of total variance = 0.004; E-Pirio: Delta AICc = 1).

Tableau 5.1 Sample size for each fitness proxy for breeding blue tits from three Corsican populations (France; 2011-2015). For survival probability, we show the number of different individuals, for annual fledgling number and mean annual fledgling mass we show the number of different observations and the number of different females (n_f) and males (n_m), and for and fledglings' recruitment probability, we show the number of different individuals and the number of different clutches ($n_{clutches}$).

Fitness proxies	D-Muro	E-Muro	E-Pirio
Survival probability	268	273	353
Annual fledgling number	261 n_f = 187 n_m = 173	172 n_f = 172 n_m = 117	198 n_f =129 n_m= 129
Mean fledgling body mass	247 n_f = 181 n_m = 167	153 n_f = 105 n_m = 100	180 n_f = 180 n_m = 119
Fledglings' recruitment probability	662 $n_{clutches}$ = 94	308 $n_{clutches}$= 58	444 $n_{clutches}$ = 92

Tableau 5.2 Mean survival and recapture probabilities with 95% confidence intervals (95% CI) from 1999 to 2015 for breeding blue tits from three Corsican populations (France).

	Survival (95% CI)	Recapture (95% CI)
D-Muro	0.398 (0.372; 0.426)	0.744 (0.700; 0.787)
E-Muro	0.586 (0.548; 0.618)	0.796 (0.742; 0.841)
E-Pirio	0.491 (0.465; 0.519)	0.800 (0.756; 0.839)

Estimates of mean survival and recapture probabilities were calculated with models including all parameters kept in the model with the lowest QAICc in Table S5.2, apart from year.

Tableau 5.3 Model selection for survival probability as a function of handling aggression (HA_i) in breeding blue tits from three Corsican populations (France; 2011 to 2015). Models were ranked according to their QAICc values, only the four best models (i.e. lowest QAICc) are presented here for each population.

Model	# Ind. Par.	Deviance	QAICc	Delta QAICc
D-Muro				
Year + Sex + HA_i + HA_i^2	8	768.9999	785.2178	0.000
Year + Age + Sex + HA_i + HA_i^2	9	767.6286	785.9014	0.684
Year + Sex + Age + Age * HA_i + Age * HA_i^2	11	765.4217	787.8229	2.605
Year + Age + HA_i + HA_i^2	8	772.0031	788.2209	3.002
E-Muro				
HA_i	3	558.3032	564.3032	0.000
Constant	2	558.5768	564.5768	0.2736
HA_i + HA_i^2	4	558.0797	566.0797	1.7765
Year + Age + Age * HA_i + Age * HA_i^2	10	550.2782	570.2782	5.975
E-Pirio				
Year + HA_i + HA_i^2	15	733.0118	748.0435	0.000
Year + Age + HA_i + HA_i^2	16	732.1471	749.307	1.264
Year +Age + Sex + HA_i + HA_i^2	17	732.1374	751.4144	3.371
Year + Year * Age + Year * HA_i^2	21	724.2939	752.2792	4.235

The recapture probability was modeled according to the first best model in Table S5.3. HA_i represents the BLUP of an individual derived from a mixed model on handling aggression scores repeated over an individual's lifetime.

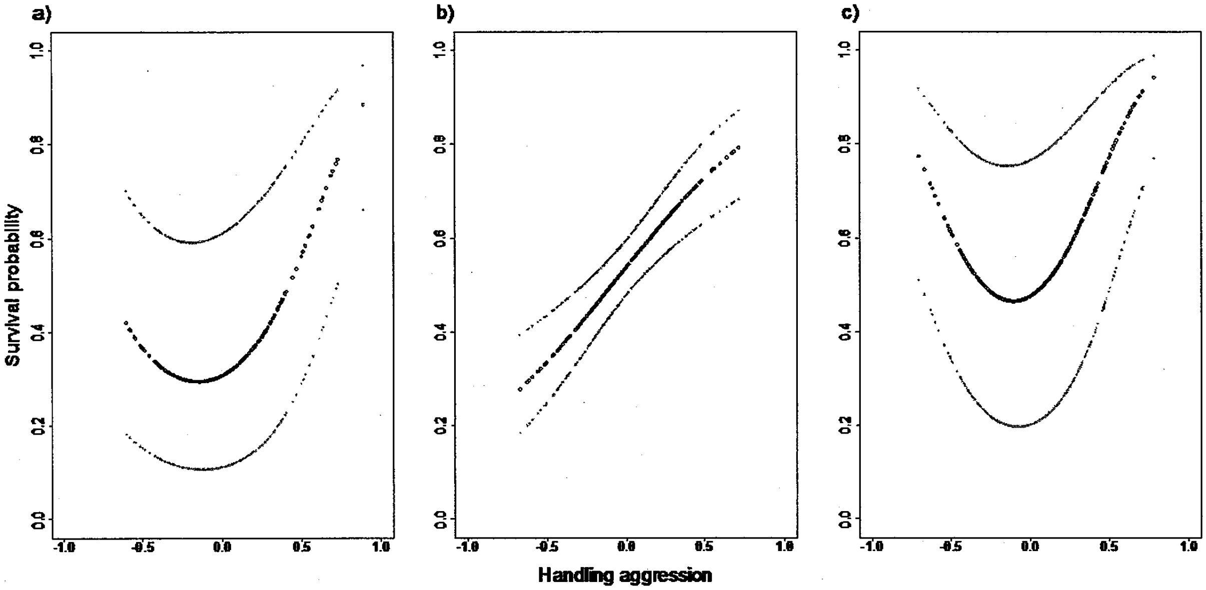

Figure 5.1 Relationship between the survival probability and handling aggression (HA_i) for breeding birds blue tits in a) D-Muro, b) E-Muro and c) E-Pirio in Corsica (France; 2011-2015). The predicted values of the survival probability as function of HA_i (black line) were obtained from the model estimates with the lowest QAICc presented in Table 5.3 and S5.3. The grey dashed lines are the lower and upper 95% confidence intervals for the predicted values. Each circle represents an individual. The intercept was fixed to the mean survival probability over all years and for females in D-Muro for representation purpose.

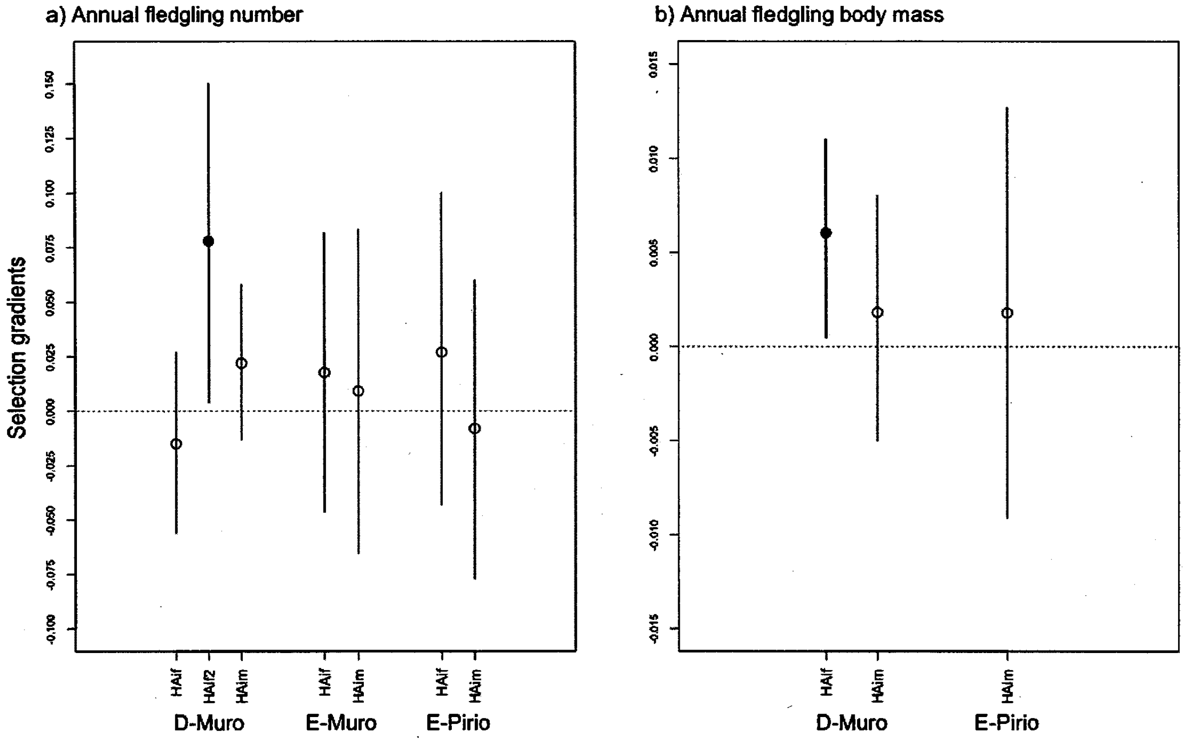

Figure 5.2 Selection gradients (and 95% CI) on handling aggression (HA_i and HA_i^2) for females (HA_f and HA_f^2) and males (HA_m) in each population using a) annual fledgling number or b) annual fledgling body mass as fitness proxies. We present the selection gradients for the model with the lowest QAICc (see text for model selection procédure and Tableau S5.5 and S5.6); there was no selection on either males or females phenotype in E-Muro for the annual fledgling body mass so there no selection gradients in the figure for this population and fitness proxy. We present with gray open circle the selection gradients for which the confidence intervals overlapped with zero and in full black circle for which it did not overlapped zero.

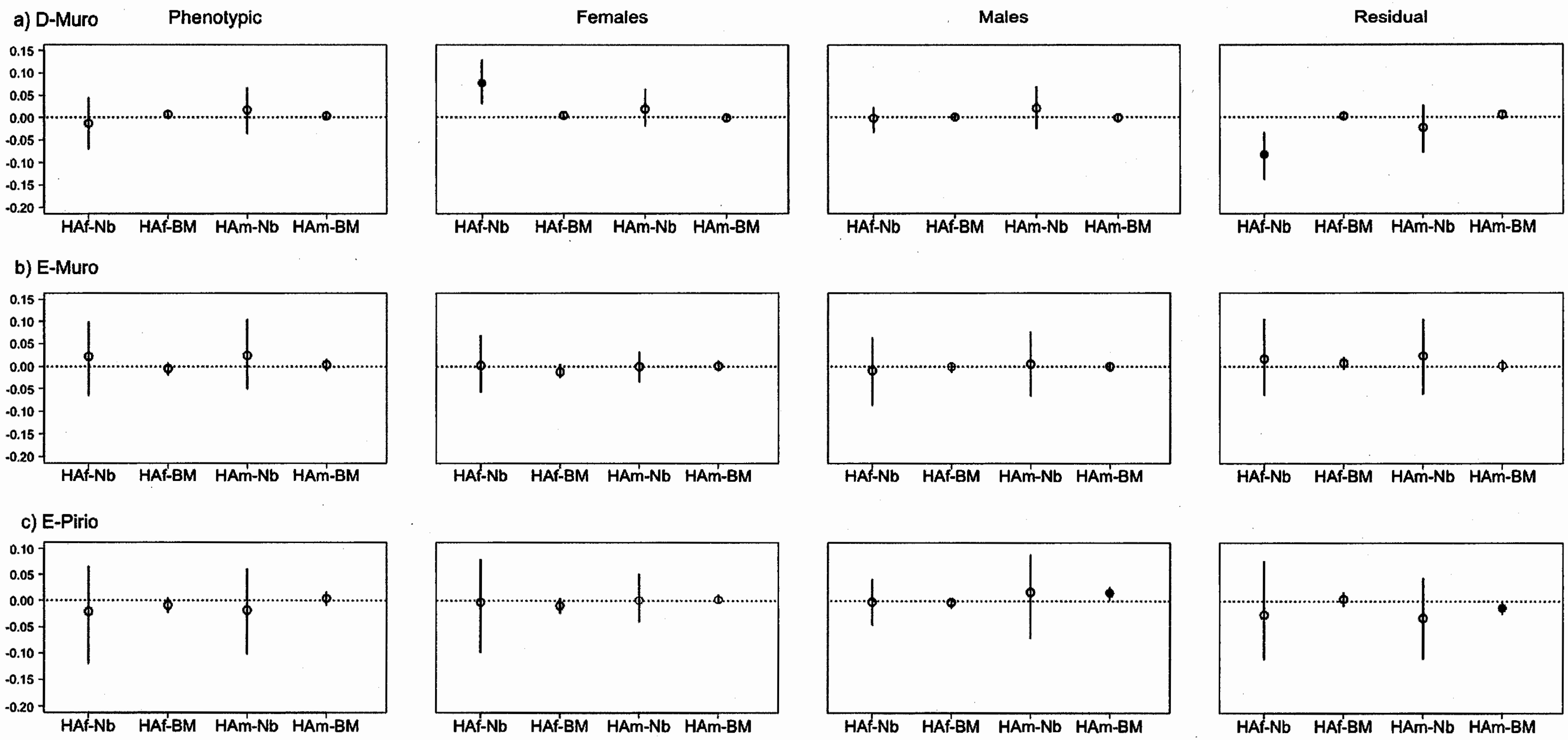

Figure 5.3 Covariances and 95% credibility intervals between female and male handling aggression phenotypes (HA_f and HA_m), the relative annual fledgling number (Nb) and the annual relative mean fledgling body mass (BM) at four hierarchical levels (phenotypic, among-females, among-males and residuals) for a) D-Muro, b) E-Muro and c) E-Pirio. We present in gray the covariances for which the confidence intervals overlapped with zero and in black for which it did not overlapped zero

5.5 Discussion

As expected, we found support for selection on handling aggression measured in both breeding and fledgling blue tits. This result adds to the growing body of evidence that personality traits can have important ecological and evolutionary consequences (Dingemanse and Réale 2005; Boon et al. 2008; Smith and Blumstein 2008; Quinn et al. 2009; Bergeron et al. 2013; Class et al. 2014; Le Galliard et al. 2015). In these blue tit populations, selection seemed to act on handling aggression mainly through differential survival of breeding individuals since selection gradients based on reproductive fitness proxies and on fledglings' recruitment were often weak and the confidence intervals around these estimates frequently included zero. Contrarily to other studies (Dingemanse et al. 2004; Boon et al. 2007; Quinn et al. 2009; Taylor et al. 2014; Nicolaus et al. 2016), we did not found fluctuating selection of handling aggression, although we found a small cohort effect for selection on fledglings' handling aggression. We found disruptive selection on handling aggression in two of the three populations, a mechanism that could participate to the maintenance of intra-specific variation in personality traits. In addition, as expected, our results suggest different selection patterns acting on handling aggression depending on the population. Overall, our results suggest that individuals with a higher handling aggression had a higher fitness in D-Muro and in the E-Muro although selection was weaker in this population (Table 5.3). In E-Pirio, our results suggest that individuals with extreme handling aggression phenotypes (both high and low) had higher fitness. These results are in part in agreement with our predictions and with the genetically higher handling aggression in D-Muro than in E-Pirio (Dubuc-Messier et al. 2016; Dubuc-Messier et al. Chap. 3) and indicate that local ecological conditions may be important in mediating the link between personality and fitness in this system.

