SHORT COMMUNICATION

When relative allocation depends on total resource acquisition: implication for the analysis of trade-offs

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Abstract

A central tenet of evolutionary biology states that life-history traits are linked via trade-offs, as classically exemplified by the van Noordwijk and de Jong model. This model, however, assumes that the relative resource allocation to a biological function varies independently of the total resource acquisition. Based on current empirical evidence, we first explored the dependency between the total resource acquisition and the relative resource allocation to reproduction and showed that such dependency is the rule rather than the exception. We then derived the expression of the covariance between traits when the assumption of independence is relaxed and used simulations to quantify the importance of such dependency on the detection of trade-offs between current reproduction and future survival. We found that the dependency between the total energy acquisition and the relative allocation to reproduction can influence the probability to detect trade-offs between survival and reproduction. As a general rule, a negative dependency between the total energy acquisition and the relative allocation to reproduction should lead to a higher probability of detecting a trade-off in species with a fast pace of life, whereas a positive dependency should lead to a higher probability of detecting a trade-off in species with a slow pace of life. In addition to confirming the importance of resource variation to reveal trade-offs, our finding demonstrates that the covariance between resource allocation and resource acquisition is generally not null and also plays a fundamental role in the detection of trade-offs.

Introduction

The hypothesis that life-history traits are linked via trade-offs is central in evolutionary ecology (Stearns, 1992). In 1986, van Noordwijk and de Jong proposed a model predicting that trade-offs between two traits should only be apparent in a population when the individual variation in current relative allocation (B) to one of the traits involved is large compared to the individual variation in the total amount of resource acquisition (A). Even if trade-offs might involve more than two

traits (e.g. Lancaster *et al.*, 2008; Cressler *et al.*, 2010), the van Noordwijk and de Jong model provides an intuitive and simple framework for the study of trade-offs and remains a milestone in evolutionary ecology (Metcalf, 2016). One of its main assumptions is that relative resource allocation to a biological function varies independently of the total resource acquisition. This assumption led to a simple expression for the covariance between the two traits involved in the trade-off. However, current theories of life-history evolution predict a positive relationship between resource acquisition and relative allocation (Erikstad *et al.*, 1998), at least within some range of resource availability (Fischer *et al.*, 2009). There is also strong empirical evidence supporting the dependency between acquisition and relative allocation (Christians, 2000; King *et al.*, 2011).

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For instance, at very low resource availability, individuals may skip a reproductive event so that their allocation to reproduction drops to zero (e.g. Pilastro *et al.*, 2003; Cubaynes *et al.*, 2011), which provides a clear example of dependency between *A* (total resource acquisition, which is a function of the resource availability) and *B* (relative resource allocation, in this case, to reproduction). Such reproductive skipping is widespread for individuals living in environments where prey availability (e.g. Kokko & Ruxton, 2000; Ruf *et al.*, 2006) or climatic conditions (e.g. Ward *et al.*, 2005) vary a lot.

In this study, we first explore, based on empirical evidence, the dependency between the total resource acquisition and the relative resource allocation to some specific life-history traits. We show that such dependency is the rule rather than the exception. Then, we derive the expression of the covariance between traits when the assumption of independence is relaxed, quantifying the importance of such dependency on the detection of trade-offs between life-history traits. We put our study in the context of the fitness costs of reproduction (i.e. allocation to reproduction and its potential reproductive and survival costs) because they correspond to the most studied life-history trade-offs (Stearns, 1992; Roff, 2002). We focus on the dependency between total resource acquisition *A* and the proportion of resource allocated to current reproduction *B*, but conclusions would be the same if we would instead consider the energy allocated to survival (1-*B*). Indeed, they have a symmetrical role and a positive covariance between *A* and *B* means a negative covariance between *A* and 1-*B*.

