

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

TESTER LE MODÈLE DE COMPROMIS ENTRE LA QUALITÉ ET LA QUANTITÉ
DE LA PROGENITURE DE VAN NOORDWIJK ET DE JONG DANS DES
ENVIRONNEMENTS HÉTÉROGÈNES

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RÉSUMÉ

La capacité d'un organisme à acquérir des ressources de l'environnement détermine la quantité d'énergie qu'il peut allouer aux fonctions biologiques. Puisque l'énergie disponible pour investir dans les fonctions biologiques est limitée, cela devrait donner lieu à des compromis. Dans la nature, les compromis sont fréquemment détectés au niveau intra-individuel, bien qu'il existe peu de preuves de tels compromis au niveau interindividuel. En 1986, van Noordwijk et de Jong ont proposé un modèle expliquant pourquoi les compromis dans la nature passent souvent inaperçus au niveau phénotypique. Ils ont proposé que lorsque la variation interindividuelle de l'acquisition (Vaq) est supérieure à la variation de l'allocation (Val), aucun compromis ne devrait être détecté et vice versa. Nous avons étudié la relation entre Vaq et Val et le compromis entre la quantité (nombre) et la qualité (taille) de la progéniture dans quatre populations de mésanges bleues eurasiennes méditerranéennes *Cyanistes caeruleus*. La plupart des études portant sur le compromis quantité-qualité à ce jour ont utilisé de simples corrélations phénotypiques ou des modèles linéaires dans leur analyse. Dans cette étude, nous avons utilisé des modèles bivariés à effets mixtes. Notre méthode nous a permis de prendre en compte des mesures répétées et de rechercher des corrélations à différents niveaux de variation, au sein d'une même population, en utilisant plusieurs covariables. Notre approche a montré l'apparition à la fois d'un compromis et d'une corrélation positive, ainsi que de compromis à plusieurs niveaux de variance dans la même population. Nous avons constaté un compromis au niveau des résidus dans trois populations sur quatre, et un compromis au niveau des femelles dans une population. Ces résultats confirment l'idée selon laquelle le compromis quantité-qualité se situe principalement au niveau interne de l'individu. De plus, les deux populations à forêt sempervirente ont montré une corrélation positive entre les années, montrant la forte variation interannuelle dans l'acquisition de ressources par les oiseaux reproducteurs qui produisent une progéniture de plus en plus petite lorsque l'environnement est plus rude. Enfin, nous avons trouvé peu ou pas d'évidence en faveur du modèle de van Noordwijk et de Jong, puisqu'une variance plus élevée dans l'acquisition ne diminuait pas la capacité à détecter le compromis quantité-qualité. Au lieu de cela, nous avons détecté les preuves les plus solides d'un compromis là où Vaq était le plus élevé. Nous avons également détecté des compromis là où le Vaq était le plus bas. Ainsi, nous avons trouvé peu de soutien à la prédiction de van Noordwijk et de Jong selon laquelle $Val > Vaq$ garantit la détection du compromis.

Mots clés : Compromis, mésange bleue, *Cyanistes caeruleus*, acquisition de ressources, allocation de ressources

CHAPITRE 1

INTRODUCTION GÉNÉRALE

The general objective of this study was to understand why expected trade-offs so often go undetected in wild populations and to see whether they could be found at different levels of variance. In this general introduction, I first present a historical overview of the optimal brood size and offspring number, followed by the investigated trade-off of this study: the trade-off between offspring size and number. I then present the van Noordwijk and de Jong model, which aims to explain why trade-offs often go undetected in nature, and finally, our objectives.

1.1 A historical overview of optimal brood size and offspring number

The study of biological trade-offs is a fundamental part of the theory of life-history evolution (Stearns 1989, 1992; Roff 1992, 2002). Trade-offs can occur because organisms that allocate resources to one trait, cannot, at the same time, allocate these resources to another trait. For example, resources allocated to somatic growth, cannot at the same time, be allocated to the production of offspring (Brown 2003). Hence, a trade-off between the resources allocated to both traits is expected, illustrated by a negative correlation between these traits. Our current understanding of trade-offs was built on the work of many previous researchers. As such, we begin by presenting some work of two prominent life history ecologists.

David Lack was a British ornithologist whose work on optimal clutch size, has been extremely influential to life history researchers (reviewed in Hutchings 2021). His theories were originally formulated on birds with altricial young, but later extended to mammals and insects. Lack hypothesized that the survival of offspring decreased with clutch size in birds (Lack 1968). In other words, the more offspring within a brood, the lower their survival. Lack hypothesized that clutch size was dependent on the number of offspring the parents could provision until fledging (Lack 1968). Parental fitness, in Lack's view, was the product between clutch size and the offspring's mean survival probability. The clutch size for a population which would ultimately result in the greatest parental fitness, was dubbed the "Lack clutch size." Lack's model, however,

was not without criticism. A review conducted by Hutchings (2021), summarized the main criticism to Lack's model: a) the model fails to incorporate parental survival, b) the Lack clutch size can vary throughout an individual's lifespan, c) the model fails to incorporate the costs associated with egg production and incubation, d) clutch size is also influenced by factors other than parental provisioning. Lastly, Lack's model is also challenged by the fact that many studies have shown that individuals can indeed support broods larger than the Lack clutch size (Gustafsson and Sutherland 1988, Pettifor et al. 1988, 2001, Dijkstra et al. 1990, Lessells 1991, Roff 1992, Stearns 1992).

Earlier work by life history researchers showed the importance of incorporating selection on offspring size, to understand selection on clutch size (Svardson 1949). In 1949, the Swedish biologist Gunnar Svardson, proposed that an individual's maximum fecundity is dependent upon the size of their offspring (Svardson 1949). His reasoning was that otherwise, selection would result in increased fecundity in the females at every generation. Svardson's reasoning was also backed by the findings that there exists a negative correlation between the number of offspring an individual female produces and their size. He also found that larger offspring hatch from larger eggs and have the greatest survival. Thus, Svardson theorized that fecundity is dependent on both the influence of offspring size on survival, and the reproductive success of the parents, which ultimately leads to a trade-off between offspring size and number, given that parental investment and care are necessarily limited. Both Lack (1968) and Svardson (1949) identified the trade-off between number of offspring and offspring survival; which ultimately limited brood size, whereas Lack hypothesized that brood size was limited by the parents' ability to provision their offspring, Svardson theorized that offspring size constrained brood size. Therefore, both researchers work demonstrate that brood size is ultimately dependent on parental energetic investment towards reproduction. The work of these two researchers would later influence the thinking of future researchers, who would incorporate parental energetic investment into life-history models (Smith and Fretwell 1974; van Noordwijk and de Jong 1986).

1.2 Energetic investments, trade-offs, and costs

The resources an organism possesses depends on the organism's ability to acquire these resources from its environment. Thus, organisms have limited resources available to invest in biological functions linked to fitness. This means, when resources are allocated to a fitness component, only the remaining resources can be allocated to the second fitness component (van Noordwijk and de Jong 1986). The limited nature of resources, available to organisms, has produced some trade-offs responsible for shaping life-history strategies.

Organisms are faced with the trade-off of investing their resources in growth/survival or reproduction. Individuals that invest more heavily in a current reproductive event, trade-off the energetic investment in growth (during their growing period) or maintenance. This leads to decreased survival and the potential to reproduce in future breeding events. Conversely, individuals may invest relatively more in future reproduction, by allocating relatively more resources to growth and survival. These individuals invest relatively less energy in a breeding event, thereby increasing their potential to reproduce in the future. This trade-off is therefore reflective of the energy invested in a breeding event, and the number of breeding events throughout the individual's lifetime (Williams 1966, Gadgil and Bossert 1970, Schaffer 1974, Charlesworth and Leon 1976, Law 1979, Michod 1979, Charlesworth 1980). Yet, within a breeding event, another trade-off exists between the quantity and the size of the offspring produced.

Both the size and number of offspring produced by an individual are crucial fitness components. Ideally, selection should favour the greatest number of offspring of the largest size. The larger the offspring, and presumably, the better nourished, the more likely they will be to survive to the age of reproduction (Smith and Fretwell 1974). Furthermore, the greater the number of offspring produced, the greater the chance that at least one will survive and reproduce (Hutchings 2021). As previously discussed, however, an individual has only so much energy to invest at any reproductive event. Thus, individuals may invest more heavily in offspring quantity or the size of their offspring (quality) (Hutchings 2021). In this manuscript, we will refer to this trade-off as the quantity-quality trade-off. Thus far, the trade-off can be thought of as solely affecting the individual that bears young, as it allocates resources towards reproduction (Christians 2000; Brown 2003; Chapin and

Chen 2018; Lasne 2018 ; Gould et al. 2022). However, the quantity-quality trade-off may also extend beyond offspring production, in species who engage in parental care.

1.3 Parental care extends parental energetic investment

Most of the studies that have investigated the quantity-quality-trade-off have been conducted on the propagules at birth (i.e., eggs, offspring, seeds) (Hutchings 2021). However, in species that engage in parental care, the parental reproductive investment extends beyond egg-laying. Passerine birds, like most birds, must incubate their eggs to optimal temperatures to allow for their proper development. Depending on the species, either the male or the female or both do incubate eggs. During the incubation stage, the non-incubating individual spends energy to feed its partner on the nest besides itself. Once hatched, parents must feed their altricial nestlings. The distance and the number of trips that parents must undertake are also energetically costly (Thomas et al. 2001). For example, blue tits *Cyanistes caeruleus* inhabiting habitats of poor quality make further and fewer foraging trips, while blue tits inhabiting higher quality habitats make shorter but more frequent foraging trips (Tremblay et al. 2005). Parent birds must also engage in nest sanitation. The white fecal sacs produced by nestlings, may increase nest visibility to predators (Tinbergen et al. 1962; Welty 1982), thus parents must invest additional energy to remove these fecal sacs from the nest. Here, we have given a non-exhaustive summary regarding how parental energetic investment extends beyond laying. The main point we aim to highlight here is how it is important to account for post-laying energetic investment while measuring the quantity-quality trade-off.

1.4 Empirical evidence for the quantity-quality trade off across taxa

Numerous studies ranging from a large range of taxa have found empirical evidence to support the quantity-quality trade-off: amphibians: (Crump 1974; Crump and Kaplan 1979; Duellman 1989; Hodl 1990; Perotti 1997), fish: (Bromage et al. 1990; Fleming and Gross 1990; Jonsson and Jonsson 1999; Lasne 2018), arachnids: (Brown 2003; Chapin and Chen 2018), birds: (Christians 2002, Guo and Lu 2022). Despite these findings, other studies did not find evidence for the quantity-quality trade-off (Horak 2008). For example, a review on the quantity-quality trade-off in birds, revealed that out of approximately 40 studies, the majority of them did not find

evidence to support the quantity-quality trade-off (Christians 2000). A lack of detection of the quantity-quality trade-off, however, does not mean that it is absent. As will be discussed in the next section, individuals within a population undergo variation in their ability to acquire resources from the environment, which can mask the detection of the trade-off within a population (van Noordwijk and de Jong 1986).