5.5.1 Disruptive selection on handling aggression

Although it is recognized that disruptive selection is a mechanism that can promote intra-specific variation (Brodie et al. 1995; Hendry et al. 2009), disruptive selection has seldom been reported for personality traits (but see Bergeron et al. 2013; Lichtenstein and Pruitt 2015; St-Hilaire et al. 2017). In this study, we found support for disruptive selection acting on handling aggression via survival probability (D-Muro and particularly in E-Pirio, Fig. 5.1, Tableau 5.3) and via the annual number of fledglings (D-Muro; Fig. 5.2a). Intra-specific competition and niche specialization are suspected to be important mechanisms by which disruptive selection could emerge (Dall et al. 2004; Bergmüller and

Taborsky 2010; Martin and Pfennig 2012; Montiglio et al. 2013). For personality traits, niche specialization could be the result of intra-specific competition for limiting resources or of small-scale environmental heterogeneity, and could imply different strategies to cope with predation threats or to find and defend important resources such as breeding territories (Dall et al. 2012). The exact proximal cause for the disruptive selection pattern on handling aggression found in this study remains to be further investigated. However, we can speculate that it is the result of distinctive strategies to cope with predation and spatial heterogeneity in predation risks (Belgrad and Griffen 2016). Indeed, docility in hand can be viewed as the reaction of individuals to a risky situation like an attack by a predator (Réale et al. 2007; Santos et al. 2015) and this trait has been linked to other personality traits related to predation risk response and to risk taking in general (Réale et al. 2007; Réale et al. 2010; Santos et al. 2015; Abbey-Lee et al. 2016). In our system, individuals with low handling aggression could be less risk prone and thus breed and forage in areas with lower predation risks that could result in a lower probability of being predated. On the contrary, individuals with a higher handling aggression could be more risk prone and occupy riskier areas but may detect predators faster and have higher escape capacities (Réale et al. 2007; Réale et al. 2010; Santos et al. 2015; Abbey-Lee et al. 2016). Such fine scale habitat-phenotype matching (Edelaar et al. 2008) could be tested by analyzing variation in personality phenotype and selection patterns at the territory scale, in comparison with local spatial variation in predation risks.

5.5.2 Contrasted selection patterns between populations

Empirical and theoretical studies suggest that personality traits could have evolved within the trade-off between current reproduction and residual reproductive value and thus be part of a pace-of-life syndrome (Wolf et al. 2007; Réale et al. 2010). For example, according to these studies risk taking should be linked to high early reproductive investment at the expense of low survival probability and low residual reproductive value (Wolf et al. 2007; Réale et al. 2010; Nicolaus et al. 2012). Corsican blue tit populations show several contrasted life history features and differences in mean personality phenotype in agreement with the predictions of the pace-of-life syndrome hypothesis. Indeed, birds from the deciduous habitat (D-Muro) invest more in current reproduction, have a lower survival probability, are in average faster explorers and display a higher mean handling aggression than birds from the evergreen habitats (Charmantier et al. 2016; Dubuc-Messier et al. 2016; Dubuc-Messier et al. Chap. 3). In addition, the results from a common garden experiment suggested that these differences in personality phenotype have a genetic origin (Dubuc-Messier Chap. 3). Overall, the results from the present study suggest that the higher handling aggression phenotype in D-Muro could have evolved in response to the local selection pressure. Indeed, we found that in D-Muro selection on handling aggression was mostly directional and positive for both viability and reproductive selection (although we also found a weak disruptive component; Fig. 5.1, Fig. 5.2, Tableau 5.3). Previous studies in this system and on personality variation suggest that handling aggression is heritable and could thus respond to selection (Réale et al. 2007; van Oers and Sinn 2011; Brommer and Kluen 2012; Class et al. 2014; Dingemanse and Dochtermann 2014).

For evergreen populations, the current selection pressures found here are not entirely in accordance with the the lower mean handling aggression found previously in these two populations. Indeed, we found mostly disruptive viability selection in E-Pirio, and a weak directional positive viability selection in E-Muro favoring individuals with a higher handling aggression phenotype (Fig. 5.1, Tableau 5.3). It is possible that the observed lower mean handling aggression phenotype in the evergreen habitats compared to the deciduous habitat is the result of a strong ongoing selection acting via other fitness proxies or of past selection pressures. Understanding the mechanistic pathway by which handling aggression translates in higher fitness in these populations should shed light on the causes of these results.

5.5.3 Mechanistic pathway linking handling aggression and fitness

An increasing number of studies are showing that personality phenotypes are under natural selection (Dingemanse and Réale 2005; Boon et al. 2008; Smith and Blumstein 2008; Quinn et al. 2009; Bergeron et al. 2013; Class et al. 2014; Le Gaillard et al. 2015), but the mechanistic pathway relating personality differences and fitness remains to be further explored in most cases. Nevertheless, a few recent studies in other species and particularly in avian species (Veerbeek et al. 1994; Dingemanse and de Goede 2004; Both et al. 2005; van Overveld and Matthysen 2010; Mutzel et al. 2013; Class et al. 2014; Santos et al. 2015; van Overveld and Matthysen 2013), provide insights on the functional role of personality traits such as handling aggression in mediating fitness in our study system. For example, the association between personality traits and survival probability has been frequently attributed to vulnerability to predation (Réale and Festa-Bianchet 2003; Bell 2005; Dingemanse et al. 2010; Santos et al. 2015; Heinen-Kay et al. 2016; Jacquin et al. 2016). As blue tits are the prey of several species it is likely that predation pressures play a key role in mediating the relationship between the personality phenotype and survival probability in this species. Moreover, some studies suggest that personality phenotypes might mediate fitness via the reproductive output trough its role in parental care. For example, Mutzel et al. (2013) have found that fast exploration in female blue tits was related to a higher fitness through high offspring provisioning rate. In addition, following a cross-fostering experiment, Class et al. (2014) found that handling aggression of foster fathers, yet not of genetic fathers, had a positive impact on fledglings' recruitment probability, suggesting that males handling aggression might have a positive effect on fitness mostly via its impact on parental care. Furthermore, several studies in great tits have suggested that associations between the personality phenotype and the reproductive output could arise via dominance and competitive ability to acquire a good breeding territory or to find food patches in an heterogeneous environment (Veerbeek et al. 1994; Dingemanse and de Goede 2004; Both et al. 2005; Overveld and Matthysen 2010; Overveld and Matthysen 2013).

Studies of natural selection on personality traits have taught us so far that selection often depends on sex, age or the local ecological conditions and is thus context-dependent (Réale and Festa-Bianchet 2003; Dingemanse et al. 2004; Both et al. 2005; Smith and Blumstein 2008; Quinn et al. 2009; Bergeron et al. 2013). For example, a study of viability selection on exploration scores in Dutch great tits over three years showed strong fluctuations in the direction of selection, which was opposite in males and females and across years (Dingemanse et al. 2004). In our populations, selection on blue tit handling aggression was age and sex dependent, although fluctuations were not as strong as in the Dutch great tits. Our study also reveals that selection on handling aggression differed according to the population, and could thus vary depending on local ecological conditions. In this context, it would be very informative to compare selection pressure at the scale of the species distribution. Interestingly, the selection patterns described here for Mediterranean blue tits contrast with a study of Finnish blue tits where there was no evidence for viability selection on breeding bird handling aggression (Class et al. 2014). Overall, the link between personality traits and fitness appears to be specific to a given age, sex, and population, and generalizing that link should be done carefully. Despite the possible complex functional role(s) of handling aggression on fitness, exploring how it affects susceptibility to predation, parental care or territory in our studied populations would be interesting research avenues for the future. Furthermore, comparing the role of handling aggression in mediating these fitness-related traits at the scale of the species distribution should provide very instructive information on the role of handling aggression in the ecology of the species and on its potential interaction with the local ecological conditions.

5.5.4 Hierarchical levels of covariation

Our results suggest that the relationship between personality and different life history traits and fitness proxies change depending on the spatial scale at which the relationship is studied. For example, at the metapopulation level, D-Muro is the population with the lowest survival probability and the highest mean handling aggression (Dubuc-Messier et al. 2016; Dubuc-Messier et al. Chap. 3). However, within D-Muro, aggressive birds had a higher survival probability. Therefore, the relationships among traits at the metapopulation level and within each population are in opposite direction. In addition, while the results for the population mean (metapopulation level) are in accordance with the pace-of-life predictions (lower mean survival probability is associated with higher mean handling aggression), within the population, the patterns of covariance seem to contradict the pace-of-life predictions. Although the support for a positive directional selection was weaker in E-Muro according to AICc (Tableau 5.3), a similar pattern emerges. At the metapopulation level, E-Muro is the population with the highest mean survival probability and the lowest mean handling aggression score, which is in accordance with the pace-of-life predictions, but within E-Muro individuals with a high handling aggression score had a higher survival probability. In E-Pirio, individuals with extreme handling aggression phenotypes had the higher survival probability. In contrast, at the metapopulation level, E-Pirio have a higher mean survival probability and a lower mean handling aggression score that D-Muro. Further investigations are needed to clarify the causes of these contrasted covariances patterns. These conflicting relationships between survival probability and handling aggression may also indicate that past selection pressures shaping the divergence of pace-of-life across deciduous and evergreen habitat patches differ from the current selection pressures measured in the present study.

Results from the multivariate analysis also revealed conflicting covariance patterns among hierarchical level of variation but at the within population level this time when we partitioned variance between the among- and within-individual levels of variation. For instance, in D-Muro we found a positive covariance at the among-female level between handling aggression and annual fledgling number, but a negative covariance between the two traits at the within-individual level (Fig. 5.3, Tableau S5.7). In short, females with higher handling aggression had overall more fledglings yet they displayed lower handling aggression in years when they had more fledglings. Similar opposing covariance patterns were observed for male handling aggression and offspring body mass in E-Pirio (Fig. 5.3, Tableau S5.7). These opposed covariance patterns among the hierarchical levels of variation within the populations could explain why we could not find strong selection gradients on traits at the phenotypic level when running classical phenotypic selection analyses (Stinchcombe et al. 2002; Brommer et al. 2014; Araya-Ajoy et al. 2016; Fig. 5.2 and 5.3). We attribute the within-individual covariance to correlated plastic response of the two traits to the same environmental factors or to stochastic events and the among-individual covariance to permanent environmental effects that affect both traits in the same direction and/or to additive genetic covariance (Dingemanse and Dochtermann 2012; Brommer 2013). A response to selection and an evolutionary change are expected only if the covariance between personality traits and fitness represents genetic covariances (Price et al. 1988; Lynch and Walsh 1998; Stinchcombe et al. 2002; Kruuk et al. 2003). If the observed between-individual covariance patterns are underpinned by genetic covariance, our present selection estimates predict an evolution towards higher handling aggression in D-Muro females and in E-Pirio males. Exploring the heritability of handling aggression for breeding birds and its genetic covariance with different fitness proxies would thus be an important next step in our study of personality evolution in this system.

Overall, the contrasting covariance patterns among levels of variation (among-population, within population, among-individual and within-individual) suggests that factors that shaped the covariance of traits at each hierarchical level may differ. Exploring the mechanistic pathway underlying the covariance between the handling aggression phenotype and fitness proxies should shed light on the causes of these contrasting covariance. In addition, these results suggest that more investigations on the role of handling aggression in mediating life-history strategies in these populations are needed.

5.5.5 Conclusion

Our study suggests that heterogeneous ecological conditions generate divergent selection patterns for handling aggression in Mediterranean blue tit populations, and that these contrasting selection patterns could be in part responsible for the observed phenotypic and genetic differentiation of these populations. Past investigations in these populations also revealed contrasting selection pressures as well as phenotypic and genetic differentiation for life-history and morphological traits (Blondel et al. 1999; Dubuc-Messier et al. Chap. 3, Charmantier et al. 2016). Taken together, studies conducted so far suggest that these Corsican blue tit populations are showing adaptations to their local ecological conditions for a variety of traits despite their spatial proximity and the connecting gene flow (Charmantier et al. 2016; Szulkin et al. 2016).

5.6 Acknowledgements

We thank the landowners for permission to work on their property. We also thank Christophe De Franceschi and the numerous field assistants for their precious work in the field, particularly Virginie Journeau, Marc-Olivier Beausoleil, Catherine Goeffroy, Karine Dubois, Simon Côté-Bougouin and Raphaëlle Mercier-Gauthier.

5.7 Supplementary materials

Adult handling aggression

The adult handling aggression trials were performed within two minutes after capture, directly after removing the bird from the trap and prior to any other manipulation. The handler held the bird in the upright position, head up, with its back facing the handler. He held the bird with one hand and placed the bird's legs between his forefinger, his middle finger and his thumb to let the bird free to move its tails and wings. The handler pointed the forefinger of his other hand at a spot about 2 to 3 cm in front of the bird's beak and noted if the bird struck at his finger, and the position of its wings and tail. After two seconds in this position, the handler moved his forefinger towards the bird's beak two or three times and recorded its reaction. The score ranged from 0 (the bird shows no reaction) to 3 (the bird spontaneously strikes the handler's fingers and spreads its wings and tail). The scoring protocol is reported in detail in Table S1. The entire test lasted less than a minute.

Tableau S5.1Blue tit handling aggression scale for adult and juveniles.

Score	Wings spread	Tail feathers spread	Bird strikes fingers
0	No	No	No
1	No	No	Yes, but only if provoked
2	No	Yes	Yes, spontaneously
3	Yes	Yes	Yes, spontaneously

When the bird displayed one reaction specific to one score and another reaction specific to another score, it received an average score between the two. For example, a bird that struck without any provocation (score 2) but did not have its wings and tail feathers spread (score 1) would be scored as 1.5.

Tableau S5.2 Model selection for survival and recapture probabilities for the long-term (1999-2015) data set of breeding blue tits in three Corsican populations (France). Models are ranked according to QAICc values, and only the four best models (i.e. lowest QAICc) are presented for each population.