Biological meaning of potential dependency between *A* (total resource acquisition) and *B* (relative resource allocation to reproduction)

The van Noordwijk and de Jong model assumes that the fraction of energy allocated to reproduction randomly varies around its average $\bar{B}$, and such variation is independent of variation in total resource acquisition *A*. However, several situations where *A* and *B* are either positively or negatively correlated may exist (Fig. 1). The most common situation is probably when *A* and *B* are positively correlated (i.e. a low relative allocation to reproduction when a low acquisition is caused by a low resource availability, and a high relative allocation to reproduction when a high acquisition occurs in response to abundant resources; Fig. 1a–c). However, a negative association between *A* and *B* may also occur. Overall, seven strategies of relative reproductive allocation can be identified, depending on the strength and direction of the correlation between *A* and *B*. For sake of clarity, we will illustrate these strategies with real case studies and discuss scenarios

with a focus on correlation between total acquisition *A* and relative allocation to reproduction *B*. We define the absolute allocation to survival as *S* and the reproductive effort as *R* (corresponding to the absolute allocation to reproduction and equal to $A \times B$) so that $A = S + R$, and the allocation to survival can be written as $S = A - R = A \times (1 - B)$.

Conservative tracking

This strategy of reproductive allocation occurs when the relative allocation to reproduction (*B*) increases at a slower rate than the total energy acquisition (*A*), allowing an increase in the absolute amount of energy allocated to both survival *S* and reproductive effort *R* (Fig. 1a). This strategy conservatively tracks environmental variation. Capital breeders (sensu Jönsson, 1997) in seasonal environments like large herbivores might display such a strategy: in good years they will increase their relative allocation to reproduction while still storing fat during the breeding season, and thereby improving their winter survival (Bårdsen *et al.*, 2008). In poor years, however, they will reduce their allocation to reproduction relative to their acquisition and will allocate resources primarily to fat stores (Bårdsen *et al.*, 2008).