1.5 The van Noordwijk and de Jong's trade-off model

An organism's ability to acquire resources from the environment determines how much resources it can allocate to fitness components, such as growth or reproduction. As such, the limited nature of the acquired resources should result in trade-offs between fitness components. However, trade-offs are not always detected among individuals, even when expected. On this basis, van Noordwijk and de Jong (1986) came up with a model to explain why expected trade-offs often go undetected within a population. Their model was based on the simple principle that there exists heterogeneity among individuals in their ability to acquire resources from the environment. They argued that when the variation in resource acquisition is high relative to variation in allocation between two biological functions, trade-offs will go undetected, but when the variation in resource acquisition is relatively low, trade-offs will be apparent. A review of the model: Their model consists of 3 parameters highlighted in equation 1.

$$A = R + S \quad \text{eq. 1}$$

Where A is the total available resources to an individual; R is the resources invested in reproduction (or any other fitness component) and S is the resources invested in somatic growth (or any other fitness component). The covariance between R and S determines the sign of the correlation between R and S. In their more detailed model, parameter B, is the total available resources that are invested into reproduction (R), or the fitness component and (1—B) is the total available resources that are invested into somatic growth (S). This can be visualized with the following figures:

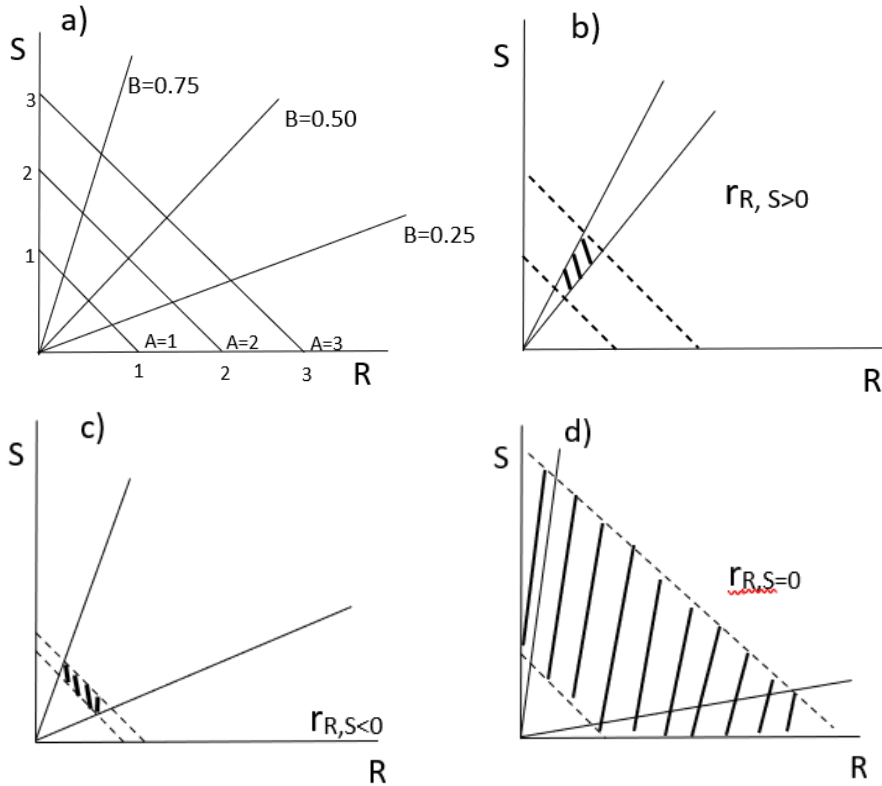


Figure 2.1 (from van Noordwijk and de Jong 1986): a) the diagonal lines intersecting S and R, called A1, A2, and A3, represent the average amount of resources in the environment available for an individual to acquire. These three lines could represent different individuals or different years within a population. Individuals, have a fixed amount of energy which they can choose to allocate to either reproduction (R) or somatic growth (S), in any combination. For example, if an individual has 3 units of energy to allocate, it may invest these 3 units of energy completely to R, completely to S, or it may partition its investment between R and S. Thus, individuals will vary in the amount of energy that they allocate to R and S, along a respective A line. Finally, parameter B represents the average proportion of the total available resource's individuals allocate to S. b) when the variation in resource acquisition between individuals or years (A) is large, compared to the variation in allocation to reproduction, R will increase with S (positive correlation: hatched area). c) when the variation in resource acquisition between individuals or years (A) is small compared to the variation in allocation to reproduction, R will decrease with S (negative correlation), showing a trade-off (hatched area). d) when both the variation in resource acquisition between individuals or years (A) and the variation in allocation to reproduction are large, R and S will be equal to zero, showing no correlation (hatched area).

1.6 Empirical evidence for van Noordwijk and de Jong's model

Since van Noordwijk and de Jong's (1986), model, many studies have not detected the quantity-quality trade-off. Christians (2002) reviewed the ornithological literature on the quantity-quality

trade-off between egg size and clutch size. He found that out of 63 studies, 73% (46 studies) showed no evidence for the QQ trade-off, 8% (5 studies) of studies showed evidence of the QQ trade-off, 38% (24 studies) of studies showed a positive relationship, and 8% of studies (5 studies) showed a significant variation between QQ but no linear pattern (these percentages not adding to 100 because some studies showed evidence for multiple different relationships). For example, a single study may have shown evidence for the QQ trade-off, a positive relationship and no relationship (Christians 2002). A lack of detection of the QQ trade-off, however, does not necessarily mean that it is absent.

Since van Noordwijk and de Jong proposed their model in 1986, some studies have found empirical evidence to support it. Christians (2000) tested van Noordwijk and de Jong's model with a between-species approach using Anseriformes (waterfowl), and various clades within the Anseriformes. The study investigated how variation in resource acquisition and allocation affected the detection of the trade-off between egg number and size. Christians' (2000) study found that the egg size and number trade-off was detected within Anseriformes, and several clades therein, when the variation in resource allocation was high, relative to the variation in resource acquisition (the total resources invested within the clutch). Thus, this study found support for van Noordwijk and de Jong's Model; although this model was originally intended for intraspecific data (Christians 2000).

Brown (2003), argues that the interpretation of the van Noordwijk and de Jong model using interspecific data, must be done with caution. He argues that variation within a population's resource acquisition and allocation, is easier to interpret from an evolutionary viewpoint given that it reflects fitness differences among individuals and selection. Conversely, interspecific data is challenging to interpret because it contains differences between individual variation within species. Different species may also reflect adaptations to different environments, resulting in fixed resource acquisition and allocation, circumventing selection on certain traits. Keeping this in mind, Brown (2003), tested the van Noordwijk and de Jong model using both interspecific and intraspecific data. In his study, he investigated differences in resource acquisition and allocation pertaining to the trade-off between offspring size and number, using 10 species of scorpions. He then compared the interspecific data to results of a single species *Centruroides vittatus*. In both levels of analysis, a trade-off between size and number of offspring was found, when the acquisition of resources

(reproductive investment) was low relative to the variance in resource allocation. Thus, this study provided support for the van Noordwijk and de Jong model using both interspecific and intraspecific data (Brown 2003).

1.7 The phenotypic gambit and heritability

Most evolutionary inferences in evolutionary ecology have come from studying phenotypes, while assuming that these phenotypes reflect the underlying genotypes (Grafen 1984). Variance in the phenotypes is composed of genetic variance (V_g), environmental variance (V_e) and the interaction between genetic and environmental variances ($V_g \times V_e$) (Falconer and MacKay 1996; Lynch and Walsh 1998). The assumption that the phenotype reflects the underlying genotype, has been dubbed the phenotypic gambit (Grafen 1984; Cheverud 1988). The phenotypic gambit can be extended to associations between traits, where the phenotypic correlation between traits is assumed to reflect their genetic correlation (Cheverud 1988; Roff 1995).

The phenotypic gambit is more reliable when the traits under study show a high heritability.

$$r_p = r_g \sqrt{h_x^2 h_y^2} + r_e \sqrt{(1 - h_x^2)(1 - h_y^2)} \quad \text{equ. 2}$$

Phenotypic correlations (r_p) between traits x and y are described by equation 2, where r_g and r_e are the genetic and environmental correlations between traits x and y , respectively, and h_x^2 h_y^2 are the heritabilities of traits x and y (Roff, 1997). This equation shows that when the heritability of traits x and y are high, the phenotypic correlation will approximate the genetic correlation and the environmental correlation will contribute little to the phenotypic correlation (Hadfield et al. 2007). By contrast, when the heritabilities of the two traits are low, the environmental variation would cause greater differences between the genetic and phenotypic correlations, making the phenotypic gambit less reliable (Cheverud 1984).

Phenotypic correlations of two traits (y and z) can also be partitioned into among-individual and within-individual correlations. When individual mean values of y (\bar{y}) correlate with individual

mean values of z (\bar{z}), an among individual correlation is formed. Conversely, when an individual's change in y between period t and $t+1$ is correlated with its change in z over the same period, a within-individual correlation is produced (Dingemanse and Dochtermann 2013). As is the case for phenotypic correlations, both within and between-individual correlations, are affected by genes, the environment, and methodological errors. Since genes belong to individuals, they therefore contribute to among-individual variation, whereas the environment can influence both among and within-individual correlations. Lastly, methodological errors, such as the error associated with the precision of an instrument, or differences in measurements among measurers, can contribute to within-individual variation, and hence within-individual correlations (Dingemanse and Dochtermann 2013).

1.8 Objectifs

Here we set out to test van Noordwijk and de Jong's model with respect to the quantity-quality trade-off in four populations of Eurasian blue tits. We considered this trade-off during the breeding season (encompassing the egg laying, and nestling provisioning stages) which is energetically demanding for both parents. Having more offspring means each offspring would receive a smaller proportion of the total amount of food provisioned by the parents. In contrast, having fewer offspring means the offspring would receive a relatively greater portion of the total food provisioned by the parents. We investigated the quantity-quality trade-off among the four populations of blue tits, using annual variation in total brood mass as a proxy for variation in resource acquisition dedicated to offspring production. We analysed the among- and within-individual (females in a pair) covariance and correlation between number of fledglings (as proxies of quantity) and mean body mass at fledging (as proxies of quality).

Hypotheses (HI) and predictions (PI):

HI.1 A trade-off should be present between the two reproductive sources of resource allocation: the quantity and quality of offspring. This is because, once a unit of energy is allocated to one biological function (e.g., quantity of offspring), only the remaining units of energy are available to be allocated to other biological functions (e.g., quality of offspring).

PI.1 We expect a negative correlation between quantity and quality of offspring illustrating the trade-off between these 2 biological functions.

HI.2 The detection of the quantity-quality trade-off is more likely to be detected in populations where average levels of acquisition are highest. However, within these populations the detection of the quantity-quality trade-off or lack thereof, will depend on the ratios of variation in resource acquisition and variation in resource allocation proposed by the van Noordwijk and de Jong (1986) model.

PI.2 Within a population, we will have evidence for the van Noordwijk and de Jong model if high variation in resource acquisition and low variation in resource allocation among years renders the quantity-quality trade-off undetectable (Figure 1.2 a). Additionally, if we find a trade-off with low variation in resource acquisition among years and high variation in resource allocation among years, we will also have evidence for the van Noordwijk and de Jong model (Figure 1.2 b). Conversely, if we find a trade-off with different ratios of variation in resource acquisition and allocation, than those proposed by van Noordwijk and de Jong, or, if we find no trade-off, despite finding the ratios of variation in acquisition and allocation proposed by van Noordwijk and de Jong, then we will have no evidence for the van Noordwijk and de Jong model. In graph b), low variation in the magnitude of resources acquired among years (blue lines) and high variation in resource allocation among years (red lines) shows the quantity-quality trade-off (black line). Inspired by van Noordwijk and de Jong 1986.