	Model	# Ind. Par.	Deviance	QAICc	Delta QAICc
D-Muro					
Recapture					
	Constant	19	3428.7825	2419.0989	0
	Year	34	3409.9743	2436.0377	16.9388
	Year + Age	35	3409.8495	2437.951	18.8521
	Year + Sex	35	3409.9553	2438.0245	18.9256
Survival					
	Year	17	3430.7759	2416.4832	0
	Year + Age	18	3428.84	2417.1389	0.6557
	Year + Sex	18	3430.6172	2418.373	1.8898
	Year + Sex + Age	19	3428.7825	2419.0989	2.6157
E-Muro					
Recapture					
	Constant	19	1972.3347	1426.9681	0
	Year	34	1946.1236	1438.5095	11.5414
	Year + Age	35	1945.0452	1439.7501	12.782
	Year + Sex	35	1945.3863	1439.9904	13.0223
Survival					
	Constant	2	1993.6084	1407.9496	0
	Year + Sex+Age	19	1972.3347	1426.9681	19.0185
	Year + Sex	18	1976.2561	1427.7296	19.78
	Year	17	1982.3845	1430.0454	22.0958
E-Pirio					
Recapture					
	Constant	19	3251.3163	2428.6737	0
	Year + Sex	35	3217.288	2435.653	6.9793
	Year + Sex + Age	36	3216.9827	2437.4284	8.7547
	Year	34	3237.7859	2448.7249	20.0512
Survival					
	Year + Sex	18	3251.5608	2426.8535	0
	Year + Sex + Age	19	3251.3163	2428.6737	1.8202
	Year	17	3256.9381	2428.8074	1.9539
	Constant	2	3364.0957	2477.5998	50.7463

Tableau S5.3 Model selection for recapture probabilities in relation to year, age, sex and handling aggression (HA_i) of breeding blue tits in three Corsican populations (France; 2011to 2015). Models are ranked according to QAICc values, and only the five best models (i.e. lowest QAICc) are presented for each population.

Models	# Id. Par.	Deviance	QAICc	Delta QAICc
D-Muro				
Constant	9	767.6286	785.9014	0.000
Year	12	764.1975	788.6723	2.771
Year + HA_i	13	763.9279	790.4828	4.581
Year + HA_i + HA_i^2	14	763.9117	792.5529	6.6515
Year + Age + HA_i + HA_i^2	15	763.2394	793.9733	8.0719
E-Muro				
Constant	9	553.4416	571.8602	0.000
Year + Age + Sex * HA_i + Sex * HA_i^2	18	534.9642	572.5889	0.727
Year + Sex * HA_i + Sex * HA_i^2	17	538.9114	574.3617	2.450
Year	12	550.4199	575.1506	3.280
E-Pirio				
Year + Age + Age * HA_i + Age * HA_i^2	17	732.1374	751.4144	0.000
Year + Age + HA_i +HA_i^2	15	737.8584	752.7858	1.371
Year + Age + HA_i	14	741.1411	753.8952	2.481
Year + Age + Sex + HA_i + HA_i^2	16	737.6186	754.6607	3.246

Survival probability was kept constant during model selection and was modeled as a function of the additive effect of time, sex, age, and the linear and quadratic effects of HA_i and HA_i^2 (see main text for details about model sélection procedure). HA_i represents the BLUP of an individual derived from a mixed model on handling aggression scores repeated over an individual's lifetime.

Tableau S5.4 Estimates of survival and recapture rates in relation to handling agression on a logit scale, with their 95% confidence intervals (CI) of breeding blue tits in three Corsican populations (France; 2011 to 2015).

Population / Parameters	Estimates	LCI	UCI
D-Muro			
Recapture			
Constant	1.720	1.118	2.322
Survival			
2011-2012	-0.813	-1.273	-0.353
2012-2013	-0.615	-1.059	-0.171
2013-2014	-0.362	-0.853	0.129
2014-2015	-0.896	-1.385	-0.408
Sex: Male	0.389	0.014	0.763
HA_i	0.807	0.172	1.442
HA_i^2	2.667	0.982	4.352
E-Muro			
Recapture			
Constant	0.840	0.739	0.907
Survival			
Constant	0.538	0.479	0.596
HA_i	0.548	0.372	0.712
E-Pirio			
Recapture			
2012	7.086	3.014	11.158
2013	7.908	3.863	11.953
2014	7.001	3.096	10.905
2015	6.078	2.210	9.946
Age: Adult	-6.125	-10.034	-2.216
Juv.: HA_i	-30.386	-39.231	-21.541
Adult: HA_i	-1.198	-2.455	0.060
Juv.: HA_i^2	36.044	35.155	36.933
Adult: HA_i^2	1.837	-0.708	4.381
Survival			
2011-2012	-0.099	-0.590	0.391
2012-2013	-0.264	-0.713	0.185
2013-2014	0.452	-0.185	1.088
2014-2015	0.854	0.094	1.615
HA_i	0.779	-0.042	1.601
HA_i^2	3.764	1.655	5.873

Results are derived from the model with the lowest QACIc (see Tables 5.2 and S5.3); juveniles (*versus* adults) and females (*versus* males) are the references. HA_i and HA_i^2 represents BLUPs of a mixed model on repeated individual values of handling aggression.

Tableau S5.5 Model selection for selection on handling aggression using annual number of fledglings as a fitness proxy in breeding blue tits from three Corsican populations (France; 2011-2015). Models were ranked according to their AICc value, and only the four best models (i.e. lowest AICc) are presented for each population.

Models / Population	AICc	Delta AICc
D-Muro		
$HA_i f + HA_i^2 f + HA_i m$	1203.61	0
$HA_i f + HA_i m$	1204.74	1.13
$HA_i f + HA_i^2 f + HA_i m + HA_i^2 m$	1204.86	1.25
$HA_i f + HA_i m + HA_i^2 m$	1205.85	2.23
E-Muro		
$HA_i f + mHA_i$	790.50	0
$HA_i f + HA_i m + HA_i^2 m$	829.36	38.86
$HA_i f + HA_i^2 f + HA_i m$	830.78	40.29
$HA_i f + HA_i^2 f + HA_i m + HA_i^2 m$	831.46	40.96
E-Pirio		
$HA_i f + HA_i m$	875.01	0
$HA_i f + HA_i^2 f + HA_i m$	876.45	1.44
$HA_i f + HA_i m + HA_i^2 m$	876.92	1.91
$HA_i f + HA_i^2 f + HA_i m + HA_i^2 m$	878.57	3.56

All models included year, laying date, and laying date^2 as fixed effect, and female and male identity as random effects. Models including interactions between year and HA_i and HA_i^2 and interactions between female and male HA_i and HA_i^2 had lower fit than these models and thus the results are not shown. HA_i represents the BLUP of an individual derived from a mixed model on handling aggression scores repeated over an individual's lifetime.

Tableau S5.6 Model selection for selection on handling aggression using annual mean fledgling body mass as a fitness proxy in breeding blue tits from three Corsican populations (France; 2011-2015). Models are ranked according to their AICc values, and only the four best models (i.e. lowest AICs) are presented for each population.

Models / Population	AICc	Delta AICc
D-Muro		
$HA_i f + HA_i m$	382.41	0
$HA_i m$	388.20	5.79
neither $HA_i m$ nor $HA_i f$	388.39	5.98
$HA_i m + HA_i m + HA_i^2 m$	388.50	6.08
E-Muro		
neither $HA_i m$ nor $HA_i f$	279.52	0
$HA_i f + HA_i m$	283.37	3.85
$HA_i m$	284.82	5.30
$HA_i f + HA_i m + HA_i^2 m$	288.30	8.77
E-Pirio		
$HA_i f$	347.98	0
$HA_i f + HA_i m$	348.25	0.27
$HA_i m + HA_i^2 m$	352.26	4.28
$HA_i f + HA_i^2 f + HA_i^2 m$	352.65	4.67

These models included year, laying date, and laying date^2 as fixed effects, and female and male identity as random effects. Models including interactions between year and HA_i and HA_i^2 and interactions between females and males HA_i and HA_i^2 had lower fit than these models and thus the results are not shown. HA_i represents the BLUP of an individual derived from a mixed model on handling aggression scores repeated over an individual's lifetime.

Tableau S5.7 Correlations (below diagonal) between female and male handling aggression (HAf and HAm), laying date (LD), relative annual fledgling number (Nb), and relative annual mean fledgling body mass (BM), at the phenotypic, among-female, among-male, and residuals levels (within-individual level; posterior mode and (95% CI)) and variance components (diagonal) for breeding blue tits in Corsica (France; 2011-2015) for a) D-Muro, b) E-Muro and c) E-Pirio populations.

a) D-Muro

	HAf	HAm	LD	Nb	BM
Phenotypic					
HAf	1.022 (0.852 ; 1.241)				
HAm	0.108 (-0.049 ; 0.278)	0.898 (0.741 ; 1.090)			
LD	-0.030 (-0.200 ; 0.127)	0.065 (-0.111 ; 0.298)	1.005 (0.857 ; 1.224)		
Nb	-0.174 (-0.355 ; 0.016)	-0.001 (-0.206 ; 0.257)	-0.147 (-0.375 ; 0.113)	0.140 (0.115 ; 0.166)	
BM	0.015 (-0.010 ; 0.038)	0.013 (-0.022 ; 0.044)	**-0.043** **(-0.080 ; -0.008)**	0.023 (-0.013 ; 0.060)	0.003 (0.002 ; 0.003)
Among-females					
HAf	0.301 (0.128 ; 0.515)				
HAm	-0.146 (-0.809 ; 0.823)	0.036 (0.002 ; 0.166)			
LD	**-0.517** **(-0.990 ; -0.070)**	-0.681 (-0.989 ; 0.368)	0.272 (0.083 ; 0.494)		
Nb	**0.686** **(0.317 ; 0.995)**	0.527 (-0.315 ; 0.989)	**-0.973** **(-0.998 ; -0.682)**	0.048 (0.025 ; 0.076)	
BM	0.037 (-0.015 ; 0.088)	-0.045 (-0.104 ; 0.042)	0.015 (-0.045 ; 0.071)	-0.001 (-0.055 ; 0.046)	0.0001 (8.176e-06 ; 0.001)
Among-males					
HAf	0.032 (0.001 ; 0.156)				
HAm	-0.894 (-0.991 ; 0.490)	0.311 (1.103 e-01 ; 0.520)			
LD	-0.739 (-0.979 ; 0.785)	0.497 (-0.482 ; 0.994)	0.025 (0.001 e-03 ; 0.204)		
Nb	-0.785 (-0.983 ; 0.749)	0.868 (-0.469 ; 0.994)	-0.695 (-0.981 ; 0.768)	0.003 (1.818 e-04 ; 0.023)	
BM	0.012 (-0.174 ; 0.228)	-0.006 (-0.217 ; 0.155)	-0.028 (-0.260; 0.155)	-0.008 (-0.201 ; 0.192)	4.79 e-05 (2.491e-06 ; 0.0004)
Residuals					
HAf	0.657 (0.478 ; 0.862)				
HAm	**0.337** **(0.083 ; 0.509)**	0.490 (0.361 ; 0.713)			
LD	0.071 (-0.148 ; 0.287)	0.059 (-0.182 ; 0.284)	0.641 (0.471 ; 0.883)		
Nb	**-0.398** **(-0.579 ; -0.171)**	-0.158 (-0.380 ; 0.119)	-0.074 (-0.270 ; 0.154)	0.077 (0.058 ; 0.105)	
BM	0.008 (-0.028 ; 0.044)	0.031 (-0.010 ; 0.067)	**-0.059** **(-0.094 ; -0.022)**	**0.039** **(0.004 ; 0.074)**	0.002 (0.002 ; 0.003)

b) E-Muro

	HAf	HAm	LD	Nb	BM
Phenotypic					
HAf	1.047 (0.836 ; 1.359)				
HAm	**0.169** **(0.017 ; 0.360)**	0.945 (0.766 ; 1.218)			
LD	0.024 (-0.123 ; 0.169)	-0.145 (-0.373 ; 0.085)	0.935 (0.755 ; 1.186)		
Nb	0.023 (-0.115 ; 0.165)	0.071 (-0.174 ; 0.301)	**-0.287** **(-0.431 ; -0.128)**	0.204 (0.167 ; 0.262)	
BM	-0.023 (-0.176 ; 0.025)	0.010 (-0.058 ; 0.093)	-0.041 (-0.148 ; 0.011)	-0.005 (-0.055 ; 0.046)	0.004 (0.003 ; 0.005)
Among-females					
HAf	0.327 (0.045 ; 0.625)				
HAm	-0.885 (-0.991 ; 0.698)	0.021 (0.001 ; 0.187)			
LD	0.915 (-0.686 ; 0.993)	-0.888 (-0.993 ; 0.619)	0.019 (0.001 ; 0.176)		
Nb	0.785 (-0.837 ; 0.976)	-0.597 (-0.947 ; 0.863)	-0.659 (-0.952 ; 0.865)	0.004 (0.0002 ; 0.027)	
BM	-0.157 (-0.709 ; 0.134)	0.080 (-0.461 ; 0.636)	-0.172 (-0.751 ; 0.865)	-0.077 (-0.556 ; 0.509)	0.001 (4.426e-05 ; 0.002)
Among-males					
HAf	0.037 (0.002 ; 0.298)				
HAm	0.727 (-0.858 ; 0.966)	0.035 (0.002 ; 0.245)			
LD	0.913 (-0.770 ; 0.993)	-0.918 (-0.995 ; 0.742)	0.167 (0.003 ; 0.447)		
Nb	-0.418 (-0.981 ; 0.803)	0.334 (-0.833; 0.983)	-0.149 (-0.799 ; 0.978)	0.046 (0.002e-03 ; 0.104)	
BM	-0.035 (-0.184; 0.091)	-0.002 (-0.138; 0.145)	-0.023 (-0.176 ; 0.104)	-0.026 (-0.163 ; 0.104)	0.001 (4.838e-06 ; 0.001)
Residuals					
HAf	0.585 (0.364 ; 0.943)				
HAm	**0.399** **(0.129 ; 0.579)**	0.802 (0.587 ; 1.062)			
LD	-0.070 (-0.398 ; 0.218)	-0.081 (-0.292 ; 0.176)	0.673 (0.441 ; 0.936)		
Nb	0.058 (-0.199 ; 0.353)	0.083 (-0.169 ; 0.300)	**-0.422** **(-0.612 ; -0.143)**	0.146 (0.099 ; 0.2050)	
BM	0.02 (-0.018 ; 0.068)	0.004 (-0.029 ; 0.038)	-0.034 (-0.082 ; 0.016)	0.010 (-0.032 ; 0.051)	0.002 (0.001 ; 0.003)