Matched tracking

This strategy of reproductive allocation occurs when the relative allocation to reproduction *B* increases at the same rate as total energy acquisition *A*, allowing the absolute allocation to survival *S* to remain constant and the absolute allocation to reproduction *R* to increase proportionally to *A* (Fig. 1b). This strategy corresponds to a perfect tracking of environmental variation, in which any extra energy is allocated to current reproduction. Such situations are likely to exist in systems where survival during the breeding season is not limited by resource availability (that is, in environments where there are always enough resources during the breeding period to ensure breeder survival) and/or where resources cannot be stored for increasing survival after the breeding season. In such situations, survival will indeed not be associated with changes in food availability. Income breeders (Jönsson, 1997) with potentially high reproductive effort like roe deer (*Capreolus capreolus*) might show matched tracking (Fig. 1b). Indeed, when energy demands peak during early lactation, roe deer females adjust their reproductive effort to the available resources within their home range, leading early survival of fawns to vary tremendously among mothers and from year to year (Gaillard *et al.*, 1997, 1998). An increase in resource acquisition (in spring–summer) is thus associated with an increase in reproductive effort but with no change in female survival, thus following a similar pattern as described in Fig. 1b.
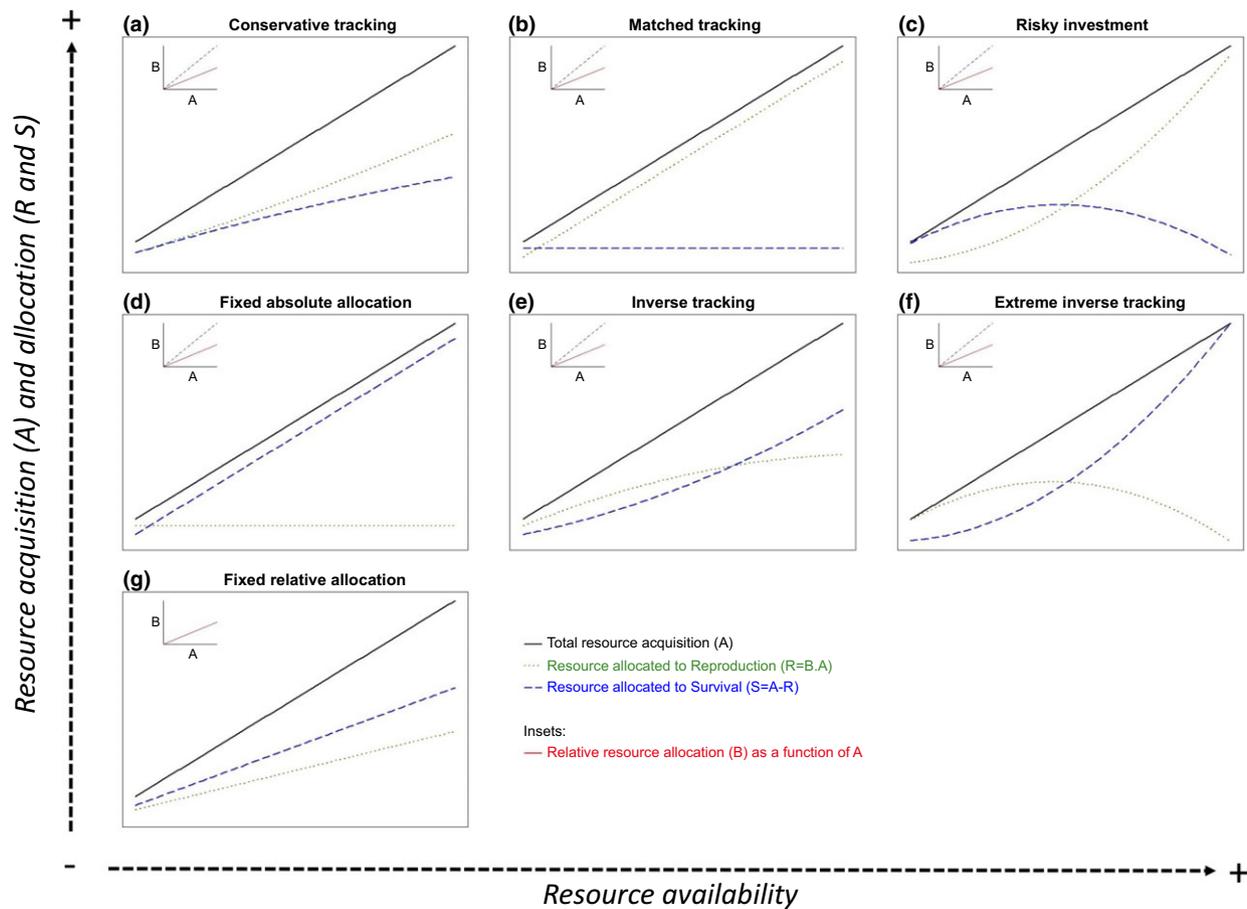
Fig. 1 Potential relationships between the absolute amount of energy acquisition A (black lines), the absolute amount of energy allocated to reproduction (i.e. reproductive effort) R (green lines), and the absolute amount of energy allocated to survival S (blue lines), as a function of a continuum of environmental quality (from low to high resource availability), and according to different patterns of dependencies between A and B (relative resource allocation to reproduction). By definition, $R = B \times A$ and $S = (1-B) \times A$. Insets in every figure represent the corresponding dependency between A and B (red line). In every inset, the dashed black line represents a relation of slope 1 (i.e. same rate of variation in A and B); the position of the red line in relation to this dashed black line indicates whether B changes faster or more slowly than A. The top three panels (a, b, c) represent situations where A and B are positively correlated. The middle panels (d, e, f) represent situations where A and B are negatively correlated. The bottom panel (g) represents the situation where A and B are independent and B is constant (as in the van Noordwijk and de Jong model).

Risky investment

This strategy of reproductive allocation occurs when the relative allocation to reproduction B increases faster than total energy acquisition A, leading the absolute allocation to survival S to decrease and the absolute allocation to reproduction R to increase (Fig. 1c). This strategy corresponds to a risky investment. As an example, edible dormice (*Glis glis*) strongly increase both absolute and relative allocation to reproduction when food resources are high and pay the cost in terms of very low future survival (Ruf *et al.*, 2006). This reproductive tactic is close to semelparity, where '*individuals 'sit tight' for several years until environmental conditions are favorable for*

reproduction' and breed only once or twice in their life (Ruf *et al.*, 2006).