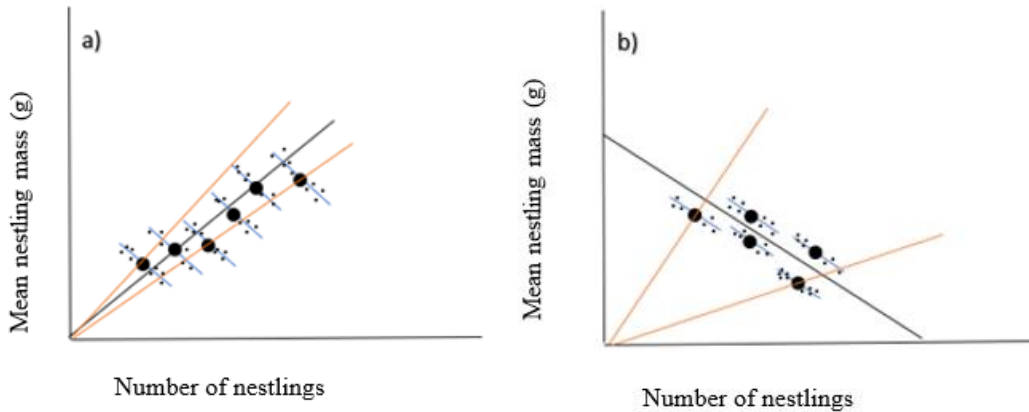


Figure 1.2 The relationship between number of nestlings (quantity) and mean nestling mass (quality). The black line shows the global model slope. The blue lines each represent a year, where a trade-off is present between mean nestling mass and number of nestlings (i.e. within-year level). The large black dots represent the mean trait value between number of nestlings and mean nestlings' mass for that year. The red lines represent the variation in resource allocation among years based on the yearly mean values (no trade-off detected at the among-year level). a), high variation in the magnitude of resources acquired among years (blue lines) and low variation in resource allocation among years (red lines) shows that the quantity-quality trade-off is obscured (black line). b), low variation in the magnitude of resources acquired among years (blue lines) and high variation in resource allocation among years (red lines) shows the quantity-quality trade-off (black line).

CHAPITRE 2

TESTING THE VAN-NOORDWIJK AND DE JONG MODEL IN FOUR BLUE-TIT POPULATIONS WITH CONTRASTED ENVIRONMENTS

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2.1 Abstract

An organism's ability to acquire resources from the environment determines how much energy it can allocate to biological functions. Since the energy available to invest in biological functions is limited, it should result in trade-offs. In nature, trade-offs are frequently detected at the within-individual level, although there is little evidence for such trade-offs at the among-individual level. In 1986, van Noordwijk and de Jong proposed a model explaining why trade-offs in nature are frequently undetected at the phenotypic level. They proposed that when among-individual variation in acquisition (V_{aq}) is higher than variation in allocation (V_{al}), no trade-off should be detected and vice versa. We investigated the relationship between V_{aq} and V_{al} and the trade-off between quantity (number) and quality (size) of offspring in four populations of Mediterranean Eurasian blue tits *Cyanistes caeruleus*. Most studies investigating the quantity-quality trade-off to date, have used simple phenotypic correlations or linear models in their analysis. In this study, we used bivariate mixed-effect models. Our method allowed us to account for repeated measurements, and to search for correlations at various levels of variation, within the same population, using multiple covariates. Our approach showed the occurrence of both a trade-off and a positive correlation, and of trade-offs at multiple levels of variance in the same population. We found a trade-off at the level of the residuals in three out of four populations, and a trade-off at the among-female level in one population. These results show evidence for the idea that the quantity-quality trade-off is mostly found at the within-individual. Additionally, the two evergreen populations showed a positive correlation among years, showing the strong interannual variation in resource acquisition by breeding birds who produce smaller and fewer offspring when the environment is harsher. Finally, we found little to no evidence for the van Noordwijk and de Jong model, since a higher variance in acquisition did not decrease the ability to detect the quantity-quality trade-off. Instead, we detected the strongest evidence for a trade-off where V_{aq} was highest. We also detected trade-offs where V_{aq} was lowest. Thus, we found little support for the van Noordwijk and de Jong prediction that $V_{al} > V_{aq}$ guarantees the detection of the trade-off.

Keywords: Trade-off, Blue tit, *Cyanistes caeruleus*, Resource acquisition, Resource allocation.

2.2. Introduction

Both the size and number of offspring produced by an individual are crucial fitness components. In theory, selection should favour the greatest number of offspring of the largest size, where larger offspring undergo increased survival to the age of reproduction (Smith and Fretwell 1974), and large clutch sizes increase the probability that at least one offspring will survive and reproduce (Hutchings 2021). Given the limited nature of resources, selection will favor the number and size of offspring size which maximizes fitness and individuals are thus faced with the trade-off of investing in offspring quantity or quality (size) (Hutchings 2021).

To date, numerous studies ranging from a large range of taxa have found empirical evidence to support the quantity-quality trade-off: amphibians: (Crump 1974; Crump and Kaplan 1979; Duellman 1989; Hodl 1990; Perotti 1997), fish: (Bromage et al. 1990; Fleming and Gross 1990; Jonsson and Jonsson 1999; Lasne 2018), arachnids: (Brown 2003; Chapin and Chen 2018), birds: (Christians 2002, Guo and Lu 2022). Despite these findings, other studies did not find evidence for the quantity-quality trade-off (Horak 2008). For example, a review on the quantity-quality trade-off in birds, revealed that out of approximately 40 studies, the majority of them did not find evidence to support the quantity-quality trade-off (Christians 2002). A lack of detection of the quantity-quality trade-off, however, does not necessarily mean that it is absent.

In nature, trade-offs are often detected at the within individual level, over successive reproductive events, but not at the among-individual level. This is due to heterogeneity among individuals in their ability to acquire and allocate resources from the environment (van Noordwijk and de Jong 1986). The variation in resource acquisition and allocation among individuals of a population may potentially mask a trade-off present at the within-individual level. According to the van Noordwijk and de Jong (1986) model, a trade-off among individuals is least likely to be detected when the variation in resource acquisition is high relative to the variation in allocation between the two biological functions. Conversely, when the variation in resource acquisition is relatively low, compared to the variation in resource allocation, a trade-off will likely be detected.

Few studies have investigated the quantity-quality trade-off while taking into account van Noordwijk and de Jong's model (but see Brown 2003, Christians 2000). Thus, in studies that did not find evidence for the quantity-quality trade-off, and which did not account for variation in resource acquisition and allocation, it is unknown whether a trade-off was inexistent or was undetected but likely present. Conversely, if a trade-off was detected, it is also unknown whether the variation in resource acquisition and allocation followed the model proposed by van Noordwijk and de Jong.

In this study, we tested the van Noordwijk and de Jong model (1986) by examining the quantity-quality trade-off in four populations of nest-box breeding Eurasian blue tits, *Cyanistes caeruleus*. We used a bivariate mixed-effect model approach to investigate the trade-offs at multiple levels of variation, including year, female and male ID and nest. We used annual variation in total brood mass as a proxy for variation in resource acquisition dedicated to offspring production. We analysed the among-and within-individual (females in a pair) covariance and correlation between number of fledglings (as proxies of quantity) and mean body mass at fledging (as proxies of quality). Given the limited nature of resources, we first predicted that a trade-off should be present between the quantity and quality of offspring, which would be indicated by a negative correlation. We predicted that when a trade-off between quantity-quality was found, we should observe $V_{aq} > V_{al}$. Conversely, if a trade-off between quantity-quality was not detected, we predicted that $V_{aq} < V_{al}$. The relationship of the quantity-quality correlation and the ratio of V_{aq} and V_{al} indicated whether we had evidence to support van Noordwijk and de Jong's model.

2.3. Methods

2.3.1. Study species and systems

The Eurasian Blue tit is a socially monogamous passerine, native to temperate and Mediterranean Europe, and western Asia. Blue tits are secondary cavity nesters, breeding in natural cavities dug by first cavity nesters such as woodpeckers, or artificial nest-boxes (Dhondt 1987). During the breeding season, Eurasian blue tits are mainly insectivorous, and depend heavily on caterpillars to feed their nestlings. In our system, they depend primarily on the green oak tortrix *Tortrix viridana*. So important are caterpillars for the nestling's diet that the tits time their laying date with the peak

of caterpillar abundance, to ensure that ample food to provision their nestlings (Zandt et al. 1990; Dias et al. 1994; Blondel et al. 1999; Blondel et al. 2006). They lay a clutch of 6–14 eggs, which the female incubates. The female thus depends on her partner to feed her during incubation. Both parents, however, share provisioning duties to their nestlings (Nilsson et al. 1988).

Our system consists of four Eurasian blue tit populations located in heterogeneous habitats in both Southern France (*Cyanistes caeruleus caeruleus*) and on the island of Corsica (France; *Cyanistes caeruleus ogliastreae*) where nest-boxes allow the close monitoring of tit populations. The La Rouvière study site was located in southern France, near the city of Montpellier (43° 40'N, 03° 40'E; 227 nest-boxes). The other three were located in North-Western Corsica, France, near the city of Calvi: E-Pirio (42° 34' N, 08° 44' E; 200 m elevation; 205 nest-boxes between two study sites), E-Muro (42° 35'N, 08° 57' E; 100 m elevation; 75 nest-boxes among three study sites), and D-Muro (42° 32'N, 08° 55'E; 350 m elevation; 110 nest-boxes among three study sites). For this study we used data that started being collected in 1987 for E-Pirio, 1991 for D-Rouvière, 1993 for D-Muro and 1998 for E-Muro and ended in 2021 for all four populations (Table 2.1).

The four populations all inhabit oak forests. However, the dominant oak species, differs between the four populations. The E-Muro, and E-Pirio populations are both dominated by the holm oak *Quercus ilex*, an evergreen species (Blondel et al. 1991), whereas D-Rouvière and D-Muro are dominated by the deciduous downy oak *Quercus pubescens*. Note that the “E” in the E-Muro and E-Pirio populations, stands for evergreen while the “D” in D-Rouvière and D-Muro stands for deciduous. The differences in dominant tree species inhabiting each population result in differences in yearly mean *Tortrix* caterpillar abundances and phenology. The differences in caterpillar abundances cause differences in habitat quality among the four Eurasian blue tit populations. The D-Rouvière and D-Muro populations contain the highest habitat quality, followed by E-Muro and E-Pirio (Blondel et al. 1993; Bondel et al. 2006). The evergreen populations, especially E-Pirio, thus supplement their nestling’s diet with arthropods other than caterpillars. In all populations, laying date coincides with the peak in caterpillar abundances. Birds from the two deciduous populations have similar average laying dates (D-Rouvière: ~ March 8, 1991-2016; D-Muro: ~ March 7th, 1993-2016, Charmantier et al. 2016). The birds in the evergreen populations lay 10 days to a month later (E-Muro: ~ March 17, 1998-2016; E-Pirio:

~ April 8, 1976-2016). D-Rouvière birds have the largest mean clutch sizes (9.95 eggs) of the four populations, followed by D-Muro (8.50 eggs), E-Muro (7.12 eggs) and E-Pirio (6.61 eggs). Mean incubation period is similar between the four populations at around 14 days. The mean number of fledglings is highest in the deciduous populations (D-Rouvière=6.24 fledglings, D-Muro=6.60 fledglings), and is both similar and lower in the evergreen populations (E-Muro=4.14 fledglings, and E-Pirio 4.15 fledglings). Mean male and female body mass are similar within each population. The largest birds are found at D-Rouvière (Males and females =11.01g), followed by D-Muro (males=9.82g, female=9.66g), E-Muro (males=9.66g, females=9.47g), and E-Pirio (males=9.37g, females=9.23g) (Charmantier et al. 2016).