c) E-Pirio

	HAf	HAm	LD	Nb	BM
Phenotypic					
HAf	0.420 (0.968 ; 1.524)				
HAm	0.146 (-0.022 ; 0.358)	0.033 (0.785 ; 1.245)			
LD	-0.010 (-0.195 ; 0.179)	-0.084 (-0.330 ; 0.131)	0.084 (0.799 ; 1.199)		
Nb	-0.036 (-0.207 ; 0.145)	-0.025 (-0.281 ; 0.222)	-0.106 (-0.329 ; 0.190)	0.004 (0.205 ; 0.311)	
BM	-0.020 (-0.119 ; 0.020)	0.008 (-0.035 ; 0.115)	-0.062 (-0.143 ; 0.017)	-0.013 (-0.092 ; 0.069)	0.0003 (0.004 ; 0.007)
Among-females					
HAf	0.420 (0.149 ; 0.763)				
HAm	-0.766 (-0.994 ; 0.424)	0.033 (0.001 ; 0.174)			
LD	**0.966** **(0.208 ; 0.997)**	-0.891 (-0.992 ; 0.472)	0.084 (5.952e-06 ; 0.31)		
Nb	0.010 (-0.976 ; 0.814)	0.801 (-0.827 ; 0.978)	-0.421 (-0.964 ; 0.846)	0.004 (0.0003 ; 0.055)	
BM	-0.087 (-0.417 ; 0.079)	0.086 (-0.155 ; 0.468)	-0.096 (-0.480 ; 0.846)	-0.023 (-0.335 ; 0.311)	0.0002 (1.192e-05 ; 0.002)
Among-males					
HAf	0.027 (0.001 ; 0.213)				
HAm	-0.208 (-0.990 ; 0.659)	0.401 (0.188 ; 0.712)			
LD	0.739 (-0.813 ; 0.975)	-0.457 (-0.973 ; 0.752)	0.019 (0.001 ; 0.156)		
Nb	-0.702 (-0.946 ; 0.873)	0.272 (-0.788 ; 0.982)	-0.830 (-0.982 ; 0.798)	0.004 (0.0003 ; 0.040)	
BM	-0.130 (-0.574 ; 0.259)	0.156 (-0.002; 0.607)	0.044 (-0.416 ; 0.428)	-0.005 (-0.431 ; 0.429)	0.002 (0.0002 ; 0.002)
Residuals					
HAf	0.669 (0.458 ; 0.954)				
HAm	**0.462** **(0.196 ; 0.664)**	0.490 (0.325 ; 0.688)			
LD	-0.179 (-0.396; 0.032)	-0.059 (-0.268 ; 0.174)	0.807 (0.628 ; 1.026)		
Nb	-0.049 (-0.274 ; 0.196)	-0.078 (-0.326 ; 0.136)	-0.043 (-0.243 ; 0.152)	0.218 (0.166 ; 0.279)	
BM	0.010 (-0.022 ; 0.043)	**-0.040** **(-0.072 ; -0.011)**	**-0.061** **(-0.096 ; -0.031)**	-0.015 (-0.048 ; 0.016)	0.003 (0.002 ; 0.005)

Estimates in bold have 95% CI that do not include zero.

Tableau S5.8 Proportion of total phenotypic variances (posterior mode and 95% CI) attributable to female and male identity, to residuals and observer identity and for female (HAf) and male (HAm) handling aggression, laying date (LD), relative annual fledgling number (Nb), and annual mean fledgling body mass (BM), in breeding blue tits from the three Corsican populations (France; 2011-2015).

	D-Muro			E-Muro			E-Pirio		
Trait	Posterior mode	Lower CI	Upper CI	Posterior mode	Lower CI	Upper CI	Posterior mode	Lower CI	Upper CI
	Among-females variance								
HAf	0.250	0.105	0.404	0.208	0.043	0.393	0.367	0.149	0.550
HAm	0.027	0.001	0.147	0.020	0.001	0.158	0.026	0.001	0.162
LD	0.258	0.091	0.450	0.020	0.001	0.177	0.082	0.005	0.230
Nb	0.354	0.198	0.499	0.011	0.001	0.123	0.023	0.001	0.208
BM	0.073	0.004	0.218	0.286	0.036	0.521	0.074	0.003	0.292
	Among-males variance								
HAf	0.015	0.001	0.123	0.033	0.001	0.188	0.020	0.001	0.164
HAm	0.279	0.103	0.447	0.279	0.102	0.447	0.423	0.208	0.601
LD	0.035	0.002	0.192	0.035	0.002	0.192	0.015	0.001	0.152
Nb	0.024	0.001	0.157	0.212	0.013	0.453	0.019	0.001	0.152
BM	0.016	0.001	0.136	0.055	0.0013	0.296	0.167	0.046	0.358
	Residual variance								
HAf	0.521	0.354	0.710	0.402	0.177	0.699	0.550	0.354	0.757
HAm	0.470	0.287	0.667	0.764	0.491	0.905	0.457	0.296	0.654
LD	0.651	0.454	0.845	0.774	0.483	0.950	0.859	0.682	0.963
Nb	0.581	0.409	0.745	0.741	0.494	0.944	0.899	0.709	0.985
BM	0.876	0.704	0.977	0.599	0.349	0.858	0.705	0.468	0.864
	Observer variance								
HAf	0.119	0.027	0.357	0.221	0.066	0.519	0.002	0.0002	0.096
HAm	0.153	0.033	0.386	0.095	0.001	0.322	0.002	0.0003	0.143

Variance component are extracted from a multivariate models performed in a Bayesian framework; see main text for details.

Tableau S5.9 Model selection for selection acting on fledglings' HA via recruitment probability in three Corsican blue tit populations (France; 2013-2014). The best model was selected according to AICc values. We present the four best models for each population.

Models / Population	AICc	Delta AICc
D-Muro		
HA * Cohort + HA^2 + Body mass	215.67	0.00
HA * Cohort + HA^2 * Cohort + Body	216.32	0.65
HA + Body mass + Cohort	217.03	1.36
HA + HA^2 + Body mass	217.44	1.77
E-Muro		
HA	166.51	0.00
HA + HA^2	168.51	2.00
HA + Body mass + Cohort	168.54	2.04
HA + HA^2 + Body mass	170.15	3.64
E-Pirio		
HA + HA^2 + Body mass	203.00	0.00
HA + HA^2 + Body mass + Cohort	203.74	0.74
HA + HA^2	204.37	1.37
HA + Body mass + Cohort	205.36	2.36

Tableau S5.10 Standardized selection gradients for fledglings' HA (linear and quadratic) in D-Muro Corsican blue tit population (France; 2013-2014) for each cohort and 95% confidence intervals.

	Cohort 2013	Cohort 2014
D-Muro		
HA	0.590 (-0.113; 1.271)	-0.297 (-0.788; 0.194)
HA^2	-1.02 (-2.591; 0.560)	0.142 (-0.827; 1.099)

These gradients were extracted from a linear mixed model using the relative recruitment probability of each fledgling for each cohort as response variable and the fixed effect structure presented in the model with the lowest AICc (Table S5.9).

CHAPITRE 6
CONCLUSIONS

6.1 Contributions et conclusions

La compréhension des mécanismes qui façonnent la diversité intraspécifique et plus particulièrement la divergence des populations sont des objectifs fondamentaux en écologie évolutive. Les études menées dans les dernières décennies nous ont permis de saisir l'importance de l'hétérogénéité environnementale pour la création de la diversité génétique et phénotypique intraspécifique et la divergence des populations (Endler 1986; Siepielski et al. 2009; Siepielski et al. 2013; Wang et Bradburd 2014). Néanmoins, il reste plusieurs zones d'ombre, notamment le rôle des flux géniques et l'importance relative de la plasticité phénotypique et des effets génétiques pour la divergence des populations à fine échelle spatiale (Richarson et al. 2014). De plus, ce n'est que récemment que les scientifiques se sont intéressés aux mécanismes qui pourraient générer une variation intraspécifique de comportements et si cette variation pouvait être adaptative (Sih et al. 2004; Réale et al. 2007). Ainsi, nous connaissons encore très peu l'importance relative des effets plastiques et génétiques pour la diversité intraspécifique de comportements.

L'objectif général de ce projet était de contribuer à améliorer notre compréhension des facteurs qui peuvent générer une variation intraspécifique de comportements. Plus spécifiquement, notre objectif était de déterminer si une forte variation de conditions écologiques à fine échelle spatiale pouvait mener à une différenciation phénotypique et génétique entre populations pour des traits de personnalité et si cette différenciation pouvait être adaptative.

La Figure 6.1 reprend les types de divergence phénotypique et les principaux processus qui les sous-tendent tels qu'illustré au Chapitre 1 (Fig. 1.1) et présente les chapitres qui les ont abordé. D'abord, aux Chapitres 2 et 4 nous avons montré une divergence de phénotype moyen de personnalité entre des adultes et des jeunes mésanges bleues qui vivent dans des populations situées dans différents types d'habitats. Puis, aux Chapitres 3 et 4, grâce à des expériences de jardins communs et de transfert réciproque de jeunes entre habitats, nous avons trouvé que ces divergences avaient une base génétique. Les résultats des Chapitres 3 et 5 ont indiqué que ces divergences ne sont pas le fruit de processus neutres tel que la dérive génique (comparaison Q_{st} - F_{st}; Chapitre 3) et que des pressions de sélection propres à chaque habitat et population pourraient plutôt en être à l'origine (Chapitre 5). De plus, les résultats du transfert réciproque de jeunes (Chapitre 4) et les nombreuses études parues sur la personnalité depuis une quinzaine d'années (revues dans van Oers et Sinn 2011; Quinn et al. 2009;

Brommer et Kluen 2012) suggèrent que les phénotypes de personnalité de ces mésanges sont héritables et pourraient donc répondre à la sélection, évoluer et former des adaptations locales.

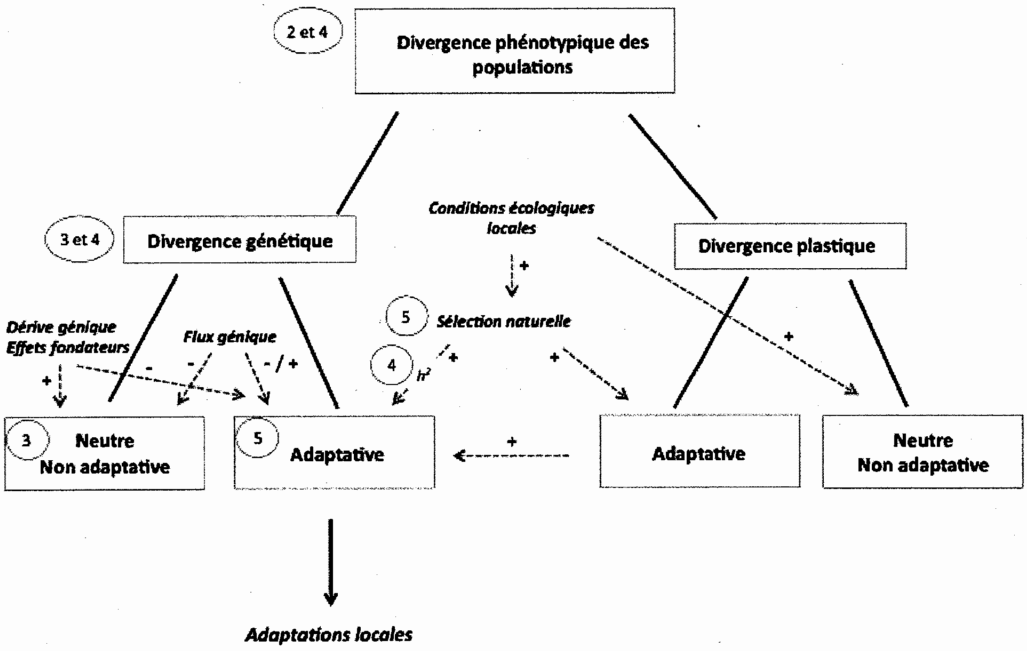

Figure 6.1 Illustration des types de divergences phénotypiques et des principaux processus qui peuvent les causer les chapitres qui ont abordé ces aspects. Cette figure est similaire à la Fig. 1.1.

Les causes écologiques de la divergence de ces populations ne sont pas connues pour le moment et feront sans doute l'objet de plusieurs études futures. Par contre, les patrons de divergences observés dans ces populations pour les traits de personnalité et pour des traits d'histoire de vie (Charmantier et al. 2016) sont en accord avec les prédictions de l'hypothèse du syndrome de train de vie (Réale et al. 2010). Selon cette hypothèse et plusieurs modèles théoriques et études empiriques, une stratégie d'histoire de vie dite « rapide », c'est-à-dire une survie limitée et un investissement massif dans la reproduction immédiate, devrait être associée à des comportements plus risqués si ces comportements maximisent la reproduction immédiate (Wolf et al. 2007; Biro et Stamps 2008; Réale et al. 2010; Nicolaus et al. 2012; Hall et al. 2015; Nicolaus et al. 2015; Sih et al. 2015). Nous avons trouvé que les mésanges qui habitent l'habitat dominé par le chêne blanc (D-Muro) ont en moyenne une probabilité de survie adulte qui est la plus faible et sont des mésanges qui investissent davantage dans la reproduction immédiate comparativement aux mésanges des habitats de chênes verts (E-Muro et E-

Pirio). Les mésanges de D-Muro ont également en moyenne un patron d'exploration plus rapide et une agressivité en main plus élevée, deux phénotypes de personnalité généralement associés à un plus grand niveau de prise de risques (Réale et al. 2010; Nicolaus et al. 2012). Ainsi, en accord avec le syndrome de train de vie, il semble que les divergences observées pourraient être le résultat de la coévolution d'un ensemble de traits formant un train de vie rapide ou lent selon conditions écologiques locales.

En somme, nos résultats suggèrent que ces populations montrent des divergences phénotypiques qui ont une base génétique et qui pourraient être adaptatives. Ainsi, cette thèse démontre que l'hétérogénéité des conditions écologiques à fine échelle spatiale peut générer des différences phénotypiques et génétiques de comportements entre des populations même si elles sont connectées par un flux génique.

6.2 Perspectives

Les résultats de cette thèse nous apportent d'importantes informations sur l'importance de l'hétérogénéité spatiale pour la divergence des populations pour des traits comportementaux. Néanmoins, à cause de contraintes logistiques cette thèse n'a pu répondre à toutes les questions pertinentes à ce sujet d'étude et nos résultats soulèvent de nombreuses questions qui n'ont pu être abordées ici, mais qui feront, je l'espère, l'objet de futures études.

Premièrement, on considère habituellement qu'il y a présence d'adaptations locales lorsque les individus ont une meilleure valeur adaptative dans leur habitat natal que dans un autre habitat aux caractéristiques écologiques différentes (Kawecki et Ebert 2004; Hereford 2009). Ainsi, la démonstration complète d'une adaptation locale nécessiterait de mesurer la valeur adaptative d'oiseaux du chêne blanc placés en chêne vert, et inversement, ce qui serait difficile à accomplir avec des animaux aussi mobiles que des oiseaux. Une alternative intéressante pour le futur serait d'utiliser de nouvelles techniques développées en génomique afin d'identifier des régions du génome qui diffèrent entre les habitats et qui portent la signature de la sélection (Storz 2005; Savolainen et al. 2013).

