



SYMPOSIUM

Using the van Noordwijk and de Jong Resource Framework to Evaluate Glucocorticoid-Fitness Hypotheses

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Synopsis Ten years ago, two reviews clarified the need to tie glucocorticoid (GC) levels directly to survival and reproductive measures. Three primary hypotheses emerged from that work: the CORT-Fitness hypothesis, the CORT-Adaptation hypothesis, and the CORT-Tradeoff hypothesis. The two reviews have since been cited nearly 900 times, but no clear consensus has emerged supporting one hypothesis over another. We propose that resource availability may be a major confound across studies. Life-history investment is determined by both allocation and acquisition, but current literature testing among the three GC-fitness hypotheses rarely incorporate metrics of resource availability. In 1986, van Noordwijk and de Jong (vN and dJ) proposed the acquisition/allocation Y-model to explain positive versus negative correlations between reproduction and survival across individuals. Their model elevated resources as critical to evaluating individual allocation strategies (favoring reproduction vs. survival), and therefore provides the ideal framework for testing across the three CORT hypotheses. Here, we review the three hypotheses in light of the last 10 years of data, introduce the vN and dJ framework as a model for fitness/GC hypothesis testing, and discuss best practices for using this framework. We believe incorporation of resource availability will reduce unexplained variability in GC-fitness tests, clarify support among the three hypotheses, and allow for greater power in testing across other context dependencies (e.g., life-history strategy) that likely regulate differential allocation to reproduction versus survival as GCs increase.

Historical perspective

Glucocorticoids (GCs) are steroids synthesized primarily in the adrenals and interrenals of vertebrates. They cycle on a diel rhythm, and regulate metabolism and activity at baseline (non-stress induced) levels (Dallman et al. 1993; Landys et al. 2006). Stress elevates GCs; stress-induced GCs have myriad suppressive, stimulatory, and preparative effects on physiology and behavior (see Sapolsky et al. 2000 for review). The term “stress” has several interpretations, and can be misused and misinterpreted depending on context. Here, we use “stress” to represent environmental or physiological challenges that increase GCs above baseline levels.

As early comparative physiologists worked to put stress-induced GC physiology into an ecological framework, a picture emerged of reproductive

suppression to possibly enhance survival. Early work in song sparrows, pied flycatchers, and side-blotched lizards showed elevated GCs reducing territoriality, parental behavior, and song production, all signs of reduced reproductive effort (Denardo and Licht 1993; Silverin 1986; Wingfield and Silverin 1986). Similarly, work across more and less extreme environments pointed to suppression of GC reactivity (the amount of GCs secreted in response to stress) to enable reproduction under harsh conditions. For example, two species of birds breeding in xeric (arid) habitats in Arizona lowered GC reactivity during breeding compared with non-breeding, while two species breeding in less extreme riparian habitat did not modulate their responses seasonally (Wingfield et al. 1992). Populations of shorebirds breeding further north along the Alaskan coast also suppressed their GC

reactivity during the breeding season, possibly to ensure a successful nesting attempt in spite of short breeding seasons (Wingfield et al. 1995). GCs seemed to be mediators of time and energy that refocused resources toward survival, away from non-essential processes such as reproduction and growth. These ideas were first formalized in a review from 1994, as part of a perspectives volume resulting from the International Society of Avian Endocrinologists (“Modulation of the adrenocortical response to stress in birds”; Wingfield 1994); and then again in 1998, in one of Wingfield’s seminal papers: “Ecological bases of hormone-behavior interactions: the “emergency life-history stage” ” (Wingfield et al. 1998). These reviews set the stage for tests of GC action in free-living vertebrates, with the assumption that decreases in reproductive function would enhance survival during environmental challenges.

However, the majority of studies on GC function in free-living animals measured just the intermediate performance metrics (e.g., territory size, song production, and parental behavior), without tying those metrics to more direct fitness metrics: reproductive output or survival. For example, GC implants increased time spent away from the nest in black-legged kittiwakes (Kitaysky et al. 2001), with the assumption that this represents reallocation of resources (foraging time) away from reproduction, toward self-maintenance. GC implants decreased territoriality in side-blotched lizards, again with the assumption of decreased final reproductive output (Denardo and Sinervo 1994).

At the same time, not all data fit the “reproductive suppression-enhanced survival” framework. Elevated GCs in Adélie penguins, tree swallows, and many amphibians and reptiles were associated with greater reproductive effort (Angelier et al. 2008; Bonier et al. 2009b; amphibian and reptile data reviewed in Moore and Jessop 2003), and this effect was variable by morph in side-blotched lizard females (Comendant et al. 2003). In several species, elevated GCs appear to be an integral part of breeding (Orchinik et al. 1988; Schiml and Rissman 1999).