The differences in life histories and behaviours result in differences in the pace-of life among the populations. Birds in the deciduous populations have a faster pace-of-life than those in the evergreen populations, because they are more aggressive, faster, and more superficial explorers (Dubuc-Messier et al. 2016). They lay larger clutches in a breeding season and have lower life expectancy (Dubuc-Messier et al. 2016; Bastianelli et al. 2021). Behaviour and life history differences among populations have a genetic basis (Dubuc-Messier et al. 2018).

We monitored nest-boxes daily or weekly, over the course of the breeding season, from early April to late June. We recorded the laying dates and clutch sizes of each brood. Parents were captured within their nest-boxes. Upon capture, parents were identified by a unique metal band number and were sexed, based on the presence or absence of a brood patch. The birds were also aged, as either adult (> 1 year of life) or juvenile (within their first year of life). Juveniles are recognizable with their less blue colour between the greater, median and lesser coverts, and the primary coverts. Un-banded individuals were banded with a metal band obtained from the Centre de Recherches sur la Biologie des Populations d'Oiseaux (CRBPO, Paris, France). Tarsus length and body mass were collected from the nestlings of each brood when the nestlings reached 15 days of age.

Second clutches are rare within each population (from 0 to 3.4% of all broods), and we thus only used first clutches in our analyses. Furthermore, we omitted clutches that underwent complete mortality, due to predation, environmental causes, disease, or abandonment before nestlings reached 15 days of age because parental energetic investment could not be calculated. Also, we excluded birds that were treated against the parasite *Protocalliphora*, Diptera: Calliphoridae,

because broods parasitized by *Protocalliphora* have lower nestling mass (Banbura et al. 2004).

We used total nestling biomass (in grams) in a clutch as an index of resource acquisition for a given blue tit pair. From the viewpoint of the brood, total nestling biomass reflects the resources acquired and directly transferred by the parents to the whole brood. We thus assumed that in the context of the quantity-quality trade-off, variance among parents or among years in the total nestling biomass would be good indicators of V_{aq} . By this index, we can estimate V_{aq} in each population and compare this variation to the correlation between offspring size and number. This comparison will indicate whether resource acquisition plays a role in affecting the trade-off between offspring size and number at the among-individual level. We used mean nestling mass at age 15 days old, as a standardized measure of the average nestling quality of a brood. Nestling mass represents a good proxy for cumulated parental energetic expenditure transferred directly to each offspring during both laying and provisioning.

2.3.2. Statistical analyses

Given that we have repeated measurements on individuals and nests across years, we used mixed-effect models to estimate the different sources of variance on the traits, using the brms package (Bürkner, 2017) in R (R Core Team, 2023).

Our first objective was to evaluate the level of variance in acquisition, which could help predict in which population we would detect the quantity-quality-trade-off, according to the van Noordwijk and de Jong model (1986). We thus ran a bivariate mixed-effect model to decompose the phenotypic variance in the total brood mass in the four populations, using year, male ID, female ID, and nest ID. We did not include any fixed effects in this model because we wanted to estimate the global proportion of the total variance in total brood mass explained by each random effect, without involving the factors related to each random effect (e.g. parent age or body mass). Variance in acquisition that may prevent us from detecting the quantity-quality trade-off could occur at the among-female, among-male, among-year, or among-nest level. The variance due to year indicates how chick biomass varies as a function of environmental conditions among years. Such environmental conditions may include interannual differences in precipitation, temperature, and the abundance of the primary food resource (*Tortrix* caterpillars). Nest effects regroup all the

characteristics of the nest and the microhabitat surrounding it, which affects chick biomass. Finally, male and female effects capture the variance in energetic investment in their brood and potential direct genetic effects which may affect a chick's ability to acquire resources from their parents and allocate these resources to different biological functions.

To analyse the trade-off between quality and quantity of offspring, we ran a bivariate mixed model built from two sub-models (Hadfield 2010). The first sub-model contained mean nestling mass (i.e., quality) as a response variable while the second sub-model contained nestling number (i.e., quantity) as a response variable, assuming they followed a Gaussian distribution. Both sub-models contained the same fixed and random effects. Mean parental mass (i.e. the mean between the mass of the male and female parent) and mean parental tarsus of a brood were used as fixed effects to account for the heritable component of nestling size (i.e., bigger parents produce bigger offspring not because they transfer more resources to them but because they share size-related genes with their offspring'). Nestling size is a function of both environmental and genetic contributions of the parents (Both et al. 2005; van Noordwijk et al. 1988). A combined effect of parental mass or size on mean nestling mass and nestling number (e.g. heavier parents produce fewer but bigger offspring) would indicate a quantity-quality trade-off, driven by parental phenotypes. We also included the male and female parent age as separate fixed effects into the models, because parent age can influence both clutch size and the number of fledglings (Auld and Charmantier 2011). Parent ages were aged categorically as juvenile or adult. A combined effect of parental age on mean nestling mass and nestling number (e.g. younger parents produce fewer but bigger offspring) would indicate a quantity-quality trade-off, driven by age.

We included male and female ID, nest ID and year as random effects. These variance components break down the phenotypic variance of mean nestling mass, number of nestlings and their covariance. Variance due to year indicates how mean nestling mass or how number of nestlings varies as a function of environmental conditions among years. The nest ID variable aimed to capture the effects of the microhabitat on both mean nestling mass and number of nestlings. The male ID and female ID variables aimed to capture differences in mean nestling mass or nestling number caused by parental features other than their mass, and size, nest. We assumed that they would represent differences in the parental abilities to transfer resources to their offspring.

A simple way of evaluating the relative importance of the variation in acquisition and allocation is to examine the residual variance of the models on total brood mass, mean nestling mass and nestling number. Residual variance equals 1 minus the sum of the variance caused by random effects. Therefore, the lower the residual variance, the higher the proportion of variance explained by all the random effects. Residual variance is thus an index of the importance of among-individual variance in acquisition or allocation caused by intrinsic (i.e. among-female or among male effects) or extrinsic factors (i.e. among-year or among-nest effects). We thus examined the residual variances estimates to predict in which population we expect to detect a trade-off.

The model also reveals which of the random effects significantly resulted in a correlation between mean nestling mass and number of nestlings. If a random showed a negative correlation, this would indicate the presence of a quantity-quality trade-off at that level. We ran each model for each population separately, with 100,000 iterations, a warm-up of 200 and a thin of 200, 2 chains and cores equal to 2.

Previous studies that tested the van Noordwijk and de Jong (1986) model with respect to the quantity-quality trade-off have used phenotypic correlations and linear models in their analysis (Blackburn 1991; Carrière and Roff 1994; Christians 2000, Brown 2003, Herreras et al. 2007). In order to compare our study with previous findings, we also conducted a simple Pearson correlation between mean nestling mass per brood and number of nestlings.

2.4 Results

2.4.1 Summary statistics

Table 2.1 Summary statistics for the four blue tit populations, in southern France and Corsica. Total and mean nestling mass per brood, number of nestlings were calculated when the nestlings reached 15 days of age (here mean values for each population are shown with 95% confident intervals). “D” refers to deciduous and “E” to evergreen populations.

Traits	D-Rouvière	D-Muro	E-Muro	E-Pirio
Number of brood-pair	611	682	266	636
Number of study years	33	28	21	32
Total brood mass (g)	88.47 (86.27, 90.67)	78.79 (77.24, 80.33)	62.18 (59.83, 64.52)	50.86 (49.63,52.09)
Mean nestling mass/brood (g)	10.76 (10.68, 10.84)	10.33 (10.29, 10.37)	10.02 (9.94,10.10)	9.47 (9.42,9.53)
Mean number of nestlings	9.27 (9.12, 9.43)	8.15 (8.02, 8.28)	6.59 (6.39,6.80)	5.99 (5.88,6.11)

We analysed between 266 and 636 broods per population. Total brood mass varied between 50.86 g (E-Pirio) and 88.47 g (D-Rouvière, Table 2.1), indicating differences in total reproductive expenditures directly transferred to the offspring and potential differences in environmental quality across populations. Additionally, mean nestling mass was highest at D-Rouvière and smallest at E-Pirio. Birds in deciduous habitats produced larger clutches than birds in the evergreen habitats.

2.4.2 Variance in total brood mass

Differences between females explained 16% and 28% of the variance in total brood mass in the two deciduous populations, but less than 6% in the evergreen populations (Figure 2.1, Table A1). Year differences explained around 20% of the variance in total brood mass in D-Rouvière and the two evergreen populations but only 5% in D-Muro (Figure 2.1).

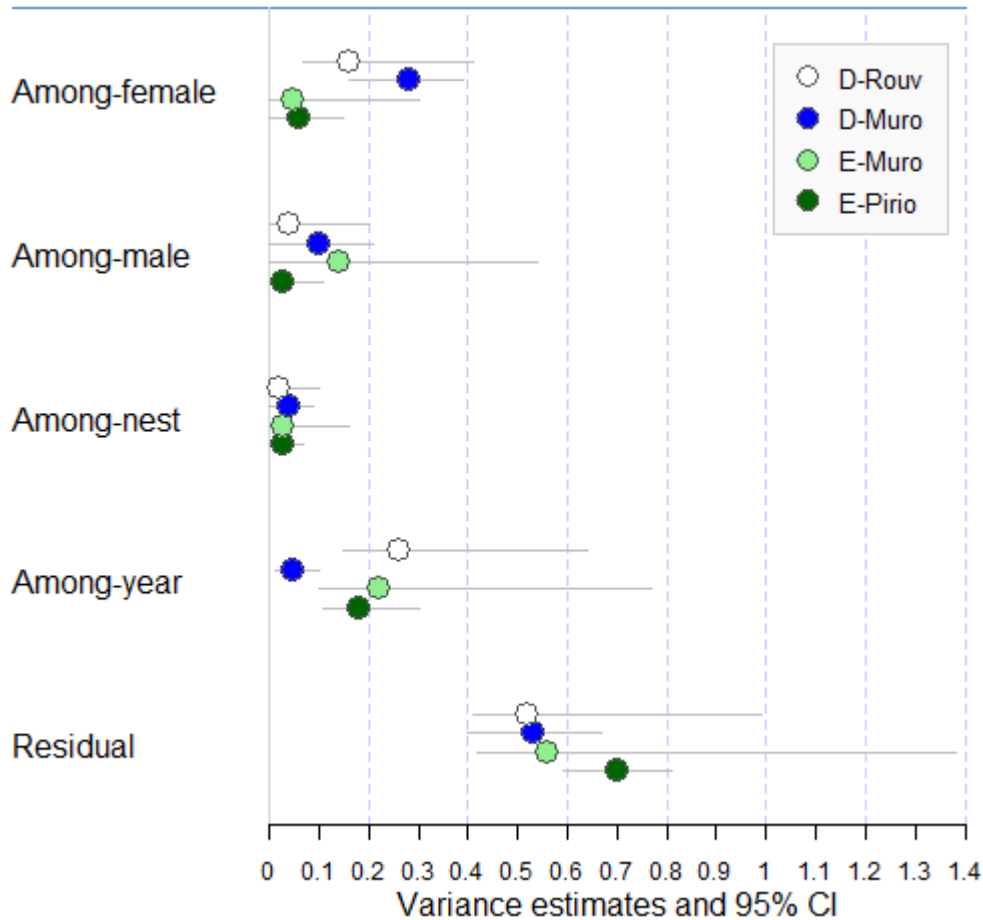


Figure 2.1 Estimates of relative variance r^2 and 95% credible intervals of total brood mass explained by differences between females, males, nests, and years in four Eurasian blue tit populations (for more information see Table A1).