Deuxièmement, pour qu'un trait puisse répondre à la sélection, évoluer et former des adaptations locales, il doit être héritable. Il est donc primordial de déterminer l'héritabilité des traits de personnalité dans notre système d'étude. Les résultats de l'expérience de transferts réciproques des jeunes (Chapitre 4) suggèrent que les phénotypes de personnalité des jeunes mésanges bleues sont héritables. De plus, les études réalisées chez d'autres espèces et chez la mésange bleue (van Oers et Sinn 2011; Brommer et Kluen 2012; Class et al. 2014) suggèrent qu'il est fort probable que le phénotype de personnalité des mésanges adultes soit également héritable. Néanmoins, les estimations d'héritabilité peuvent changer en fonction des conditions environnementales (Charmantier et Garant 2005) et des effets d'environnement précoce (de la ponte à 3 jours) auraient pu influencer nos estimations d'héritabilité chez les jeunes (Kruuk et Hadfield 2007; Brommer et Kluen 2012). Il est donc important que les études futures sur ce système confirment l'héritabilité des traits étudiés. Le modèle statistique le plus couramment utilisé actuellement pour estimer l'héritabilité des traits en milieu naturel est le « modèle animal » (Lynch et Walsh 1998; Kruuk 2004; Wilson et al. 2010). Il utilise le pedigree de la population pour estimer la covariance entre le phénotype de différentes paires d'individus et leur degré d'apparentement. La quantité d'individus étudiés jusqu'à présent n'était pas suffisante pour faire ces analyses dans le cadre de cette thèse, mais pourrait l'être prochainement.

Troisièmement, un des aspects importants de l'hypothèse du syndrome de train de vie est que les traits de personnalité pourraient avoir coévolué avec les traits d'histoire de vie s'ils interviennent dans la manière dont les individus négocient les compromis d'histoire de vie, telle que l'investissement dans la reproduction immédiate et la reproduction future (Wolf et al. 2007; Réale et al. 2010; Sih et al. 2015). Les compromis d'histoire de vie se négocient au niveau des individus. Bien que les divergences observées soient en accord avec l'hypothèse du syndrome de train de vie au niveau des moyennes populationnelles, les associations entre traits au niveau des individus ne sont pas en accord avec les prédictions du syndrome de train de vie (Chapitre 5). De plus, nous ne connaissons pas pour l'instant si les traits de personnalité étudiés interviennent dans les compromis d'histoire de vie des individus. Des études plus approfondies sur le lien entre le phénotype de personnalité étudié et différentes facettes de l'écologie de la mésange bleue sont nécessaires pour y voir plus clair. Plusieurs études réalisées chez la mésange charbonnière (*Parus major*) ont suggéré que les phénotypes de personnalité ont un rôle important à jouer dans l'investissement dans les soins parentaux (Mutzel et al. 2013a; Class et al. 2014), l'acquisition et la défense d'un territoire de reproduction (Verbeek et al. 1994; Dingemanse et de Goede 2004; Araya-Ajoy et Dingemanse 2015) et la reproduction hors couple (Araya-Ajoy et al. 2016). Il est donc possible que les traits de personnalité étudiés interviennent dans les compromis d'histoire de vie chez la mésange bleue par ces aspects de leur écologie. Il serait intéressant que de futures études sur ce système s'intéressent à ces aspects. Par ailleurs, on peut s'attendre à ce que la coévolution entre les phénotypes de personnalité et les stratégies d'histoire de vie dépendent des pressions de sélection locales et donc varie selon les populations (Réale et al. 2010). Les populations étudiées dans le cadre de cette thèse sont localisées à l'extrême sud de l'aire de distribution de la mésange bleue. Il serait donc intéressant d'inclure des populations localisées à différents endroits dans leur aire de distribution et d'établir des collaborations avec des équipes de recherche dans différents pays d'Europe.

Quatrièmement, des études suggèrent que des divergences génétiques sont possibles malgré un flux de gènes si les pressions de sélection sont fortes et que la dispersion des individus entre les habitats et les populations est non aléatoire (Garant et al. 2007; Edelaar et Bolnick 2012; Richardson et al. 2014). Les résultats de cette thèse et les études précédentes menées chez ces populations montrent qu'il y a effectivement différents régimes de sélection dans chacune des populations étudiées (Charmantier et al. 2016). Plusieurs études ont montré que la personnalité des individus pourrait intervenir dans leur patron de dispersion (revue par Cote et al 2010). Néanmoins, les patrons de dispersion des mésanges entre ces populations ne sont pas encore connus. Une étude en cours (de Franceschi et al. in prep) pourra nous renseigner sur la distance de dispersion des jeunes mésanges nées dans nos stations d'études et sur son lien avec leur phénotype de personnalité. Il n'en reste pas moins que l'étude des patrons précis de dispersion des petits passereaux à l'aide par exemple d'émetteurs ou GPS est difficile, à cause notamment de la taille de l'organisme, des risques de prédation et des distances parcourues. Une autre possibilité pour des études futures sur ce sujet serait de recourir à des méthodes de mesures indirectes par exemple en étudiant la signature isotopique de l'habitat d'origine dans les plumes des mésanges (Charmantier et al. 2014).

Cinquièmement, nous avons montré que les divergences phénotypiques entre ces populations ont une base génétique pour plusieurs traits (Chapitre 3 et Chapitre 4). Néanmoins, la plasticité et les effets génétiques ne sont pas nécessairement mutuellement exclusifs et un trait peut être simultanément influencé par les deux processus. D'ailleurs, la forte variation annuelle de phénotype moyen de personnalité des adultes (Chapitre 2) et les divergences génétiques plus fortes que les divergences phénotypiques (fréquence cardiaque sous-contrainte, agressivité en main des jeunes) suggèrent que les traits étudiés sont également sujets à des variations de type plastique. En outre, un nombre croissant d'études suggèrent que la plasticité phénotypique peut elle-même varier selon les populations, avoir une base génétique et représenter une adaptation aux conditions écologiques locales (Nussey et al. 2007; Porlier et al. 2012b). Porlier et al. (2012b) ont d'ailleurs montré qu'il existe une variation interindividuelle de plasticité dans la date de ponte dans ces populations de mésanges et que certaines populations sont composées d'individus plus plastiques que d'autres. De plus, certaines études ont suggéré que la plasticité phénotypique pourrait être reliée aux phénotypes de personnalité des individus (Dingemanse et al. 2010). Ainsi, une avenue intéressante de recherche pour le futur serait de déterminer s'il existe des variations interpopulationnelles et interindividuelles de plasticité pour les phénotypes de personnalité dans ce système d'étude, si ces variations ont une base génétique, si elles impliquent plusieurs types de traits dont des traits d'histoire de vie et si les patrons de plasticité sont soumis à la sélection.

Finalement, plusieurs études ont montré que les traits de personnalité peuvent être corrélés entre eux au niveau phénotypique et génétique pour former des syndromes comportementaux (Sih et al. 2004; Dochtermann 2011; Brommer et Kluen 2012; Dochtermann et Dingemanse 2013). Les syndromes comportementaux concernent les corrélations entre les traits de personnalité qui ont lieu au niveau interindividuel, c'est-à-dire au niveau de la composante répétable des phénotypes de personnalité (Dingemanse et Dochtermann 2012). Pour bien mettre en évidence les syndromes comportementaux, il est préférable d'utiliser de nombreux tests répétés par individus et des modèles statistiques mixtes multivariés (Brommer 2013; Dingemanse et Dochtermann 2013). L'étude des syndromes comportementaux n'était pas l'objectif de cette thèse, et la taille de l'échantillon récolté n'était pas suffisante pour bien départager la composante interindividuelle de la composante intraindividuelle (résiduelle) dans chaque population. Néanmoins, ce type d'analyse devrait être réalisable prochainement. En plus des syndromes comportementaux, les données récoltées dans les prochaines années pourraient nous permettre de déterminer la covariance génétique entre les traits de personnalité, mais également entre des traits de personnalité et d'autres types de traits comme des traits d'histoires de vie. Les matrices de covariances génétiques ainsi générées pourraient nous renseigner sur les pressions de sélection passées, mais aussi sur d'éventuelles contraintes à l'évolution indépendante des traits dans ces populations (Docthermann et Dingemanse 2013; Brommer 2013).

6.3 Conclusion générale

Cette thèse souligne l'importance de l'hétérogénéité environnementale pour la diversité intraspécifique et montre qu'une divergence phénotypique et génétique adaptative est possible pour des traits comportementaux souvent considérés comme plus plastiques et moins sujets aux divergences génétiques. Nous espérons que les résultats de cette étude stimuleront d'autres équipes de recherche à intégrer une dimension comportementale à leur programme et à développer des stations d'études qui couvrent différentes conditions écologiques à fine échelle spatiale. De plus, les résultats de cette thèse ouvrent la voie à de nombreuses pistes de recherches sur ce système d'étude que je trouve très stimulantes et qui je crois, apporteront beaucoup à l'écologie comportementale et à l'écologie évolutive.

REFERENCES

Abbey-Lee, R. N., Mathot, K. J., et Dingemanse, N. J. (2016). Behavioral and morphological responses to perceived predation risk: a field experiment in passerines. *Behavioral Ecology*, *27*(3), 857- 864. https://doi.org/10.1093/beheco/arv228

Ågren, J., et Schemske, D. W. (2012). Reciprocal transplants demonstrate strong adaptive differentiation of the model organism *Arabidopsis thaliana* in its native range. *New Phytologist*, *194*(4), 1112- 1122. https://doi.org/10.1111/j.1469-8137.2012.04112.x

Araya-Ajoy, Y. G., et Dingemanse, N. J. (2015). Characterizing behavioural « characters »: an evolutionary framework. *Proceedings of the Royal Society B: Biological Sciences*, *281*(1776), 20132645 - 20132645. https://doi.org/10.1098/rspb.2013.2645

Araya-Ajoy, Y. G., Kuhn, S., Mathot, K. J., Mouchet, A., Mutzel, A., Nicolaus, M., Wijmenga, J.J., Kempenaers, B. et Dingemanse, N. J. (2016). Sources of (co)variation in alternative siring routes available to male great tits (*Parus major*). *Evolution*, *70*(10), 2308 - 2321 https://doi.org/10.1111/evo.13024

Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Campbell-Nelson, S., Robertson, K. W., et Ketterson, E. D. (2012). Boldness behavior and stress physiology in a novel urban environment suggest rapid correlated evolutionary adaptation. *Behavioral Ecology*, *23*(5), 960 - 969. https://doi.org/10.1093/beheco/ars059

Atwell, J. W., Cardoso, G. C., Whittaker, D. J., Price, T. D., et Ketterson, E. D. (2014). Hormonal, behavioral, and life-history traits exhibit correlated shifts in relation to population establishment in a novel environment. *The American Naturalist*, *184*(6), E147–E160.

Banbura, J., Lambrechts, M. M., Blondel, J., Perret, P., et Cartan-Son, M. (1999). Food handling time of blue tit chicks: constraints and adaptation to different prey types. *Journal of Avian Biology*, *30*(3), 263. https://doi.org/10.2307/3677352

Bates, D., Mächler, M., Bolker, B.M., et Walker, S.C. (2014). Fitting linear mixed-effects models using lme4., *available at https://cran.r-project.org/web/packages/lme4/vignettes.*

Belgrad, B. A., et Griffen, B. D. (2016). Predator–prey interactions mediated by prey personality and predator hunting mode. *Proceedings of the Royal Society B: Biological Sciences*, *283*(1828), 20160408. https://doi.org/10.1098/rspb.2016.0408

Bell, A. M. (2005). Behavioural differences between individuals et two populations of stickleback (*Gasterosteus aculeatus*): behavioural syndromes. *Journal of Evolutionary Biology*, *18*(2), 464 - 473. https://doi.org/10.1111/j.1420-9101.2004.00817.x

Bell, A. M., Hankison, S. J., et Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, *77*(4), 771 - 783. https: //doi.org/10.1016/ j.anbehav. 2008.12.022

Bell, A. M., et Stamps, J. A. (2004). Development of behavioural differences between individuals and populations of sticklebacks, *Gasterosteus aculeatus*. *Animal Behaviour*, *68*(6), 1339- 1348. https://doi.org/10.1016/j.anbehav.2004.05.007

Bergeron, P., Montiglio, P.-O., Réale, D., Humphries, M. M., Gimenez, O., et Garant, D. (2013). Disruptive viability selection on adult exploratory behaviour in eastern chipmunks. *Journal of*

Evolutionary Biology, *26*(4), 766‑774. https://doi.org/10.1111/jeb.12081

Bergmüller, R., et Taborsky, M. (2010). Animal personality due to social niche specialisation. *Trends in Ecology and Evolution*, *25*(9), 504‑511. https://doi.org/10.1016/j.tree.2010.06.012

Biro, P. A., et Stamps, J. A. (2008). Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, *23*(7), 361‑368. https://doi.org/10.1016/j.tree.2008.04.003

Blanquart, F., Kaltz, O., Nuismer, S. L., et Gandon, S. (2013). A practical guide to measuring local adaptation. *Ecology Letters*, *16*(9), 1195‑1205. https://doi.org/10.1111/ele.12150

Blondel, J., Dias, P. C., Maistre, M., et Lambrechts, M. M. (1999). Selection-bsed biodiversity at a small spatial scale in a low-dispersing insular bird. *Science*, *285*(5432), 1399‑1402.

Blondel, J., Perret, P., Anstett, M.-C., et Thebaud, C. (2002). Evolution of sexual size dimorphism in birds: test of hypotheses using blue tits in contrasted Mediterranean habitats. *Journal of Evolutionary Biology*, *15*(3), 440–450.

Blondel, J., Thomas, D. W., Charmantier, A., Perret, P., Bourgault, P., et Lambrechts, M. M. (2006). A thirty-year study of phenotypic and genetic variation of blue tits in Mediterranean habitat mosaics. *Bioscience*, *56*(8), 661–673.

Boon, A. K., Réale, D., et Boutin, S. (2007). The interaction between personality, offspring fitness and food abundance in North American red squirrels. *Ecology Letters*, *10*(11), 1094‑1104. https://doi.org/10.1111/j.1461-0248.2007.01106.x

Both, C., Dingemanse, N. J., Drent, P. J., et Tinbergen, J. M. (2005). Pairs of extreme avian personalities have highest reproductive success. *Journal of Animal Ecology*, *74*(4), 667‑674. https://doi.org/10.1111/j.1365-2656.2005.00962.x

Bouwhuis, S., Charmantier, A., Verhulst, S., et Sheldon, B. C. (2010). Trans-generational effects on ageing in a wild bird population. *Journal of Evolutionary Biology*, *23*(3), 636‑642. https://doi.org/10.1111/j.1420-9101.2009.01929.x

Bouwhuis, S., Quinn, J. L., Sheldon, B. C., et Verhulst, S. (2013). Personality and basal metabolic rate in a wild bird population. *Oikos*, *123*(1), 56‑62. https://doi.org/10.1111/j.1600-0706.2013.00654.x

Braillet, C., Charmantier, A., Archaux, F., Dos Santos, A., Perret, P., et Lambrechts, M.M. (2002). Two blue tit *Parus caeruleus* populations from Corsica differ in social dominance. *Journal of Avian Biology*, *33*, 446‑450.