Total energy acquisition A and relative allocation to reproduction B may also be negatively correlated. This means that the proportion of resources allocated to reproduction (B) increases, and therefore, the proportion of resources allocated to survival ($1-B$) decreases, when the total resource acquisition (A) decreases. Such a situation could, for example, correspond to a terminal investment in which individuals trade their survival (or future reproduction) for their current reproduction when the environmental conditions deteriorate. Different strategies can be identified here (Fig. 1d–f), again depending on the strength of the negative covariation between A and B.

Fixed absolute allocation

This strategy of reproductive allocation occurs when A and B are negatively correlated but change at the same rate, so that the absolute allocation to reproduction R remains constant, and the absolute allocation to survival S decreases when total energy acquisition A decreases (Fig. 1d). Individuals playing this strategy consistently allocate the same absolute amount of energy to reproduction irrespective of the environmental conditions, possibly due to a phylogenetic constraint or a canalization process. We were unable to find any empirical example of such strategy. Note that this differs from the van Noordwijk and de Jong model's *fixed relative allocation strategy*, where B instead of R remains constant with changes in total energy acquisition A (Fig. 1g).

Inverse tracking

This strategy of reproductive allocation occurs when A and B are negatively correlated but change at a different rate. The relative allocation to reproduction B may increase at a slower (Fig. 1e) or faster (Fig. 1f) rate than the rate of decrease in total energy acquisition A. Absolute allocation to survival S declines when A decreases whatever the trend in absolute allocation to R (Fig. 1e,f). Individuals playing this extremely conservative strategy reduce their relative allocation to reproduction B when resource availability increases, thereby improving their condition in anticipation of future reproductive attempts. This strategy could be played by primiparous individuals in highly iteroparous species. As an example, young male bison (*Bison bison*) do not increase their reproductive effort during the rut even when intraspecific competition with mature males decreases (Komers *et al.*, 1994).

Consequently, a diversity of situations occurs when A and B covary, either positively or negatively (see, e.g. Christians, 2000; Fischer *et al.*, 2009; King *et al.*, 2011). Understanding such covariance is important to assess fitness costs of reproduction because the detection of costs depends on the relationship linking A and B. The effect of cov*(A, B)* on cov*(R, S)* is investigated in more details in the following section.

Dependency between *A* and *B* and the sign of the covariance between *R* and *S*

As discussed previously, a dependency between the total resource acquisition A and the relative resource allocation to reproduction B is likely to exist in most circumstances. To what extent this dependency affects the detection of trade-offs, however, remains unanswered to date. We start with the equation of the van Noordwijk and de Jong model, based on four quantities: the total amount of resources acquired (A) by an individual, two life-history traits in which these resources can be allocated, that is

reproductive effort (R) and survival (S), and the fraction B of the total energy acquired (A) that is allocated to R. To derive a comprehensive equation defining cov(R, S) as a function of A and B, we assumed bivariate normality for A and B. This assumption is likely relevant for A, the total resource acquisition, but may not be a good approximation for B, the allocation to reproduction. Indeed, B is a proportion bounded between 0 and 1, and hence, a beta distribution is more realistic. However, to our knowledge, it is not possible to calculate analytically the covariance or correlation between A and B (or R and S) when B follows a beta distribution. We thus only aimed to assess the robustness of assuming a normal distribution for B instead of analytically looking for the effects of the dependency between A and B on the model outcome when B follows a beta distribution. Our simulations indicate that the equation based on a binormal distribution for A and B (see eqn 4 below) provides robust results when B follows a beta distribution, especially when the dependency between A and B is taken into account and σ_B^2 is not too high, that is $\sigma_B^2 < 0.05$ in our simulations (see Appendix S1). A $\sigma_B^2 < 0.05$ (equivalent to a standard deviation $\sigma_B = 0.22$) represents a very high variation in resource allocation; in most situations, the variance in resource allocation B will likely be $\ll 0.05$ and the normal approximation for B should give reliable results.