Furthermore, among-male variance was negligible and their credible intervals consistently overlapped zero. The residual variance represented more than 50% of the variance in total brood mass in all populations (Figure 2.1). Residual variance was higher in E-Pirio compared to the three other populations, indicating a potentially higher probability of detecting a trade-off in that population.

Upon adding the variance captured by the random effects of which the credible intervals did not overlap zero, we found that most of the variance in total brood mass was captured at D-Rouvière (42%), E-Pirio (33%), D-Muro (22%) and E-Muro (18%) (Table A1).

2.4.3. Variance in mean nestling mass and number of nestlings

Mean nestling mass increased with mean parent mass in all populations (Table 2.2). Number of nestlings decreased with mean parental mass in E-Pirio and D-Rouvière, although the 95% CI did slightly overlap with 0 in this second population (Table 2.2). Number of nestlings increased with mean parent mass in D-Muro, but here again 95% CI did overlap with 0. There was no clear relationship between nestling number and mean parent mass in E-Muro (Table 2.2). Mean parent tarsus had no effect on mean nestling mass nor nestling number in any population (Table 2.2).

Table 2.2 Fixed effects of parental features on mean nestling mass and nestling number, in four Eurasian blue tit populations. The reference category for the age was adult male and adult female. In bold, estimates with 95%CI not overlapping 0.

Trait	Parameter	D-Rouvière	D-Muro	E-Muro	E-Pirio
		V (95%CI)	V (95%CI)	V (95%CI)	V (95%CI)
Mean nestling mass	Intercept	10.24 (9.95, 10.52)	10.39 (10.29, 10.49)	10.26 (10.07, 10.44)	9.86 (9.70, 10.02)
	Mean parent mass	0.42 (0.28, 0.57)	0.32 (0.24, 0.40)	0.43 (0.27, 0.59)	0.37 (0.26, 0.47)
	Mean parent tarsus	-0.06 (-0.16, 0.05)	0.04 (-0.01, 0.09)	0.07 (-0.02, 0.16)	-0.05 (-0.11, 0.03)
	Juvenile male	0.03 (-0.12, 0.17)	-0.03 (-0.09, 0.04)	-0.17 (-0.31, -0.02)	-0.07 (-0.19, 0.05)
	Juvenile female	-0.09 (-0.23, 0.05)	0.01 (-0.06, 0.08)	-0.20 (-0.34, -0.06)	-0.15 (-0.25, -0.04)
Number of nestlings	Intercept	9.7 (9.15, 10.26)	8.29 (8.00, 8.56)	6.71 (6.22, 7.18)	5.94 (5.63, 6.27)
	Mean parent mass	-0.27 (-0.61, 0.01)	0.27 (-0.25, 0.10)	-0.07 (-0.53, 0.43)	-0.25 (-0.50, -0.01)
	Mean parent tarsus	0.07 (-0.15, 0.30)	-0.08 (-0.25, 0.10)	0.08 (-0.19, 0.34)	0.00 (-0.15, 0.15)
	Juvenile male	-0.07 (-0.38, 0.25)	-0.08 (-0.31, 0.15)	-0.35 (-0.80, 0.10)	-0.34 (-0.62, -0.07)
	Juvenile female	-0.25 (-0.58, 0.06)	-0.23 (-0.46, 0.00)	-0.21 (-0.69, 0.28)	-0.18 (-0.42, 0.07)

We found weak evidence that male age affected mean nestling mass or nestling number (Table 2.2). Juvenile females produced less offspring, but the 95% CI overlapped with 0 in all the populations. Juvenile females produced lighter nestlings than adult females in evergreen populations only, and adult females respectively (Table 2.2). In E-Pirio, juvenile females also had lower mean nestling mass and lower number of nestlings than adult females.

Differences between females explained 26% to 18% of the variance in mean nestling mass in the two deciduous populations, and 7% to 15% in the two evergreen populations (Figure 2.2a, Table A2). Among-male and among-nest variances represented less than 12% of the total variance in mean nestling mass and their 95% CI consistently overlapped zero. Year differences explained

17% to 22% of the variance in mean nestling mass in the deciduous populations and 20% to 33% of the variance in the evergreen populations (Figure 2.2 a, Table A2).

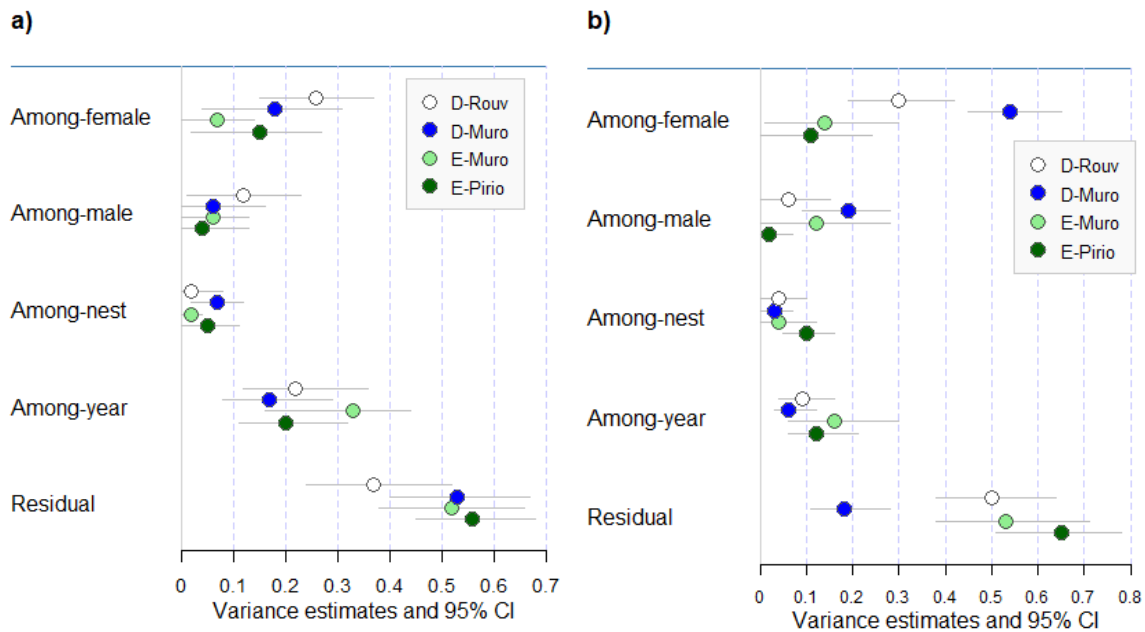


Figure 2.2 Relative variance components and their 95% credible intervals of mean nestling mass (a) and nestling numbers (b) in four blue tit populations. For more information see Table A2.

Residual variance in mean nestling mass explained 18% to 50% of the variance in deciduous populations and 53 to 65% of the variance in evergreen populations (Figure 2.2 a, Table A2). Residual variance in allocation of resources to mean nestling mass was lower in D-Rouvière than in the three other populations, indicating a potentially higher probability of detecting a trade-off in that population.

Females explained between 30% to 54% of variance in number of nestlings in deciduous populations (Figure 2.2b). In E-Muro, females captured 14% of the variance, but the 95% CI approximated 0. In E-Pirio, females captured 11% of the variance in number of nestlings but the 95% CI overlapped zero (Figure 2.2b, Table A2). Variance among males was low, with confidence intervals overlapping zero in all populations except for D-Muro, where males explained 19% of the variance (Figure 2.2b, Table A2). Among-nest variance captured 3% to 4% of the variance in number of nestlings in the deciduous populations, but their 95% CI overlapped 0 (Figure 2.2b,

Table A2). E-Muro captured 4% variance, and the 95% CI overlapped zero. E-Pirio captured 10% variance (Figure 2.2b, Table A2). Among-year variance captured 6% to 9% variance in nestling number in deciduous populations, and 12% to 16% in evergreen populations (Figure 2.2b, Table A2). Residuals captured 18% to 50% variance in number of nestlings in deciduous populations, and 55% to 65% of variance in evergreen populations (Figure 2.2b, Table A2). Residual variance in allocation of resources to number of nestlings was lower in D-Muro than in the three other populations, indicating a potentially higher probability of detecting a trade-off in that population.

Upon adding the variance in mean nestling mass captured by the random effects of which the credible intervals did not overlap zero, we found that most of the variance was captured at D-Rouvière (60%), E-Pirio (35%), D-Muro (33%) and E-Muro (20%) (Table A2). Upon adding the variance in nestling number captured by the random effects of which the credible intervals did not overlap zero, we found that most of the variance was captured at E-Pirio (79%), D-Rouvière (39%), D-Muro (16%) and E-Muro (22%) (Table A2).

2.4.4 Correlations between mean nestling mass and number of nestlings

The among-female correlation between mean nestling mass and number of nestlings was strongly negative in D-Rouvière (-0.41), the associated 95% CI overlapped with 0 in the three other populations (figure 2.3. Table A2). The among-male and among-nest correlations between mean nestling mass and number of nestlings had 95% CI which always overlapped zero in all populations (Figure 2.3. Table A2). The among-year correlation between mean nestling mass and number of nestlings was positive in both deciduous populations but the 95% CI overlapped zero in both cases (Figure 2.3. Table A2). The among-year correlation between mean nestling mass and number of nestlings was strongly positive in both evergreen populations and 95% CI did not overlap 0. The correlation between mean nestling mass and number of offspring was strongly negative in all populations, and with their 95% CI not overlapping 0, except for D-Muro where the correlation was only slightly negative and where the 95% CI overlapped 0.

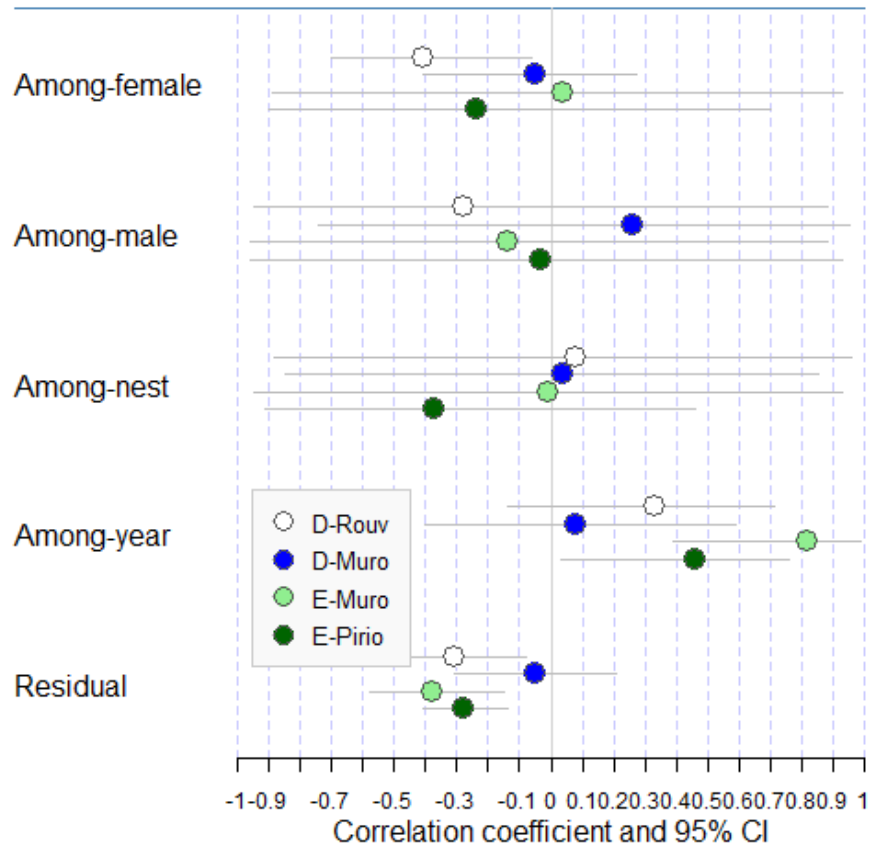


Figure 2.3 Correlations (95%CI) between mean nestling mass and number of nestlings in four blue tit populations.