Brodie III, E. D., Moore, A. J., et Janzen, F. J. (1995). Visualizing and quantifying natural selection. *Trends in Ecology and Evolution*, *10*(8), 313‑318.

Brommer, J. E. (2013). On between-individual and residual (co)variances in the study of animal personality: are you willing to take the « individual gambit »? *Behavioral Ecology and Sociobiology*, *67*(6), 1027‑1032. https://doi.org/10.1007/s00265-013-1527-4

Brommer, J. E., et Class, B. (2015). The importance of genotype-by-age interactions for the development of repeatable behavior and correlated behaviors over lifetime. *Frontiers in zoology*, *12*(1), 1-13

Brommer, J. E., Karell, P., Ahola, K., et Karstinen, T. (2014). Residual correlations, and not individual properties, determine a nest defense boldness syndrome. *Behavioral Ecology*, *25*(4), 802‑812.

https://doi.org/10.1093/beheco/aru057

Brommer, J. E., et Kluen, E. (2012). Exploring the genetics of nestling personality traits in a wild passerine bird: testing the phenotypic gambit. *Ecology and Evolution*, *2*(12), 3032‑3044. https://doi.org/10.1002/ece3.412

Careau, V., et Garland, T. (2012). Performance, personality, and energetics: correlation, causation, and mechanism. *Physiological and Biochemical Zoology*, *85*(6), 543‑571. https://doi.org/10.1086/666970

Careau, V., Montiglio, P.-O., Garant, D., Pelletier, F., Speakman, J. R., Humphries, M. M., et Réale, D. (2015). Energy expenditure and personality in wild chipmunks. *Behavioral Ecology and Sociobiology*, *69*(4), 653‑661. https://doi.org/10.1007/s00265-015-1876-2

Carere, C., et van Oers, K. (2004). Shy and bold great tits (*Parus major*): body temperature and breath rate in response to handling stress. *Physiology and Behavior*, *82*(5), 905‑912. https://doi.org/10.1016/j.physbeh.2004.07.009

Charmantier, A., Blondel, J., Perret, P., et Lambrechts, M. M. (2004). Do extra-pair paternities provide genetic benefits for female blue tits *Parus caeruleus*? *Journal of Avian Biology*, *35*(6), 524–532

Charmantier, A., Doutrelant, C., Dubuc-Messier, G., Fargevieille, A., et Szulkin, M. (2016). Mediterranean blue tits as a case study of local adaptation. *Evolutionary Applications*, *9*(1), 135‑152. https://doi.org/10.1111/eva.12282

Charmantier, A., et Garant, D. (2005). Environmental quality and evolutionary potential: lessons from wild populations. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1571), 1415‑1425. https://doi.org/10.1098/rspb.2005.3117

Charmantier, A., Kruuk, L. E. B., Blondel, J., et Lambrechts, M. M. (2004). Testing for microevolution in body size in three blue tit populations. *Journal of Evolutionary Biology*, *17*(4), 732‑743. https://doi.org/10.1111/j.1420-9101.2004.00734.x

Charmantier, A., McCleery, R. H., Cole, L. R., Perrins, C., Kruuk, L. E. B., et Sheldon, B. C. (2008). Adaptive phenotypic plasticity in response to climate change in a wild bird population. *Science*, *320*(5877), 800‑803. https://doi.org/10.1126/science.1157174

Charmantier, A., et Réale, D. (2005). How do misassigned paternities affect the estimation of heritability in the wild? *Molecular Ecology*, *14*(9), 2839‑2850. https://doi.org/10.1111/ j.1365-294X.2005.02619.x

Cheverud, J. M. (1996). Developmental integration and the evolution of pleiotropy. *American Zoologist*, *36*(1), 44–50.

Cheverud, J. M., Rutledge, J. J., et Atchley, W. R. (1983). Quantitative genetics of development: genetic correlations among age-specific trait values and the evolution of ontogeny. *Evolution*, *37*(5), 895-905. https://doi.org/10.2307/2408405

Cheverud, J.M., et Marroig, G. (2007). Comparing covariances matrices: Random skewers method compared to the common principal components model. *Genetics abd Molecular Biology*, *30*(2)

Choquet R, Rouan L, Pradel R. (2009). Program E-SURGE: a software application for fitting Multievent models. Dans : Thomson DL, Cooch EG, Conroy MJ, éditeurs. Series: *Environmental and Ecological Statistics*. 3: 845-865.

Clark CW. (1994). Antipredator behavior and the asset-protection principle. *Behavioral Ecology* 5: 159-170.

Class, B., et Brommer, J. E. (2015). A strong genetic correlation underlying a behavioural syndrome disappears during development because of genotype–age interactions. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1809), 20142777. https://doi.org/10.1098/rspb.2014.2777

Class, B., Kluen, E., et Brommer, J. E. (2014). Evolutionary quantitative genetics of behavioral responses to handling in a wild passerine. *Ecology and Evolution*, *4*(4), 427-440. https://doi.org/10.1002/ece3.945

Cole, E. F., et Quinn, J. L. (2014). Shy birds play it safe: personality in captivity predicts risk responsiveness during reproduction in the wild. *Biology Letters*, *10*(5), 20140178 -20140178. https://doi.org/10.1098/rsbl.2014.0178

Conover, D.O., et Schultz, E.T. (1995). Phenotypic similarity and evolutionary significance of contergradient variation. *Trends in Ecology and Evolution*, *10*(6), 248-252

Cote, J., et Clobert, J. (2007). Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1608), 383-390. https://doi.org/10.1098/rspb.2006.3734

Dall, S. R. X., Bell, A. M., Bolnick, D. I., et Ratnieks, F. L. W. (2012). An evolutionary ecology of individual differences. *Ecology Letters*, *15*(10), 1189-1198 https://doi.org/10.1111/j.1461-0248.2012.01846.x

Dall, S. R. X., Houston, A. I., et McNamara, J. M. (2004). The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, *7*(8), 734-739. https://doi.org/10.1111/j.1461-0248.2004.00618.x

Dammhahn, M. (2012). Are personality differences in a small iteroparous mammal maintained by a life-history trade-off? *Proceedings of the Royal Society B: Biological Sciences*, *279*(1738), 2645-2651. https://doi.org/10.1098/rspb.2012.0212

Danecek, P., Auton, A., Abecasis, G., Albers, C. A., Banks, E., DePristo, M. A., et al. (2011). The variant call format and VCFtools. *Bioinformatics*, *27*(15), 2156-2158. https://doi.org/10.1093/bioinformatics/btr330

Dingemanse, N. J. (2004). The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology*, *15*(6), 1023-1030. https://doi.org /10.1093/ beheco/arh115

Dingemanse, N. J., Barber, I., Wright, J., et Brommer, J. E. (2012). Quantitative genetics of behavioural reaction norms: genetic correlations between personality and behavioural plasticity vary across stickleback populations: Behavioural reaction norm quantitative genetics. *Journal of Evolutionary Biology*, *25*(3), 485-496. https://doi.org/10.1111/j.1420-9101.2011.02439.x

Dingemanse, N. J., Both, C., Drent, P. J., van Oers, K., et van Noordwijk, A. J. (2002). Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, *64*(6), 929-938. https://doi.org/10.1006/anbe.2002.2006

Dingemanse, N. J., et de Goede, P. (2004). The relation between dominance and exploratory behavior is context-dependent in wild great tits. *Behavioral Ecology*, *15*(6), 1023-1030. https://doi.org/10.1093/beheco/arh115

Dingemanse, N. J., et Dochtermann, N. A. (2013). Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology*, *82*(1), 39‐54. https://doi.org/10.1111/1365-2656.12013

Dingemanse, N. J., et Dochtermann, N. A. (2014). Individual behaviour: behavioural ecology meets quantitative genetics. Dans: *Quantitative genetics in the wild.* Charmantier, A., Garant, D., et Kruuk, L. E. (éditeurs) B. Oxford University Press.

Dingemanse, N. J., Dochtermann, N., et Wright, J. (2010). A method for exploring the structure of behavioural syndromes to allow formal comparison within and between data sets. *Animal Behaviour*, *79*(2), 439‐450. https://doi.org/10.1016/j.anbehav.2009.11.024

Dingemanse NJ, Réale D. 2013. What is the evidence for natural selection maintaining animal personality variation? In: Carere C, Maestripieri D. *Animal Personalities: Behavior, Physiology and Evolution.* Chicago University. Chicago. 201-220.

Dochtermann, N. A. (2011). Testing Cheverud's conjecture for behavioral correlations and behavioral syndromes. *Evolution*, *65*(6), 1814‐1820. https://doi.org/10.1111/j.1558-5646.2011.01264.x

Dochtermann, N. A., et Dingemanse, N. J. (2013). Behavioral syndromes as evolutionary constraints. *Behavioral Ecology*, *24*(4), 806‐811. https://doi.org/10.1093/beheco/art002

Conrad, J.L. Weinersmith, K.L., Brodin, T., Saltz, J.B., Sih, A. (2011). Behavioral syndromes in fishes: a review with implications for ecology and fisheries management. *Journal Fish Biology*. 78: 395-435.

Drent, P. J., Oers, K. v., et Noordwijk, A. J. v. (2003). Realized heritability of personalities in the great tit (*Parus major*). *Proceedings of the Royal Society B: Biological Sciences*, *270*(1510), 45‐51. https://doi.org/10.1098/rspb.2002.2168

Dubuc-Messier, G., Réale, D., Perret, P., et Charmantier, A. (2016). Environmental heterogeneity and population differences in blue tits personality traits. *Behavioral Ecology*, arw148. https://doi.org/10.1093/beheco/arw148

Edelaar, P., et Bolnick, D. I. (2012). Non-random gene flow: an underappreciated force in evolution and ecology. *Trends in Ecology and Evolution*, *27*(12), 659‐665. https://doi.org/10.1016/j.tree.2012.07.009

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

Ellner, S., et Hairston Jr, N. G. (1994). Role of overlapping generations in maintaining genetic variation in a fluctuating environment. *The American Naturalist*, *143*(3), 403–417.

Endler, J.A. (1986). *Natural selection in the wild.* Princeton : Princeton University Press.

Ferns, P. N., et Hinsley, S. A. (2010). How blue are british tits? Sex, age and environmental effects. *Bird Study*, *57*(3), 315‐329. https://doi.org/10.1080/00063651003716770

Ferrari, C., Pasquaretta, C., Carere, C., Cavallone, E., von Hardenberg, A., et Réale, D. (2013). Testing for the presence of coping styles in a wild mammal. *Animal Behaviour*, *85*(6), 1385‐1396. https://doi.org/10.1016/j.anbehav.2013.03.030

Fitzpatrick, B. M. (2012). Underappreciated consequences of phenotypic plasticity for ecological speciation. *International Journal of Ecology*, *2012*, 1 - 12. https://doi.org/10.1155/2012/256017

Foll, M., et Gaggiotti, O. (2008). A genome-scan method to identify selected loci appropriate for both dominant and codominant markers: A bayesian perspective. *Genetics*, *180*(2), 977 - 993. https://doi.org/10.1534/genetics.108.092221

Fournier, D.A., Skaug, H.J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder,M., Nielsen, A. et Sibert, J. (2012). AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. *Optimization Methods Software*. 27:233-249.

Fraser, D.F., Gilliam, J.F. (1987). Feeding under predation hazard: response of the guppy and Hart's rivulus from sites with contrasting predation hazard. *Behavavioral Ecology Sociobiology*. 21: 203-209.

Fresneau, N., Kluen, E., et Brommer, J. E. (2014). A sex-specific behavioral syndrome in a wild passerine. *Behavioral Ecology*, *25*(2), 359 - 367. https://doi.org/10.1093/beheco/aru008

Fucikova, E., Drent, P. J., Smits, N., et van Oers, K. (2009). Handling stress as a measurement of personality in great tit nestlings (*Parus major*). *Ethology*, *115*(4), 366 - 374. https://doi.org/10.1111/j.1439-0310.2009.01618.x

Garant, D., Forde, S. E., et Hendry, A. P. (2007). The multifarious effects of dispersal and gene flow on contemporary adaptation. *Functional Ecology*, *21*(3), 434 - 443. https://doi.org/10.1111/j.1365-2435.2006.01228.x

Goudet, J. (2005). HIERFSTAT, a package for R to compute and test hierarchical F-statistics. *Molecular Ecology Notes*, *5*, 184 - 186.

Green, J. A. (2011). The heart rate method for estimating metabolic rate: review and recommendations. *Comparative Biochemistry and Physiology Part A: Molecular and Integrative Physiology*, *158*(3), 287 - 304. https://doi.org/10.1016/j.cbpa.2010.09.011

Groothuis, T. G. G., et Carere, C. (2005). Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, *29*(1), 137 - 150. https://doi.org/10.1016/j.neubiorev.2004.06.010

Groothuis, T. G. G., et Trillmich, F. (2011). Unfolding personalities: the importance of studying ontogeny. *Developmental Psychobiology*, *53*(6), 641 - 655. https://doi.org/10.1002/dev.20574

Grosbois, V., Henry, P.-Y., Blondel, J., Perret, P., Lebreton, J.-D., Thomas, D. W., et Lambrechts, M. M. (2006). Climate impacts on Mediterranean blue tit survival: an investigation across seasons and spatial scales. *Global Change Biology*, *12*(12), 2235 - 2249. https://doi.org/10.1111/j.1365-2486.2006.01286.x

Hadfield, J. (2010). MCMC Methods for multi-response generalized linear mixed models: the MCMCglmm R Package. *Journal of Statistical Software*, *33*, 1 - 22.

Hadfield, J. D., Heap, E. A., Bayer, F., Mittell, E. A., et Crouch, N. M. A. (2013). Disentagling genetic and prenatal sources of familiar resemblance across ontogeny in wild passerine: eggs versus genes. *Evolution*, *67*(9), 2701 - 2713. https://doi.org/10.1111/evo.12144

Hakkarainen, H., Korpimäki, E. (1994). Nest defense of Tengmalm's owls reflects offspring survival prospect under fluctuating food conditions. *Animal Behaviour*. 48: 843-849.

Hall, M. L., van Asten, T., Katsis, A. C., Dingemanse, N. J., Magrath, M. J. L., et Mulder, R. A.