Assuming bivariate normality for A and B, we can write (Bohrnstedt & Goldberger, 1969):

$$\mathrm{cov}(R,S) = \mathrm{cov}(AB, A - AB) = \mathrm{cov}(A, AB) - \mathrm{var}(AB) \quad (1)$$

and

$$\mathrm{cov}(A, AB) = \bar{A}\,\mathrm{cov}(A, B) + \bar{B}\sigma_A^2 \quad (2)$$

$$\mathrm{var}(AB) = \bar{A}^2\sigma_B^2 + \bar{B}^2\sigma_A^2 + 2\bar{A}\bar{B}\,\mathrm{cov}(A, B) + \sigma_A^2\sigma_B^2 + \mathrm{cov}(A, B)^2 \quad (3)$$

where σ_A^2 is the variance in total energy acquisition A and σ_B^2 the variance in relative allocation to reproduction B. By replacing (2) and (3) in (1), we obtain:

$$\mathrm{cov}(R,S) = \left[\bar{B}(1 - \bar{B})\sigma_A^2 - \bar{A}^2\sigma_B^2 - \sigma_A^2\sigma_B^2\right] + \mathrm{cov}(A, B)[\bar{A}(1 - 2\bar{B}) - \mathrm{cov}(A, B)]$$

Or, using cor*(A, B)* instead of cov*(A, B)*:

$$\mathrm{cov}(R,S) = \left[\bar{B}(1 - \bar{B})\sigma_A^2 - \bar{A}^2\sigma_B^2 - \sigma_A^2\sigma_B^2\right] + \mathrm{cor}(A, B)\sigma_A\sigma_B[\bar{A}(1 - 2\bar{B}) - \mathrm{cor}(A, B)\sigma_A\sigma_B] \quad (4)$$

The first term corresponds to the van Noordwijk and de Jong model (situation where A and B are

independent and cor*(A, B)* = 0). When cor*(A, B)*≠0, the sign of the covariance between R and S is affected by the sign and magnitude of the correlation between A and B.

Figure 2 represents the effect of taking this dependency between A and B into account on the probability to obtain a negative covariance between R and S (and thus on the probability to detect fitness costs of reproduction). Our procedure to quantify this effect was as follows: for each combination of cor*(A, B)* and $\bar{B}$, 1000 simulations were performed with different average total energy acquisition $\bar{A}$ and different variances for A and