2.4.5 Comparing method performances in the detection of the quantity-quality trade-off

We ran a Pearson correlation between mean nestling mass per brood and number of nestlings both across the 4 populations (pooled data) and among the 4 populations. Our Pearson correlation across populations revealed a positive correlation ($R_p=0.24$, 95% CI=0.20,0.28). Within the populations, our Pearson correlation detected a trade-off at D-Rouvière ($R_p = -0.25$, 95% CI=-0.32,-0.18) and E-Pirio ($R_p = -0.17$ 95%CI=-0.24, -0.09). The correlation was weak and negative at E-Muro, with the 95% CI overlapping zero ($R_p = -0.01$ (95% CI= -0.13, 0.11)). We found a weak positive correlation at D-Muro, with the 95% CI also overlapping zero ($R_p = 0.03$, 95 % CI =-0.05, 0.10). Therefore, compared to the bivariate model, the Pearson correlation only detected two trade-offs with confidence.

2.5. Discussion

We found evidence for both a quantity-quality trade-off and variance in acquisition in the four blue tit populations we studied. However, the results were more complex than we expected as we found the trade-off at different hierarchical levels depending on the population (for a summary see Table 2.3). Contrary to what we predicted, a higher variance in acquisition relative to the variance in allocation did not lead to a decreased ability to detect the quantity-quality trade-off. Following the van Noordwijk and de Jong (1986) model, the detection of the quantity-quality trade-off is more likely in populations where average levels of acquisition are highest. In our study, the chance of detecting a trade-off would decline from D-Rouvière to D-Muro, to E-Muro, and to E-Pirio (i.e. total brood mass in Table 2.1).

Table 2.3 Summary of all findings based on the models of resource acquisition and quantity-quality trade-off model.

Prediction	D-Rouvière	D-Muro	E-Muro	E-Pirio
Evidence for variation in acquisition				
Among-female variance in total brood mass	Yes	Yes	No	No
Among-male, or among-nest variance in total brood mass	No	No	No	No
Among-year variance in total brood mass	Yes	No	Yes	Yes
Positive among-year correlation between average chick mass and chick number	No	No	Yes	Yes
Positive among-nest correlation between average chick mass and chick number	No	No	No	No
Evidence for variation in allocation				
Among-female, among-male, or among-year variance in nestling number or mean nestling mass	Medium	Strong	Weak	Weak
Evidence for quantity-quality trade-off				
Negative Pearson's correlation coefficient	Yes	No	No	Yes
Negative among-female correlation between mean nestling mass and number	Yes	No	No	No
Negative among-male, among-nest or among-year correlation between mean nestling mass and number	No	No	No	No
Negative within-pair (residual) correlation between mean nestling mass and number	Yes	No	Yes	Yes
Larger parents produced fewer but bigger offspring	Yes*	No	No	Yes
Juvenile males produce fewer but bigger offspring than adult males	No	No	No	No
Juvenile females produce fewer but bigger offspring than adult females	No	No	No	No

* 95% CI slightly overlap 0.

Furthermore, a low variation in resource acquisition relative to variation in allocation (i.e. high V_{al}/V_{aq}) should make the quantity-quality trade-off more likely to be detected. From the residual variance in the models on total brood mass, mean nestling mass and number of nestlings, we could see that E-Pirio showed the lowest potential for variation in acquisition (Figure 2.1), and that D-Muro and D-Rouvière show the highest potential for variation in allocation (Figure 2.2). Our chance of detecting a trade-off should thus decrease from E-Pirio and D-Muro to D-Rouvière, and to E-Muro. This is, however, not what we found. Our results show that evidence for the quantity-quality trade-off was more prominent at D-Rouvière (i.e. within-pair and among-female levels, effects of mean parent mass, Pearson's correlation coefficient; Table 2.3), at E-Pirio (i.e. within-pair levels and effect of mean parent mass, Pearson's correlation coefficient), and to a lower extent at E-Muro (i.e. only at the within-pair level). We, however, did not find any trade-off in D-Muro. We thus have weak evidence to support the prediction of the van Noordwijk and de Jong model that a low variance in acquisition relative to the variance in allocation guarantees the detection of the trade-off.

We found stronger evidence of a trade-off at the within-pair (residual) level, in three out of the four populations (Figure 2.3, Table 2.3), indicating that when a pair produced more offspring these offspring were smaller on average. These results confirm the idea that the quantity-quality trade-off is mostly found at the within-individual (within-pair) level (Stearns 1989, 1992; van Noordwijk and de Jong 1986).

2.5.1 Using bivariate mixed-effect models vs traditional methods in calculating the quantity-quality trade-off

Many studies investigating the quantity-quality trade-off have used correlations and linear models in their analysis (Blackburn 1991; Carrière and Roff 1994; Christians 2000, Brown 2003, Herreras et al. 2007). In this study we used bivariate mixed-effect models (Hadfield 2010; Bürkner 2021), which allowed us to estimate correlations between the traits at different hierarchical levels, within the same population, using multiple covariates. Unlike the Pearson correlation coefficient, the bivariate mixed model does not conflate correlation estimates at the different levels (i.e. among-individual and residual) into one phenotypic correlation coefficient, which may prevent the

detection of the trade-off at underlying levels (Dingemanse and Dochtermann 2012). Our bivariate mixed models found evidence for trade-offs in three out of the four populations. In contrast, the Pearson's correlation coefficient was only negative at D-Rouvière and E-Pirio. Additionally, the bivariate model yielded two positive correlations at the level of year in the two evergreen populations, which the Pearson correlation did not detect. Lastly, we ran a Pearson correlation between quantity-quality using the pooled data from the 4 populations. This analysis resulted in a positive correlation across populations. This may have been due to variation in acquisition among the different covariates (detected in the bivariate model) within each respective population. This variation in acquisition could be masking the underlying quantity-quality trade-offs, as suggested by the van Noordwijk and de Jong (1986) model. Finally, compared to Pearson correlations, our study shows that bivariate models are more informative than traditional methods of analyses.

A notable disadvantage of the applicability of bivariate models is that they are reliant upon large datasets to converge properly and provide reliable parameter estimates, and they are computationally intensive. This explains the large 95% CI associated with several moderate correlation coefficients (Figure 2.2, Table A2), which prevent us from interpreting these results as important. Furthermore, little to no variance for either mean nestling mass or number of nestlings will likely result in either no covariance, or the correlation estimates will be associated with large 95% CI. For example, among-female variance in evergreen habitats are small for both mean nestling mass and number of nestlings. Thus, it is expected to find large 95% CI associated with among-females correlations in these two pops. In contrast, residual variances are much higher and the 95% CI associated with residual correlations are thus smaller. This ultimately means that it is easier to detect a trade-off at this level of variation.

2.5.1 Variance and correlation estimated at the among-year level

Among-year variance represented around 20% of the total variation in brood mass in all the populations except D-Muro (<5%). Among-year variance also represented between 17 and 33% of the total variation in mean nestling mass. However, among-year variance represented only a small proportion (i.e. 6 to 16%) of the total variation in number of nestlings. We also found a highly positive correlation among years, between offspring mass and number, in both evergreen populations, but not in deciduous populations. Given that our measure of nestling mass and number

of nestlings excludes the effects of predation or total nest fatalities due to intense weather patterns (i.e., extreme heat or cold), variation in food resources could be responsible for this finding. This finding suggests that the evergreen habitats show more temporal variation than the deciduous habitats, for example, by producing smaller and fewer offspring when the environment is harsher. Caterpillars are a crucial food source for nestling blue tits (Blondel et al. 1991). In evergreen populations, this food source is limited (Zandt et al. 1990; Dias et al. 1994, Charmantier et al 2016). Thus, interannual differences in caterpillar availability, could help explain the positive relationship between offspring size and number in evergreen populations. The absence of a positive correlation between quantity-quality at the level of year, in deciduous populations, may be because caterpillar abundance is relatively higher there, and not a limited resource. Thus, deciduous birds do not show temporal variation in their investment in quantity and quality as evergreen birds do. Further studies, such as a common garden experiment, could shed light on whether these differences between habitats are the results of evergreen birds showing more plastic responses to environmental changes, as compared to deciduous populations.

2.5.2 Females as main energetic investors

We found that females were important in explaining variation in total brood mass; our index of resource acquisition, in deciduous populations but not in evergreen populations (Figure 2.2). One potential explanation could be associated to variation in laying date. We did not include laying date in our models, but we could assume that adding it would potentially reduce among-female variance in total brood mass and lead to a decrease in total brood mass with time. Laying date differs across the four populations (Charmantier et al 2016) and is heritable (Caro et al. 2009; Charmantier et al 2016; Thorley and Lord 2015).

In our system, a mismatch between breeding dates and the annual peak in caterpillar abundance has strong fitness consequences, such as smaller brood mass, increased metabolic rates, and increased rearing costs per nestling (Thomas et al. 2001). Deciduous populations have relatively more prominent annual peaks in caterpillar abundances, compared to evergreen populations (Zandt et al. 1990; Dias et al. 1994, Charmantier et al 2016). Caterpillars are also the main food item used to provision nestlings in deciduous populations, whereas in evergreen populations, both caterpillars and other arthropods are used (Tremblay et al. 2005). Thus, a mismatch between laying date and

peak caterpillar abundance may potentially have greater consequences in deciduous populations, as compared to evergreen populations.

Other potential explanations could be associated with the populations age structure. Annual reproductive performance varies with female age showing a quadratic effect. Inexperienced young birds and older senescing females have lower reproductive success as compared to middle-aged females. However, annual reproductive success was not affected by the interaction of age and laying date (Bonamour et al. 2020). Furthermore, we included age in our models, although with only two categories, juveniles and adults.

Differences in variance among females in nestling mass could also be explained by differences in the heritability of body mass among the populations. Charmantier et al. (2004) found a lower heritability for body mass at E-Pirio (0.27) than at D-Rouvière (0.35) and D-Muro (0.68). We included mean parent mass in the models, which should have partly accounted for genetics and maternal effects on chick growth and body mass.