(2015). Animal personality and pace-of-life syndromes: do fast-exploring fairy-wrens die young? *Frontiers in Ecology and Evolution, 3*. https://doi.org/10.3389/fevo.2015.00028

Heinen-Kay, J. L., Schmidt, D. A., Stafford, A. T., Costa, M. T., Peterson, M. N., Kern, E. M. A., et Langerhans, R. B. (2016). Predicting multifarious behavioural divergence in the wild. *Animal Behaviour, 121*, 3‑10. https://doi.org/10.1016/j.anbehav.2016.08.016

Hendry, A. P., Huber, S. K., De Leon, L. F., Herrel, A., et Podos, J. (2009). Disruptive selection in a bimodal population of Darwin's finches. *Proceedings of the Royal Society B: Biological Sciences, 276*(1657), 753‑759. https://doi.org/10.1098/rspb.2008.1321

Herczeg, G., Ab Ghani, N. I., et Merilä, J. (2013). Evolution of stickleback feeding behaviour: genetics of population divergence at different ontogenetic stages. *Journal of Evolutionary Biology, 26*(5), 955‑962. https://doi.org/10.1111/jeb.12103

Hereford, J. (2009). A Quantitative Survey of Local Adaptation and Fitness Trade-Offs. *The American Naturalist, 173*(5), 579‑588. https://doi.org/10.1086/597611

Hurtrez-Boussès, S., Garine-Wichatitsky, M. de, Perret, P., Blondel, J., et Renaud, F. (1999). Variations in prevalence and intensity of blow fly infestations in an insular Mediterranean population of blue tits. *Canadian Journal of Zoology, 77*(2), 337–341.

Jacques-Hamilton, R., Hall, M. L., Buttemer, W. A., Matson, K. D., Gonçalves da Silva, A., Mulder, R. A., et Peters, A. (2017). Personality and innate immune defenses in a wild bird: Evidence for the pace-of-life hypothesis. *Hormones and Behavior, 88*, 31‑40. https://doi.org/10.1016/j.yhbeh.2016.09.005

Jacquin, L., Reader, S. M., Boniface, A., Mateluna, J., Patalas, I., Pérez-Jvostov, F., et Hendry, A. P. (2016). Parallel and nonparallel behavioural evolution in response to parasitism and predation in Trinidadian guppies. *Journal of Evolutionary Biology, 29*(7), 1406‑1422. https://doi.org/10.1111/jeb.12880

Karlsson Green, K., Eroukhmanoff, F., Harris, S., Pettersson, L. B., et Svensson, E. I. (2016). Rapid changes in genetic architecture of behavioural syndromes following colonization of a novel environment. *Journal of Evolutionary Biology, 29*(1), 144‑152. https://doi.org/10.1111/jeb.12769

Kawecki, T. J., et Ebert, D. (2004). Conceptual issues in local adaptation. *Ecology Letters, 7*(12), 1225‑1241. https://doi.org/10.1111/j.1461-0248.2004.00684.x

Kingsolver, J. G., Diamond, S. E., Siepielski, A. M., et Carlson, S. M. (2012). Synthetic analyses of phenotypic selection in natural populations: lessons, limitations and future directions. *Evolutionary Ecology, 26*(5), 1101‑1118. https://doi.org/10.1007/s10682-012-9563-5

Kluen, E., et Brommer, J. E. (2013). Context-specific repeatability of personality traits in a wild bird: a reaction-norm perspective. *Behavioral Ecology, 24*(3), 650‑658. https://doi.org/10.1093/beheco/ars221

Kluen, E., Siitari, H., et Brommer, J. E. (2014). Testing for between individual correlations of personality and physiological traits in a wild bird. *Behavioral Ecology and Sociobiology, 68*(2), 205‑213. https://doi.org/10.1007/s00265-013-1635-1

Kontiainen, P., Pietiainen, H., Huttunen, K., Karell, P., Kolunen, H., et Brommer, J. E. (2009). Aggressive Ural owl mothers recruit more offspring. *Behavioral Ecology, 20*(4), 789‑796. https://doi.org/10.1093/beheco/arp062

Koolhaas, J. M., de Boer, S. F., Buwalda, B., et van Reenen, K. (2007). Individual variation in coping with stress: a multidimensional approach of ultimate and proximate mechanisms. *Brain, Behavior and Evolution*, *70*(4), 218‑226. https://doi.org/10.1159/000105485

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

Korsten, P., Mueller, J. C., HermannstäDter, C., Bouwman, K. M., Dingemanse, N. J., Drent, P. J. et al. (2010). Association between DRD4 gene polymorphism and personality variation in great tits: a test across four wild populations. *Molecular Ecology*, *19*(4), 832‑843. https://doi.org/10.1111/j.1365-294X.2009.04518.x

Korsten, P., van Overveld, T., Adriaensen, F., et Matthysen, E. (2013). Genetic integration of local dispersal and exploratory behaviour in a wild bird. *Nature Communications*, *4*. https://doi.org/10.1038/ncomms3362

Krebs, J.R. et Davies, N. B. (1997). *Behavioural Ecology: An Evolutionary Approach.* 4^{e} Edition. Oxford: Wiley-Blackwell.

Kruuk, L. E. B. (2004). Estimating genetic parameters in natural populations using the « animal model ». *Philosophical Transactions of the Royal Society B: Biological Sciences*, *359*(1446), 873‑890. https://doi.org/10.1098/rstb.2003.1437

Kruuk, L. E. B., et Hadfield, J. D. (2007). How to separate genetic and environmental causes of similarity between relatives: Separating genetic and environmental effects. *Journal of Evolutionary Biology*, *20*(5), 1890‑1903. https://doi.org/10.1111/j.1420-9101.2007.01377.x

Kruuk, L. E., Merilä, J., et Sheldon, B. C. (2003). When environmental variation short-circuits natural selection. *Trends in Ecology and Evolution*, *18*(5), 207–209.

Lambrechts, M. M., Blondel, J., Hurtez-Bousses, S., Maistre, M., et Perret, P. (1997). Adaptive inter-population differences in blue tit life-history traits on Corsica. *Evolutionary Ecology*, *11*, 599‑612.

Lambrechts, M. M., Perret, P., Maistre, M., et Blondel, J. (1999). Do experiments with captive non–domesticated animals make sense without population field studies? A case study with blue tits' breeding time. *Proceedings of the Royal Society of London B: Biological Sciences*, *266*(1426), 1311–1315.

Lande, R., et Arnold, S. J. (1983). The measurement of selection on correlated characters. *Evolution*, *37*(6), 1210. https://doi.org/10.2307/2408842

Lebreton, J.-D., Burham, K., Clobert, J., et Anderson, D. R. (1992). Modeling and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs*, *62*(1), 67-118

Le Galliard, J.-F., Paquet, M., Cisel, M., et Montes-Poloni, L. (2013). Personality and the pace-of-life syndrome: variation and selection on exploration, metabolism and locomotor performances. *Functional Ecology*, *27*(1), 136‑144. https://doi.org/10.1111/1365-2435.12017

Le Galliard, J.-F., Paquet, M., et Mugabo, M. (2015a). An experimental test of density-dependent selection on temperament traits of activity, boldness and sociability. *Journal of Evolutionary Biology*, *28*(5), 1144‑1155. https://doi.org/10.1111/jeb.12641

Le Galliard, J.-F., Paquet, M., et Mugabo, M. (2015b). An experimental test of density-dependent selection on temperament traits of activity, boldness and sociability. *Journal of Evolutionary Biology*, *28*(5), 1144‑1155. https://doi.org/10.1111/jeb.12641

Leinonen, T., McCairns, R. J. S., O'Hara, R. B., et Merilä, J. (2013). QST–FST comparisons: evolutionary and ecological insights from genomic heterogeneity. *Nature Reviews Genetics*, *14*(3), 179‑190. https://doi.org/10.1038/nrg3395

Lenormand, T. (2002). Gene flow and the limits to natural selection. *Trends in Ecology and Evolution*, *17*(4), 183‑189.

Lichtenstein, J. L. L., et Pruitt, J. N. (2015). Similar patterns of frequency-dependent selection on animal personalities emerge in three species of social spiders. *Journal of Evolutionary Biology*, *28*(6), 1248‑1256. https://doi.org/10.1111/jeb.12651

Loiselle, B. A., Sork, V. L., Nason, J., et Graham, C. (1995). Spatial genetic structure of a tropical understory shrub, *Psychotria officinalis* (*Rubiaceae*). *American Journal of Botany*, *82*(11), 1420. https://doi.org/10.2307/2445869

Lovegrove, B. G. (2003). The influence of climate on the basal metabolic rate of small mammals: a slow-fast metabolic continuum. *Journal of comparative physiology. B, Biochemical, systemic, and environmental physiology*, *173*(2), 87–112.

Lynch, M. et Walsh, B. (1998). *Genetics and analysis of quantitative traits*. Sunderland : Sinauer Associates.

MacArthur, R.H., Wilson, E.O. (1967). *Theory of island biogeography*. Pinceton: Princeton University press.

Maes, J., Van Damme, R., et Matthysen, E. (2013). Individual and among-population variation in dispersal-related traits in Natterjack toads. *Behavioral Ecology*, *24*(2), 521‑531. https://doi.org/10.1093/beheco/ars193

Martin, R. A., et Pfennig, D. W. (2012). Widespread disruptive selection in the wild is associated with intense resource competition. *BMC Evolutionary Biology*, *12*(136), 1‑13.

Mazerolle, M.J. (2016) AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R package version 2.1-0. https://cran.r-project.org/package=AICcmodavg.

Meirmans, P. G., et Van Tienderen, P. H. (2004). genotype and genodive: two programs for the analysis of genetic diversity of asexual organisms. *Molecular Ecology Notes*, *4*(4), 792‑794. https://doi.org/10.1111/j.1471-8286.2004.00770.x

Merilä, J., Hendry, A.P. (2014). Climate change, adaptation, and phenotypic plasticity: the problem and the évidence. *Evolutionary Applications,* *7*(1):1-14.

Miranda, A. C., Schielzeth, H., Sonntag, T., et Partecke, J. (2013). Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? *Global Change Biology*, *19*(9), 2634‑2644. https://doi.org/10.1111/gcb.12258

Moller, A. P., et Nielsen, J. T. (2014). Parental defense of offspring and life history of a long-lived raptor. *Behavioral Ecology*, *25*(6), 1505‑1512. https://doi.org/10.1093/beheco/aru130

Montiglio, P.-O., Dammhahn, D., Dubuc-Messier, G., Réale, D. In prep. When should animals be paceless? Integrating the role of the ecological conditions and natural history into the pace of life syndrome hypothesis.

Montgomerie, R.D., Weatherhead, P.J. (1988). Risks and rewards of nest defense by parent birds. *Quaterly Review Biology* 63:167-187.

Montiglio, P.-O., Ferrari, C., et Réale, D. (2013). Social niche specialization under constraints: personality, social interactions and environmental heterogeneity. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *368*(1618), 20120343‑20120343. https://doi.org/10.1098/rstb.2012.0343

Montiglio, P.-O., Garant, D., Bergeron, P., Dubuc-Messier, G., et Réale, D. (2014). Pulsed resources and the coupling between life-history strategies and exploration patterns in eastern chipmunks (*Tamias striatus*). *Journal of Animal Ecology*, *83*(3), 720‑728. https://doi.org/10.1111/1365-2656.12174

Mutzel, A., Blom, M. P. K., Spagopoulou, F., Wright, J., Dingemanse, N. J., et Kempenaers, B. (2013). Temporal trade-offs between nestling provisioning and defence against nest predators in blue tits. *Animal Behaviour*, *85*(6), 1459‑1469. https://doi.org/10.1016/j.anbehav.2013.03.043

Mutzel, A., Dingemanse, N. J., Araya-Ajoy, Y. G., et Kempenaers, B. (2013). Parental provisioning behaviour plays a key role in linking personality with reproductive success. *Proceedings of the Royal Society B: Biological Sciences*, *280*(1764), 20131019‑20131019. https://doi.org/10.1098/rspb.2013.1019

Naguib, M., Flörcke, C., et van Oers, K. (2011). Effects of social conditions during early development on stress response and personality traits in great tits (*Parus major*). *Developmental Psychobiology*, *53*(6), 592‑600. https://doi.org/10.1002/dev.20533

Nakagawa, S., et Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological Reviews* 85: 935-956 . https://doi.org/10.1111/j.1469-185X.2010.00141.x

Nicolaus, M., Tinbergen, J. M., Bouwman, K. M., Michler, S. P. M., Ubels, R., Both, C., Kempensers, B., Dingemanse, N. J. (2012). Experimental evidence for adaptive personalities in a wild passerine bird. *Proceedings of the Royal Society B: Biological Sciences*, *279*(1749), 4885‑4892. https://doi.org/10.1098/rspb.2012.1936

Nicolaus, M., Tinbergen, J. M., Ubels, R., Both, C., et Dingemanse, N. J. (2016). Density fluctuations represent a key process maintaining personality variation in a wild passerine bird. *Ecology Letters*, *19*(4), 478‑486. https://doi.org/10.1111/ele.12584

Niemela, P. T., Dingemanse, N. J., Alioravainen, N., Vainikka, A., et Kortet, R. (2013). Personality pace-of-life hypothesis: testing genetic associations among personality and life history. *Behavioral Ecology*, *24*(4), 935‑941. https://doi.org/10.1093/beheco/art014

Nosil, P., Vines, T. H., et Funk, D. J. (2005). Perspective: reproductive isolation caused by natural selection against immigrants from divergent habitats. *Evolution*, *59*(4), 705‑719.

Nussey, D. H., Wilson, A. J., et Brommer, J. E. (2007). The evolutionary ecology of individual phenotypic plasticity in wild populations. *Journal of Evolutionary Biology*, *20*(3), 831‑844. https://doi.org/10.1111/j.1420-9101.2007.01300.x

O'Hara, R. B., et Mërila, J. (2005). Bias and precision in QST estimates: problems and some solutions. *Genetics*, *171*(3), 1331‑1339. https://doi.org/10.1534/genetics.105.044545

Perrins C. 1979. *Bristish tits*. Collins. Cornell University.

Petelle, M. B., Martin, J. G. A., et Blumstein, D. T. (2015). Heritability and genetic correlations of personality traits in a wild population of yellow-bellied marmots (*Marmota flaviventris*). *Journal of Evolutionary Biology*, *28*(10), 1840‑1848. https://doi.org/10.1111/jeb.12700

Pianka, E. R. 1970. On *r* et *K* selection. *American Naturalist 104*: 592-597

Pigliucci, M. (2005). Evolution of phenotypic plasticity: where are we going now? *Trends in Ecology and Evolution*, *20*(9), 481‑486. https://doi.org/10.1016/j.tree.2005.06.001

Pinheiro, J.C., Bates, D.M. 2000. *Mixed effects models in S and S-PLUS*. New York. United State of America. Springer.

Porlier, M., Garant, D., Perret, P., et Charmantier, A. (2012a). Habitat-linked population genetic differentiation in the Blue tit *Cyanistes caeruleus*. *Journal of Heredity*, *103*(6), 781‑791. https://doi.org/10.1093/jhered/ess064

Porlier, M., Charmantier, A., Bourgault, P., Perret, P., Blondel, J., et Garant, D. (2012b). Variation in phenotypic plasticity and selection patterns in blue tit breeding time: between- and within-population comparisons: Variation in plasticity among populations. *Journal of Animal Ecology*, *81*(5), 1041‑1051. https://doi.org/10.1111/j.1365-2656.2012.01996.x

Price, T. P., Kirkpatrick, M., et Arnold, S. J. (1988). Directional selection and the evolution of breeding date in birds. *Science*, *240*(4853), 798‑799.