B (i.e. σ_A^2 and σ_B^2). Cov*(R, S)* was then calculated using both eqn 4 (model where A and B are correlated) and the model from van Noordwijk & de Jong (1986) that assumes independence between A and B (i.e. eqn 4 with cor*(A, B)* = 0). The y-axis (Fig. 2) represents the number of simulations where eqn 4 gives a negative cov*(R, S)* divided by the number of simulations where the van Noordwijk and de Jong model gives a negative cov*(R, S)*. As an example, if we get 300 and 200 simulations with a cov*(R, S)* < 0 using eqn 4 and the van Noordwijk and de Jong model, respectively, the y-value reported here would be $\frac{300}{200} = 1.5$, which means that it
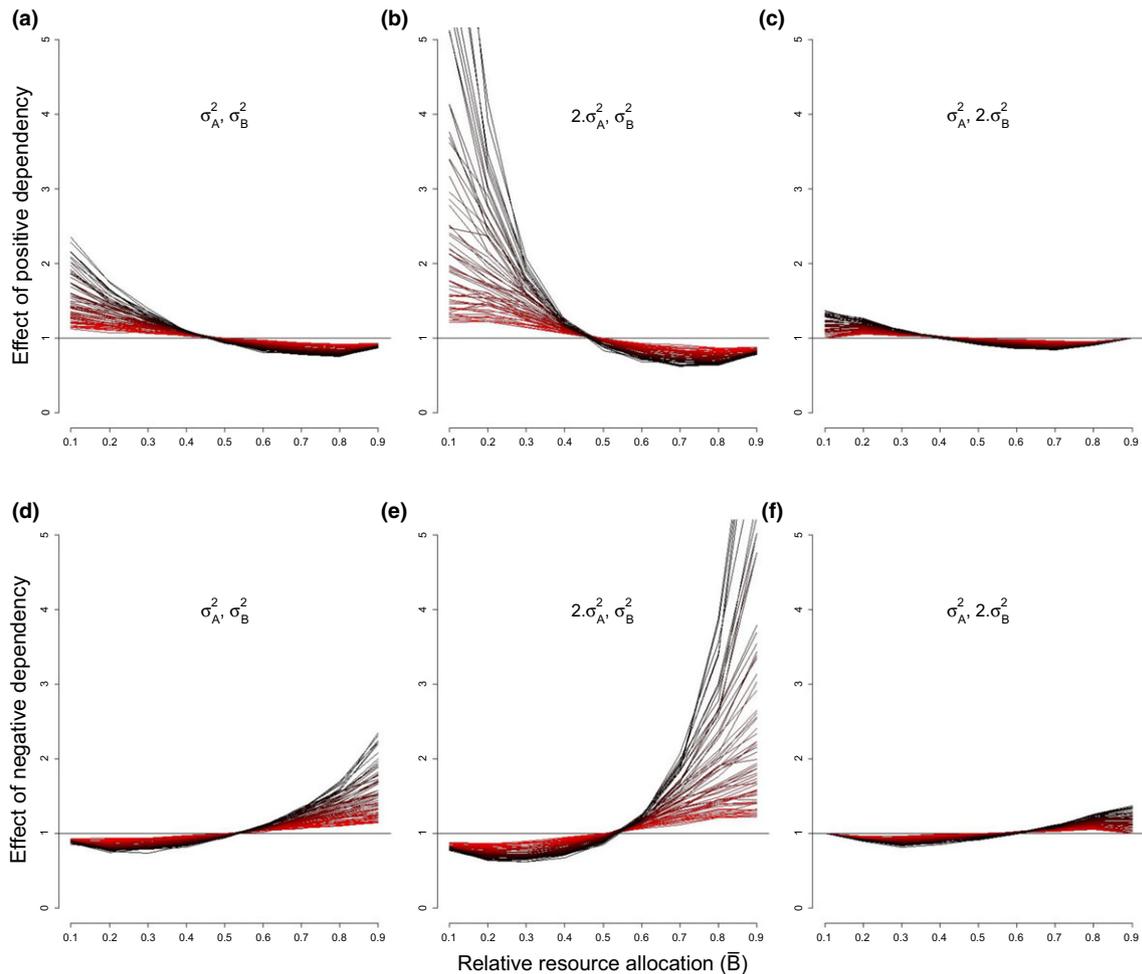

Fig. 2 Effect of the dependency between the absolute energy acquisition A and the relative energy allocation to reproduction B on the sign of the covariance between the absolute allocation to reproduction R and survival S. Curves depict different correlation coefficients between A and B ranging from 0.1 to 0.8 (panels a, b and c), and from −0.8 to −0.1 (panels d, e and f). In each panel, the darker the red, the larger the absolute magnitude of the correlation. The x-axis represents the average relative allocation to reproduction $\bar{B}$. The y-axis represents the effect of taking into account the dependency between A and B (upper panels: positive dependency; lower panels: negative dependency) on the chance to detect a negative covariance, and hence a trade-off, between R and S (see text for details). A y-value of 1.5 means that it is 1.5 times more likely to get a negative cov*(R, S)* when taking into account the dependency between A and B. Central panels (b and e) correspond to increased variance in energy acquisition σ_A^2 (from σ_A^2 to $2\times \sigma_A^2$, while keeping all other parameters constant) and right panels (c and f) to increased variance in energy allocation σ_B^2 (from σ_B^2 to $2\times \sigma_B^2$, while keeping all other parameters constant). Parameter values used in our simulations are given in Appendix S3.

is 1.5 more likely to get a negative cov(R, S) when taking into account the dependency between A and B.