Provisioning rates could also be important in determining offspring mass. In blue tits, both parents provision the offspring. Differences between male and female provisioning rates could potentially explain why females seem to invest more in the nestlings than males. However, it is not necessarily the case that higher provisioning rates result in increased nestling mass given that provisioning rates also vary with the size and quality of the prey brought back to the nestlings (Gibb 1955; Royama 1966; van Balen 1973). D-Muro birds provision at higher rates than birds at E-Pirio, but E-Pirio birds compensate by bringing back larger prey items to the nestlings (Tremblay et al. 2005). It is not known, however, how much provisioning rates differ within populations in our system. Females of D-Muro, E-Muro and E-Pirio explore the environment at slower rates than males of the same population (Charmantier et al. 2016). This could mean that within a population, and relative to males, females are more thorough foragers and bring back larger prey items than males. This could partially explain our finding that females invest more in offspring mass than males. Alternatively, males are faster explorers within each population (Charmantier et al. 2016). If males are also superficial explorers and bring back smaller prey sizes more frequently, they may contribute equally to offspring size, just as the females do. Therefore, the relationship between

provisioning rates, prey size, sex, and nestling mass at the within population level would need to be studied.

Note that for the sake of simplicity in the analyses we considered mean nestling mass only, not the variance among nestlings in body mass. Variance in offspring mass may vary among females, or any other random effects. Variance in offspring mass within each brood could reflect some bet-hedging strategies (Valcu et al. 2019) that could depend on parents' traits, habitat characteristics or year variation in food abundance and climate. Although these questions would be interesting to explore, they were out of the scope of our paper, and we wanted to focus on the quantity quality trade-off.

2.5.3 Males captured little variance in nestling mass and number

Males captured little variation in total brood mass, mean nestling mass or number, in all populations (Table A1). This suggests that males are more similar in their contribution to nestling mass and number as opposed to females. Perhaps this is because males show more consistent foraging strategies, within each respective population, whereas females' foraging strategies are more variable within a population. As previously mentioned, males are faster explorers relative to females in all populations, which suggests that they also provision more frequently than females. Still, we do not know the differences in both provisioning rates and prey sizes between the sexes for a population. This information could help us better understand whether foraging strategies vary within a population and whether they determine offspring size or number. Lastly, the low among-male variance in mean nestling mass and number also explains the very large 95% CI associated with the among-male correlations; given that the low variance among males for the traits, the correlation could not be estimated precisely.

2.5.4 The importance of nest site

Our results show that among-nest variance in total brood mass, and mean nestling mass and number was negligible in the four blue tit populations. Furthermore, we did not find any correlations nor trade-offs at the level of the nest. Because we removed all the nests that failed before fledging because of predation, or abandonment, this result suggests that microhabitat around the nests did

not play any role in chick rearing, other than through the risk of predation. One potential reason for the absence of variation among nests in mean nestling mass is that birds in our system travel large distances while foraging. In D-Muro, the mean foraging distance is 25.2 ± 12.3 m, while at E-Pirio, the mean is much larger: 53.2 ± 22.9 m (Tremblay et al. 2005). Thus, nests and their surrounding microhabitats may not influence parents' ability to raise their offspring. However, we excluded broods that underwent complete nest failures in our analyses, as nests differ in their occupation rate over the years, and as occupation rate decreases with the risk of nest failure (Dion-Phenix et al., unpublished). Thus, microhabitats around the nest may be more important for blue tit success in terms of fatal predation and parasitism events than in terms of chick provisioning.

2.5.5 The role of parent mass and size on offspring size and number

We found that mean parental tarsus length, our proxy for skeletal size (Both et al. 2005), had no effect on mean nestling mass nor mean nestling number (Table A3). Heavier parents produced heavier offspring in all populations, which is suggestive of the genetic effect that parents play in offspring size. This supports the findings of previous studies that body mass is strongly heritable in these populations (Perrier et al. 2018). However, note that nestling and parental mass were taken at different ages. Heavier parents may also bring more food to their offspring. Additionally, we found that juvenile males produce smaller nestlings than adult males in E-Muro but not in other populations. We also found that juvenile females produce smaller nestlings than adult nestlings in evergreen populations but not in deciduous populations. It is difficult to make any conclusions regarding these results given that we aged the blue tits as chick, juvenile or adult, instead of a numerical age. As mentioned previously, reproductive success does increase with female age in our system, and plateaus at about age 3 years old, and finally decreases with age (Bonamour et al. 2020).

2.5.6 Conclusion

Evolutionary biology has had a long history of debates about the existence of trade-offs (Brommer 2013; Cheverud 1988; Doehtermann 2011; Falconer and MacKay 1996; Grafen 1984; Hadfield et al. 2007; Kruuk et al. 2008; Lack 1968; Lynch and Walsh 1998; Reznick et al. 2000; Roff 1995; Roff 1996; Rose and Charlesworth 1981; Smith and Fretwell 1974; Svardson 1949;

van Noordwijk and de Jong 1986). One main explanation for the contradictory results of studies on trade-offs is that they are difficult to detect because of all the sources that may affect the relationship between two conflicting traits, and the noise surrounding this relationship. In this study we used a bivariate mixed model and detected the quantity-quality trade-off in all but one population. Our approach revealed that the sources of variation in acquisition that may hide the trade-off and the trade-off itself can be found at multiple levels of variation within a population. Furthermore, our results did not support the prediction of van Noordwijk and De Jong model that a low variance in acquisition relative to the variance in allocation would facilitate the detection of a trade-off. This study highlights the complexity of the processes involved in the acquisition and allocation of resources to competing biological functions.

CHAPITRE 3

CONCLUSION GÉNÉRALE

The objective of this study was to test the van Noordwijk and de Jong model (1986) by examining the quantity-quality trade-off in four populations of nest-box breeding Eurasian blue tits, *Cyanistes caeruleus*. We used a bivariate approach to investigate the trade-offs at multiple levels of variation, including year, female and male ID and nest. We used annual variation in total brood mass as a proxy for variation in resource acquisition dedicated to offspring production. We analyse the among-and within-individual (females and males in a pair) covariance and correlation between number of fledglings (as proxies of quantity) and mean body mass at fledging (as proxies of quality) to see if we had evidence for the van Noordwijk and de Jong (1986) model. In this conclusion, we review the main findings of our study, how they contribute to life history ecology, our study limitations, and potential future research directions.

3.1 Contribution to life history ecology

Our study contributed to life history ecology, by demonstrating that trade-offs at the among-individual level, can be detected at different levels of variation, within a population. Also, our study shows that a trade-off or lack thereof, may be present at the same, or at a different hierarchical level, in another population of the same species. This means that generalizations regarding a trade-off, for a species, may be at best difficult to make. Lastly, our study showed that we have little evidence to support van Noordwijk and de Jong's (1986) model, given that trade-offs were detected when variation of resource acquisition was both high, and low, relative to the variation in resource allocation.

3.1.1 Trade-offs and correlations at multiple levels of variance.

Many studies investigating trade-offs at the phenotypic level, have not partitioned the variance at multiple hierarchical levels (Bromage et al. 1990; Chapin and Chen 2018; Fleming and Gross 1990; Song et al. 2016). Failing to do so, such as in the case of a Pearson correlation analysis, conflates the correlation estimates at both the among-individual and residual levels, resulting in a single phenotypic correlation coefficient. Thus, this method of analysis, may mask underlying

trade-offs, and positive correlations at different levels of variance. Pearson correlations are therefore less precise and less biologically informative, as opposed to a bivariate mixed model approach, which can detect correlations at multiple levels of biologically relevant covariates. For example, our bivariate model found a trade-off at the level of females (D-Rouvière), showing that females that produced more offspring also produced smaller ones. Similarly, our finding of a trade-off at the within-pair level due to the residuals (D- Rouvière, E-Muro and E-Pirio) indicated that when a pair produced more offspring these offspring were smaller on average (Figure 2.3, Table A2). With respect to our bivariate model, this also meant that some unaccounted factor was responsible for the trade-off. Furthermore, the positive correlation at the level of year (E-Muro and E-Pirio), indicated that over the years, mean nestling mass increased with number of nestlings. This finding suggests that the evergreen habitats show more temporal variation than the deciduous habitats, or that evergreen birds show more plastic responses to environmental changes, for example, by producing smaller and fewer offspring when the environment is harsher. Lastly, given that caterpillars are a limited resource in evergreen populations, interannual differences in caterpillar availability, could help explain the positive relationship between offspring size and number. By contrast, the absence of a relationship between year and quantity-quality in deciduous populations, may be because caterpillar abundance is relatively higher there, and thus not a limited resource.

3.1.2 The generalizability of trade-offs within a species.

Interspecific comparisons of the quantity-quality trade-off are difficult to interpret, due to the challenge of disentangling the variation associated with different life histories of the difference species, from individual variation in resource acquisition and allocation. Conversely, a population should reflect differences in resource acquisition and allocation more obviously than a study among species (Brown 2003). However, a notable exception may potentially occur, when different populations of a single species differ significantly in their life histories and behaviours. These differences may lead to differing detections of trade-offs and correlations among the covariates in the different populations.

Our study investigated the quantity-quality trade-off in four populations of Eurasian blue tits *Cyanistes caeruleus* which differed in their life histories and behaviours. We found a positive

correlation between quantity-quality components across populations. However, we found both trade-offs and positive correlations within the populations at differing levels of variance. The positive correlation across populations could be due to differing levels of resource acquisition among different covariates within the 4 populations, which thus masked the underlying trade-offs in accordance with the van Noordwijk and de Jong (1986) model. Furthermore, we might expect that populations with similar life histories and behaviours show trade-offs and correlations at similar levels of variance. We found evidence for this in the evergreen populations, where a trade-off was detected at the level of the residuals, and a positive correlation was found between quantity-quality at the level of year. However, we have evidence to the contrary in the deciduous populations, where no trade-off was found at D-Muro, and two trade-offs were found at D-Rouvière (female level and residual level). Thus, our study demonstrates that generalizations of the detection of a trade-off of a single species, are at best difficult to make. It is therefore important for researchers to keep this in mind when comparing trade-offs at the population level, among different species.

3.1.3 Support for the van Noordwijk and de Jong (1986) model.

Our study showed little support for the van Noordwijk and de Jong prediction that low variance in acquisition relative to the variance in allocation will result in the detection of a trade-off. A higher variance in acquisition did not lead to a decreased ability to detect the quantity-quality trade-off. Based on our model on total brood mass we expected to find a trade-off more easily in the evergreen population (i.e. negligible variance in acquisition among females or males) than in the deciduous ones (i.e. higher variance in acquisition among females and some variance among years; Figure 2.1. and Table A1). Our results, however, show that evidence for the quantity-quality trade-off was more prominent at D-Rouvière (i.e. within-pair, among-female and mean parent mass levels), at E-Pirio (i.e. within-pair and mean parent mass levels), at E-Muro (i.e. only at the within-pair level), and we did not find any trade-off in D-Muro. Therefore, we found little evidence for van Noordwijk and de Jong prediction that $V_{al} > V_{aq}$ guarantees the detection of a trade-off.

3.2 Limitations

3.2.1 Bayesian bivariate analysis

Our analysis utilized Bayesian bivariate models. These models are computationally intensive and reliant upon large datasets. In our study, data collection spanned 34 years, from 1987 to 2021. This involved, the yearly monitoring of hundreds of nest-boxes on both the island of Corsica and mainland France. Thus, sufficient funds and manpower must achieve comparable datasets. Additionally, although Bayesian statistics have gained popularity among researchers, many universities teach Bayesian statistics only at the graduate level, if at all (Dogucu and Hu 2022). Therefore, there still exists a learning gap among researchers who are used to a frequentist approach of analysis.