Quinn, J. L., Patrick, S. C., Bouwhuis, S., Wilkin, T. A., et Sheldon, B. C. (2009). Heterogeneous selection on a heritable temperament trait in a variable environment. *Journal of Animal Ecology*, *78*(6), 1203‑1215. https://doi.org/10.1111/j.1365-2656.2009.01585.x

R Core Team (2015). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna. Austria.

Räsänen, K., et Kruuk, L. E. B. (2007). Maternal effects and evolution at ecological time-scales. *Functional Ecology*, *21*(3), 408‑421. https://doi.org/10.1111/j.1365-2435.2007.01246.x

Rausher, M. (1992). The measurement of selection on quantitative traits: biases due to environmental covariances between traits and fitness. *Evolution*, *46*(3), 616‑626.

Réale, D., et Festa-Bianchet, M. (2003). Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, *65*(3), 463‑470. https://doi.org/10.1006/anbe.2003.2100

Réale, D., Festa-Bianchet, M., et Jorgenson, T.J. (1999). Heritability of body mass varies with age and season in wild bighorn sheep. *Heredity*, *83*, 526‑532.

Réale, D., Gallant, B. Y., Leblanc, M., et Festa-Bianchet, M. (2000). Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*, *60*(5), 589‑597. https://doi.org/10.1006/anbe.2000.1530

Réale, D., Garant, D., Humphries, M. M., Bergeron, P., Careau, V., et Montiglio, P.-O. (2010). Personality and the emergence of the pace-of-life syndrome concept at the population level.

Philosophical Transactions of the Royal Society B: Biological Sciences, *365*(1560), 4051‑4063. https://doi.org/10.1098/rstb.2010.0208

Réale, D., Martin, J., Coltman, D. W., Poissant, J., et Festa-Bianchet, M. (2009). Male personality, life-history strategies and reproductive success in a promiscuous mammal. *Journal of Evolutionary Biology*, *22*(8), 1599‑1607. https://doi.org/10.1111/j.1420-9101.2009.01781.x

Réale, D., McAdam, A. G., Boutin, S., et Berteaux, D. (2003). Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1515), 591‑596. https://doi.org/10.1098/rspb.2002.2224

Réale, D., Reader, S. M., Sol, D., McDougall, P. T., et Dingemanse, N. J. (2007). Integrating animal temperament within ecology and evolution. *Biological Reviews*, *82*(2), 291‑318. https://doi.org/10.1111/j.1469-185X.2007.00010.x

Reparaz, L. B., van Oers, K., Naguib, M., Doutrelant, C., Visser, M. E., et Caro, S. P. (2014). Mate preference of female blue tits varies with experimental photoperiod. *PLoS ONE*, *9*(3), e92527. https://doi.org/10.1371/journal.pone.0092527

Revell, L. J. (2007). The G matrix under fluctuating correlational mutation and selection. *Evolution*, *61*(8), 1857‑1872. https://doi.org/10.1111/j.1558-5646.2007.00161.x

Revell, L. J. (2012). phytools: an R package for phylogenetic comparative biology (and other things): phytools: R package. *Methods in Ecology and Evolution*, *3*(2), 217‑223. https://doi.org/10.1111/j.2041-210X.2011.00169.x

Reznick, D., Bryant, M. J., et Bashey, F. (2002). r-and K-selection revisited: the role of population regulation in life-history evolution. *Ecology*, *83*(6), 1509–1520.

Reznick, D., Butler IV, M. J., et Rodd, H. (2001). Life-History evolution in guppies. VII. The comparative ecology of high- and low-predation environments. *The American Naturalist*, *157*(2), 126‑140. https://doi.org/10.1086/318627

Richardson, J. L., Urban, M. C., Bolnick, D. I., et Skelly, D. K. (2014). Microgeographic adaptation and the spatial scale of evolution. *Trends in Ecology and Evolution*, *29*(3), 165‑176. https://doi.org/10.1016/j.tree.2014.01.002

Ricklefs, R. E., et Wikelski, M. (2002). The physiology/life-history nexus. *Trends in Ecology and Evolution*, *17*(10), 462–468.

Roff, D. A., et Fairbairn, D. J. (2012). A test of the hypothesis that correlational selection generates genetic correlations. *Evolution*, *66*(9), 2953‑2960. https://doi.org/10.1111/j.1558-5646.2012.01656.x

Santos, C. D., Cramer, J. F., Pârâu, L. G., Miranda, A. C., Wikelski, M., et Dechmann, D. K. N. (2015). Personality and morphological traits affect pigeon survival from raptor attacks. *Scientific Reports*, *5*, 15490. https://doi.org/10.1038/srep15490

Skaug, H., Fournier, D., Bolker, B., Magnusson, A. et Nielsen, A. (2016).Generalized linear mixed models using 'AD Model Builder'. R package version 0.8.3.3

Savolainen, O., Lascoux, M., et Merilä, J. (2013). Ecological genomics of local adaptation. *Nature Reviews Genetics*, *14*(11), 807‑820. https://doi.org/10.1038/nrg3522

Schielzeth, H., Stoffel, M. et Nakagawa, S. (2016). rptR: repeatability estimation for Gaussian and non-Gaussian data. R package version 0.9.0. http://CRAN.R-project.org/package=rptR

Schielzeth, H., et Forstmeier, W. (2009). Conclusions beyond support: overconfident estimates in mixed models. *Behavioral Ecology*, *20*(2), 416‐420. https://doi.org/10.1093/beheco/arn145

Schuett, W., Tregenza, T., et Dall, S. R. X. (2010). Sexual selection and animal personality. *Biological Reviews*, *85*(2), 217‐246. https://doi.org/10.1111/j.1469-185X.2009.00101.x

Siepielski, A. M., DiBattista, J. D., et Carlson, S. M. (2009). It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecology Letters*, *12*(11), 1261‐1276. https://doi.org/10.1111/j.1461-0248.2009.01381.x

Siepielski, A. M., Gotanda, K. M., Morrissey, M. B., Diamond, S. E., DiBattista, J. D., et Carlson, S. M. (2013). The spatial patterns of directional phenotypic selection. *Ecology Letters*, *16*(11), 1382‐1392. https://doi.org/10.1111/ele.12174

Sih, A., Bell, A. M., Johnson, J. C., et Ziemba, R. E. (2004). Behavioral syndromes: an integrative overview. *The quarterly review of biology*, *79*(3), 241–277.

Sih, A., Mathot, K. J., Moirón, M., Montiglio, P.-O., Wolf, M., et Dingemanse, N. J. (2015). Animal personality and state–behaviour feedbacks: a review and guide for empiricists. *Trends in Ecology and Evolution*, *30*(1), 50‐60. https://doi.org/10.1016/j.tree.2014.11.004

Sinn, D. L., Perrin, N. A., Mather, J. A., et Anderson, R. C. (2001). Early temperamental traits in an octopus (*Octopus bimaculoides*). *Journal of Comparative Psychology*, *115*(4), 351.

Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science*, *236*(4803), 787‐792.

Smith, B. R., et Blumstein, D. T. (2008). Fitness consequences of personality: a meta-analysis. *Behavioral Ecology*, *19*(2), 448‐455. https://doi.org/10.1093/beheco/arm144

Smith, B. R., et Blumstein, D. T. (2010). Behavioral types as predictors of survival in Trinidadian guppies (*Poecilia reticulata*). *Behavioral Ecology*, *21*(5), 919‐926. https://doi.org/10.1093/beheco/arq084

Stearns, S.C. (1992). *The evolution of life histories.* Oxford: Oxford University Press.

Stamps, J. A. (2007). Growth-mortality tradeoffs and personality traits in animals. *Ecology Letters*, *10*(5), 355‐363. https://doi.org/10.1111/j.1461-0248.2007.01034.x

Stamps, J., et Groothuis, T. G. G. (2010). The development of animal personality: relevance, concepts and perspectives. *Biological Reviews*, *85*(2), 301‐325. https://doi.org/10.1111/j.1469-185X.2009.00103.x

St-Hilaire, E., Réale, D., Garant, D. 2017. Determinants, selection and heritability of docility in wild eastern chipmunks. *Journal of Evolutionary Biology*. In review.

Stinchcombe, J. R., Agrawal, A. F., Hohenlohe, P. A., Arnold, S. J., et Blows, M. W. (2008). Estimating nonlinear selection gradients using quadratic regression coefficients: double of nothing? *Evolution*, *62*(9), 2435‐2440. https://doi.org/10.1111/j.1558-5646.2008.00449.x

Stinchcombe, J. R., Rutter, M. T., Burdick, D. S., Tiffin, P., Rausher, M. D., et Mauricio, R. (2002).

Testing for Environmentally Induced Bias in Phenotypic Estimates of Natural Selection: Theory and Practice. *The American Naturalist*, *160*(4), 511 - 523. https://doi.org/10.1086/342069

Storz, J. F. (2005). Using genome scans of DNA polymorphism to infer adaptive population divergence. *Molecular Ecology*, *14*(3), 671 - 688. https://doi.org/10.1111/j.1365-294X.2005.02437.x

Sultan, S. E., et Spencer, H. G. (2002). Metapopulation structure favors plasticity over local adaptation. *The American Naturalist*, *160*(2), 271 - 283. https://doi.org/10.1086/341015

Szulkin, M., Gagnaire, P.-A., Bierne, N., et Charmantier, A. (2016). Population genomic footprints of fine-scale differentiation between habitats in Mediterranean blue tits. *Molecular Ecology*, *25*(2), 542 - 558. https://doi.org/10.1111/mec.13486

Taylor, R. W., Boon, A. K., Dantzer, B., Réale, D., Humphries, M. M., Boutin, S., Gorrel, J.C., Colman, D.W. et McAdam, A. G. (2012). Low heritabilities, but genetic and maternal correlations between red squirrel behaviours: G-matrix of red squirrel personality traits. *Journal of Evolutionary Biology*, *25*(4), 614 - 624. https://doi.org/10.1111/j.1420-9101.2012.02456.x

Taylor, R. W., Boutin, S., Humphries, M. M., et McAdam, A. G. (2014). Selection on female behaviour fluctuates with offspring environment. *Journal of Evolutionary Biology*, *27*(11), 2308 - 2321. https://doi.org/10.1111/jeb.12495

Teplitsky, C., Tarka, M., Møller, A. P., Nakagawa, S., Balbontín, J., Burke, T. A., et al. Assessing Multivariate constraints to evolution across ten long-term avian studies. *PLoS ONE*, *9*(3), e90444. https://doi.org/10.1371/journal.pone.0090444

Tinbergen, J. M., et Boerlijst, M. C. (1990). Nestling weight and survival in individual great tits (*Parus major*). *The Journal of Animal Ecology*, *59*(3), 1113. https://doi.org/10.2307/5035

Tremblay, I., Thomas, D. W., Lambrechts, M. M., Blondel, J., et Perret, P. (2003). Variation in blue tit breeding performance across gradients in habitat richness. *Ecology*, *84*(11), 3033–3043.

Trivers RL. 1972. Parental investment and sexual selection. In: Campbell B, editeur. *Sexual selection and the descent of man: the Darwinian pivot.* Chicago. United States of America. Transaction Publishers. p. 136-179.

van Oers, K., Klunder, M., Drent, P.J. (2005). Context dependence of personalities: risk-taking behavior in a social and a nonsocial situation. *Behavioral Ecology* 16: 716-723.

van Oers, K., Kohn, G.M., Hinde, C.A., et Naguib, M. (2015). Parental food provisioning is related to nestling stress response in wild great tit nestlings: implications for the development of personality. *Frontiers in zoology*, *12*, 1 - 10.

van Oers, K., et Sinn, D. L. (2011). Toward a basis for the phenotypic gambit: advances in the evolutionary genetics of animal personality. Dans M. Inoue-Murayama, S. Kawamura et A. Weiss, editeurs, *From Genes to Animal Behavior*.Tokyo: Springer Japan. p. 165 - 183.

van Overveld, T., et Matthysen, E. (2010). Personality predicts spatial responses to food manipulations in free-ranging great tits (*Parus major*). *Biology Letters*, *6*(2), 187 - 190. https://doi.org/10.1098/rsbl.2009.0764

van Overveld, T., et Matthysen, E. (2013). Personality and information gathering in free-ranging great tits. *PloS one*, *8*(2), e54199.

Verbeek, M., Drent, P. J., et Wiepkema, P. R. (1994). Consistent individual differences in early exploratory behaviour of male great tits. *Animal Behaviour*, *48*, 1113‑1121.

Wang, I. J., et Bradburd, G. S. (2014). Isolation by environment. *Molecular Ecology*, *23*(23), 5649‑5662. https://doi.org/10.1111/mec.12938

Wiersma, P., Muñoz-Garcia, A., Walker, A., et Williams, J. B. (2007). Tropical birds have a slow pace of life. *Proceedings of the National Academy of Sciences*, *104*(22), 9340–9345.

Wikelski, M., Spinney, L., Schelsky, W., Scheuerlein, A., et Gwinner, E. (2003). Slow pace of life in tropical sedentary birds: a common-garden experiment on four stonechat populations from different latitudes. *Proceedings of the Royal Society B: Biological Sciences*, *270*(1531), 2383‑2388. https://doi.org/10.1098/rspb.2003.2500

Wilson, A. J., Pemberton, J. M., Pilkington, J. G., Clutton-Brock, T. H., Coltman, D. W., et Kruuk, L. E. B. (2007). Quantitative genetics of growth and cryptic evolution of body size in an island population. *Evolutionary Ecology*, *21*(3), 337‑356. https://doi.org/10.1007/s10682-006-9106-z

Wilson, A. J., Réale, D., Clements, M. N., Morrissey, M. M., Postma, E., Walling, C. A., … Nussey, D. H. (2010). An ecologist's guide to the animal model. *Journal of Animal Ecology*, *79*(1), 13‑26. https://doi.org/10.1111/j.1365-2656.2009.01639.x

Wolf, M., van Doorn, G. S., Leimar, O., et Weissing, F. J. (2007). Life-history trade-offs favour the evolution of animal personalities. *Nature*, *447*(7144), 581‑584. https://doi.org/10.1038/nature05835

Wright, S. (1949). The genetical structure of populations. *Annals of Human Genetics*, *15*(1), 323‑354.

Zandt H, Strijkstra A, Blondel J, van Balen H. (1990). Food in two mediterranean blue tit populations: Do differences in caterpillar availability explain differences in timing of the breeding season? Dans Blondel J, Gosler A, Lebreton JD, McCleery R, éditeurs. *Population Biology of Passerine Birds: An Integrated Approach*. Berlin: Springer-Verlag. Pages 145–155.