Our simulation results (Fig. 2) confirm that considering the dependency between the total energy acquisition A and the relative allocation to reproduction B can greatly affect the probability to detect trade-offs (between survival and reproduction in our example). One of the main conclusions of van Noordwijk and de Jong was that trade-offs were harder to detect when the variation in resource acquisition σ_A^2 was large compared to the variation in resource allocation σ_B^2 (Fig. 1b,c in van Noordwijk & de Jong, 1986). This conclusion still holds when A and B are not independent (Appendix S2), and when σ_A^2 increases, the probability to detect trade-offs decreases (Appendix S2). Moreover, when σ_A^2 increases (Fig. 2, central panels), the effect of taking the dependency between A and B into account on the probability to detect trade-offs increases. When σ_B^2 increases, the probability to detect trade-offs increases (Appendix S2) and taking into the dependency between A and B has little effect (Fig. 2, right panels).

Moreover, irrespective of σ_A^2 and σ_B^2, the effect of a dependency between A and B on the probability to detect trade-offs is especially pronounced in two situations: first, when A and B are positively correlated (Fig. 2, upper panels) and $\bar{B}$ is low; and second, when A and B are negatively correlated (Fig. 2, lower panels) and $\bar{B}$ is high. In these two situations, a higher correlation between A and B is associated with a stronger effect on the probability to detect a trade-off. When cor$(A, B) > 0$ and B is high or when cor$(A, B) < 0$ and B is low, considering the dependency between A and B has a negative but limited effect on the probability to detect a trade-off between survival and reproduction.

Therefore, our results show that, as a general rule, a negative dependency between the total energy acquisition A and the relative allocation to reproduction B should lead to a higher probability of detecting trade-offs in species with high average relative allocation to reproduction $\bar{B}$, that is species with a fast pace of life with high R and low S. Conversely, a positive dependency between A and B should lead to a higher probability of detecting trade-offs in species with low average relative allocation to reproduction $\bar{B}$, that is species with a slow pace of life with high S and low R.

Conclusion

Both current theory and recent empirical studies indicate that the assumption of independence between the fraction of energy acquired that is allocated to reproduction B and the total energy acquired A is likely to be violated (Christians, 2000; Fischer *et al.*, 2009; King *et al.*, 2011; Robinson & Beckerman, 2013). As the assumption of independence is central to the van Noordwijk and de Jong model, we aimed to develop this model further to assess the consequences of

relaxing this assumption on the probability of detecting trade-offs. We have demonstrated here that a positive or a negative covariation between A and B should occur in various life-history strategies and that both the sign and the strength of the association between A and B have a marked influence on the chances of detecting evolutionary trade-offs. Nevertheless, the relationship between the total energy acquisition and the relative allocation has rarely been evaluated from field studies, and seldom has the covariance between A and B been accounted for when studying fitness costs of reproduction. Moreover, the dependency between A and B (and thus between R and S) may not necessarily be linear (see Appendix S4 for an example). In such situations, estimating the covariance between R and S can be meaningless and lead to erroneous results and interpretations. Assessing whether or not B is dependent on A, and what is the shape of their relationship is therefore of primary importance to study evolutionary trade-offs between life-history traits.

The van Noordwijk and de Jong model has played a crucial role in evolutionary ecology by allowing researchers to understand the importance of controlling for individual differences in resource acquisition when studying trade-offs both in the laboratory and in the wild. This simple model has a high heuristic value and is still frequently used to explain the probability of detecting life-history trade-offs (Metcalf, 2016). Our findings confirm that the take-home message of van Noordwijk and de Jong holds even when relaxing the assumption of independence between resource acquisition and resource allocation. Our work goes one step further by demonstrating that the covariance between total resource acquisition and resource allocation also plays a fundamental role in the detection of trade-offs. Thereby, our finding improves our current understanding of the detection of life-history trade-offs by providing a new theoretical framework, independently of the type of approach (i.e. observational or experimental) applied to collect empirical data on resource acquisition and allocation. Our work calls for the necessity for future studies to assess the covariance between the total energy acquisition and the relative allocation to the focal trait to assess reliably trade-offs among life-history traits.

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Supporting information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1 Robustness of the normal distribution assumption for resource allocation, *B*.

Appendix S2 Relationships between cov(R, S), σ_A^2 and σ_B^2 when A and B are not independent.

Appendix S3 Parameter values used to produce Fig. 2.

Appendix S4 Example of a nonlinear relationship between A and B and between R and S when B follows a beta distribution.