3.2.2 Underestimating the importance of nest site.

Our results show that among-nest variance in total brood mass, and mean nestling mass and number was negligible in the four blue tit populations. Furthermore, we did not find any correlations nor trade-offs at the level of nest. This suggests that microhabitat around the nests did not play any role in chick rearing. However, we excluded broods that underwent complete nest failures in our analyses, and we know that nest differ in their occupation rate over the years, and that occupation rate is negatively related to nest failure (Dion-Phenix et al., unpublished). Thus, microhabitats around the nest may be more important for blue tit success in terms of fatal predation and parasitism events than in terms of chick provisioning.

3.2.3 Nestling and parental mass were taken at different ages

Heavier parents produced heavier offspring in all populations, which is suggestive of the genetic effect that parents play in offspring size. This supports the findings of previous studies that body mass is strongly heritable in these populations (Perrier et al. 2018). Additionally, we found that juvenile males produce smaller nestlings than adult males in E-Muro but not in other populations. We also found that juvenile females produce smaller nestlings than adult nestlings in evergreen populations but not in deciduous populations. It is difficult to make any conclusions regarding

these results because age was assigned categorically as chick, juvenile or adult, as opposed to a numerical age. An ideal approach would have been to measure both the parent and offspring mass, at the same numerical age, preferably at adult hood once they stopped growing in size. However, this would have relied on recapturing the offspring the following year, which is highly impractical. Additionally, recapture rates are low in our system, meaning that our sample size would be greatly decreased. Alternatively, we could also have standardized our mass measurements by using egg mass of the parents and offspring. However, this would also require that the parents be born in our system, in order for their egg mass to be measured, and would again decrease our sample size.

3.3 Potential future research directions

Future studies could investigate the role of foraging strategies between the sexes on variation in brood mass, within each respective population. We found that females were important in explaining variation in total brood mass; our index of resource acquisition, in deciduous populations but not in evergreen populations (Figure 2.2, Table A1). Conversely, we found that males captured very little variation in total brood mass in any population (Figure 2.2, Table A1). In our system, the birds of deciduous populations are faster and more superficial explorers, whereas those from evergreen populations are slower and thorough explorers (Charmantier 2016). Females also explore the environment slower than males within each respective population (Charmantier 2016). We also know that birds from deciduous populations provision at higher rates than birds in evergreen populations, who compensate by bringing back larger prey items to the nestlings (Tremblay et al. 2005). However, we do not have data on the differences between male and female provisioning rates within populations. Future studies could therefore investigate whether foraging strategies differ between the sexes in relation to offspring size. Foraging strategies may be more similar within a sex and between sexes in evergreen populations where food is limited. Conversely, deciduous populations may show a wider range of foraging strategies among the sexes given that food is more abundant and more variable among years. As such, in a future study, the provisioning rates, prey size, and speed of exploration between the sexes within a population, could be analysed in relation to offspring size.

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APPENDICE

Table A1 Variance components (V) and 95% credible intervals (95% CI) of total brood mass in four Eurasian blue tit populations. r^2 (95% CI) refers to the relative variances and their respective credible intervals.

Population	D-Rouviere		D-Muro		E-Muro		E-Pirio	
	V(95% CI)	r^2 (95% CI)	V(95% CI)	r^2 (95% CI)	V(95% CI)	r^2 (95% CI)	V(95% CI)	r^2 (95% CI)
Random effect								
Female ID	128.41 (52.16, 206.03)	0.16 (0.07, 0.41)	121.02 (72.06, 170.92)	0.28 (0.16, 0.39)	20.36 (0.17, 62.27)	0.05 (0.00, 0.30)	14.42 (0.32, 37.81)	0.06 (0.00, 0.15)
Male ID	35.33 (0.28, 101.08)	0.04 (0.00, 0.20)	44.83 (1.75, 92.04)	0.10 (0.00, 0.21)	53.47 (1.91, 111.72)	0.14 (0.00, 0.54)	8.79 (0.05, 29.59)	0.03 (0.00, 0.11)
Nest ID	16.41 (0.25, 47.52)	0.02 (0.00, 0.10)	18.22 (1.39, 38.37)	0.04 (0.00, 0.09)	10.429 (0.06, 33.43)	0.03 (0.00, 0.16)	7.47 (0.18, 18.10)	0.03 (0.00, 0.07)
Year	202.49 (117.93, 319.456)	0.26 (0.15, 0.64)	21.65 (6.45, 44.21)	0.05 (0.01, 0.10)	87.30 (40.80, 158.72)	0.22 (0.10, 0.77)	47.54 (27.31, 78.57)	0.18 (0.11, 0.30)
Residual	409.68 (326.92, 493.35)	0.52 (0.41, 0.99)	231.26 (176.86, 292.83)	0.53 (0.40, 0.67)	218.97 (162.55, 283.52)	0.56 (0.42, 1.38)	180.16 (152.25, 208.39)	0.70 (0.59, 0.81)
Fixed effect								
(Intercept)	7603.84 (6789.96, 8398.47)		6157.90 (5831.23, 6498.60)		3740.95 (3282.10, 4229.72)		2621.12 (2396.15, 2860.49)	

Table A2 Variance components (V), relative variance and correlations (r^2) estimates and 95% credibility intervals, for mean nestling mass and number of nestlings in four blue tit populations.

Population	Trait	Parameter	D-Rouviere		D-Muro		E-Muro		E-Pirio	
			V(95% CI)	r^2 (95% CI)	V(95% CI)	r^2 (95% CI)	V(95% CI)	r^2 (95% CI)	V(95% CI)	r^2 (95% CI)
Mean nestling mass	Female ID	0.25 (0.14, 0.34)	0.26 (0.15, 0.37)	0.04 (0.01, 0.07)	0.18 (0.04, 0.31)	0.03 (0.00, 0.07)	0.07 (0.00, 0.14)	0.07 (0.01, 0.13)	0.15 (0.02, 0.27)	
	Male ID	0.11 (0.01, 0.21)	0.12 (0.01, 0.23)	0.01 (0.00, 0.04)	0.06 (0.00, 0.16)	0.02 (0.00, 0.07)	0.06 (0.00, 0.13)	0.02 (0.00, 0.06)	0.04 (0.00, 0.13)	
	Nest ID	0.02 (0.00, 0.07)	0.02 (0.00, 0.08)	0.02 (0.00, 0.03)	0.07 (0.02, 0.12)	0.01 (0.00, 0.02)	0.02 (0.00, 0.04)	0.02 (0.00, 0.05)	0.05 (0.00, 0.11)	
	Year	0.20 (0.11, 0.33)	0.22 (0.12, 0.36)	0.04 (0.02, 0.07)	0.17 (0.08, 0.29)	0.13 (0.06, 0.23)	0.33 (0.16, 0.44)	0.10 (0.05, 0.16)	0.20 (0.11, 0.32)	
	Residual error	0.34 (0.22, 0.48)	0.37 (0.24, 0.52)	0.12 (0.09, 0.16)	0.53 (0.40, 0.67)	0.21 (0.15, 0.26)	0.52 (0.38, 0.66)	0.27 (0.21, 0.33)	0.56 (0.45, 0.68)	
Number of nestlings	Female ID	1.18 (0.75, 1.63)	0.30 (0.19, 0.42)	1.77 (1.45, 2.11)	0.54 (0.45, 0.65)	0.45 (0.02, 0.93)	0.14 (0.01, 0.30)	0.26 (0.01, 0.55)	0.11 (0.00, 0.24)	
	Male ID	0.23 (0.00, 0.60)	0.06 (0.00, 0.15)	0.62 (0.28, 0.93)	0.19 (0.09, 0.28)	0.39 (0.01, 0.89)	0.12 (0.00, 0.28)	0.04 (0.00, 0.16)	0.02 (0.00, 0.07)	
	Nest ID	0.18 (0.01, 0.40)	0.04 (0.00, 0.10)	0.08 (0.00, 0.22)	0.03 (0.00, 0.07)	0.14 (0.00, 0.38)	0.04 (0.00, 0.12)	0.24 (0.12, 0.37)	0.10 (0.05, 0.16)	
	Year	0.36 (0.16, 0.63)	0.09 (0.04, 0.16)	0.20 (0.08, 0.39)	0.06 (0.03, 0.12)	0.50 (0.20, 0.95)	0.16 (0.06, 0.30)	0.27 (0.14, 0.47)	0.12 (0.06, 0.21)	
	Residual error	1.95 (1.49, 2.48)	0.50 (0.38, 0.64)	0.59 (0.37, 0.92)	0.18 (0.11, 0.28)	1.69 (1.20, 2.23)	0.53 (0.38, 0.71)	1.49 (1.18, 1.80)	0.65 (0.51, 0.78)	
Cor(Mean nestling mass, Number of nestlings)	Female ID		-0.41 (-0.70, -0.06)		-0.05 (-0.41, 0.27)		0.04 (-0.89, 0.93)		-0.24 (-0.9, 0.7)	
	Male ID		-0.28 (-0.95, 0.88)		0.26 (-0.74, 0.95)		-0.14 (-0.96, 0.88)		-0.03 (-0.96, 0.93)	
	Nest ID		0.08 (-0.88, 0.96)		0.04 (-0.85, 0.85)		-0.01 (-0.95, 0.93)		-0.37 (-0.91, 0.46)	
	Year		0.33 (-0.14, 0.71)		0.08 (-0.40, 0.59)		0.82 (0.39, 0.99)		0.46 (0.03, 0.79)	
	Residual		-0.31 (-0.52, -0.08)		-0.05 (-0.31, 0.21)		-0.38 (-0.58, -0.15)		-0.28 (-0.41, -0.14)	

Table A3 Table 2.2 Fixed effects of parental features on mean nestling mass and nestling number, in four Eurasian blue tit populations. The reference category for the age was adult male and adult female. In bold, estimates with 95% CI not overlapping 0.

Population		D-Rouvière	D-Muro	E-Muro	E-Pirio
Trait	Parameter	V(95% CI)	V(95% CI)	V(95% CI)	V(95% CI)
Mean nestling mass	(Intercept)	10.24 (9.95, 10.52)	10.39 (10.29, 10.49)	10.26 (10.07, 10.44)	9.86 (9.70, 10.02)
	Mean parent mass	0.42 (0.28, 0.57)	0.32 (0.24, 0.40)	0.43 (0.27, 0.59)	0.37 (0.26, 0.47)
	Mean parent tarsus	-0.06 (-0.16, 0.05)	0.04 (-0.01, 0.09)	0.07 (-0.02, 0.16)	-0.05 (-0.11, 0.03)
	Juvenile male	0.03 (-0.12, 0.17)	-0.03 (-0.09, 0.04)	-0.17 (-0.31, -0.02)	-0.07 (-0.19, 0.05)
Number of nestlings	(Intercept)	9.7 (9.15, 10.26)	8.29 (8.00, 8.56)	6.71 (6.22, 7.18)	5.94 (5.63, 6.27)
	Mean parent mass	-0.27 (-0.61, 0.01)	0.27 (-0.03, 0.57)	-0.07 (-0.53, 0.43)	-0.25 (-0.50, -0.01)
	Mean parent tarsus	0.07 (-0.15, 0.30)	-0.08 (-0.25, 0.10)	0.08 (-0.19, 0.34)	0.00 (-0.15, 0.15)
	Juvenile male	-0.07 (-0.38, 0.25)	-0.08 (-0.31, 0.15)	-0.35 (-0.80, 0.10)	-0.34 (-0.62, -0.07)
	Juvenile female	-0.25 (-0.58, 0.06)	-0.23 (-0.46, 0.00)	-0.21 (-0.69, 0.28)	-0.18 (-0.42, 0.07)