Three hypotheses emerge

In 2008 and 2009, two reviews highlighted the variety of assumptions rampant in the discussion of fitness effects of GCs. Breuner et al. (2008) pointed to the dearth of direct fitness measures in studies of corticosterone (CORT: the primary GC in birds, reptiles, amphibians, mice, and rats) effects. If we are to claim that CORT suppresses reproduction to enhance survival, we need actual measures of fitness

(or as close as we can get), not just measures of performance that hand-wave to fitness effects. Bonier et al. (2009a) also emphasized the need for a greater focus on fitness measures, and, most importantly, pointed out that comparing GC effects across stressed and non-stressed individuals are unlikely to find an enhancement of any function, survival, or otherwise. They clarified that stress (any environmental challenge) represents a decrease in environmental quality; if elevated GCs are associated with a decline in environmental quality, then elevated GCs should always result in a decline in performance metrics, and therefore fitness.

Since publication, these two reviews have been cited almost 900 times, and tests of GC-fitness relationships have exploded. Across stress physiology, there are now many hypotheses regarding the role of GCs in fitness (reviewed in Schoenle et al. 2018). However, three central, competing, testable hypotheses have emerged (Fig. 1).

The CORT-Tradeoff hypothesis: This represents the historic view that GCs redirect physiology and behavior away from reproduction to ensure survival through the challenge. Reproduction and survival trade-off across organisms (Stearns 1992) and this hypothesis predicts a shift toward survival as GCs increase. These ideas have been prevalent in the literature since Wingfield’s reviews (1994, 1998), reaffirmed by Wingfield and Sapolsky review (2003), and named as the CORT-Tradeoff hypothesis by Patterson et al. (2014).

The CORT-Adaptation hypothesis posits that elevated GCs increase reproductive effort. Bonier et al. (2009a) proposed that when challenges are associated with reproduction, resources may be reallocated to reproductive effort, increasing reproductive success. There is no expectation in this hypothesis for allocation to survival-related processes.

The CORT-Fitness hypothesis predicts that as challenge/stress increase, all fitness metrics will decline. Animals facing environmental challenge should have not only elevated GCs but also lower fitness, as compared with non-challenged animals. So when comparing animals facing different levels of challenge, an increase in CORT should reflect a decline in overall fitness. Bonier et al. (2009a) formalized this line of thought with the CORT-Fitness hypothesis, we demonstrate this here (Fig. 1) with predicting a decline in both survival and reproduction under this hypothesis.

Both Breuner et al. (2008) and Bonier et al. (2009a) reviewed the literature to evaluate whether elevated GCs (at either baseline or stress-induced levels) predicted increases or decreases in survival-

or reproduction-related performance metrics. The majority of studies across reviews (75%) supported a decrease in reproduction-related performance metrics with increased GCs, whereas survival-related metrics were split almost 50/50. Only a fraction of the studies presented measured reproductive output or survival—instead of intermediate performance metrics with assumed fitness consequences—but results from those studies were also mixed.

However, studies on GCs and fitness have exploded over the last decade. A recent Web of Science search produced almost 1000 papers concerning “fitness AND (GCs OR corticosterone OR cortisol).” This increase in attention should result in differentiation between hypotheses. Unfortunately, data remain inconclusive. Increased GCs are associated with increased and decreased reproductive output, and increased and decreased survival. Several examples are shown in Fig. 2, all finding clear relationships between GC physiology (plasma, fecal, or feather GCs) and either direct measures of reproductive output: (a) number of young fledged (Patterson et al. 2014), and (b) the choice to attempt breeding or not (Hansen et al. 2016) or survival: (c) days survived after fledge

(Rivers et al. 2012), and (d) return rate to the next breeding season (Koren et al. 2012).

A resource framework for the study of GC-fitness relationships

There is no consensus in the current literature on GC-fitness relationships; however, we believe that current tests are confounded by approach. Two separate processes determine investment in life history traits: allocation and acquisition (Fig. 3; Glazier 1999; Morehouse 2014). Current approaches test only allocation, comparing individuals’ performance without controlling for resource availability (acquisition). In their seminal paper, van Noordwijk and de Jong (1986) clarify the need to consider resources when measuring allocation differences between individuals. Their Y-model took ideas proposed by Lack (1947), Williams (1966) and Stearns (1977), and put them into a framework that could explain both tradeoffs between reproduction and survival, as well as situations that result in positive correlations between the two. They use the following framework (Fig. 3) to illustrate how resource variation (acquisition) can mask expected tradeoffs between survival and reproduction. In this framework, distance from the origin represents the amount of resources available (green lines A1–4). Meanwhile, individuals also fall on allocation lines (orange lines B1–4), which describe the proportion of resources they spend on survival versus reproduction. If there is large variation in allocation strategy (orange lines) and small variation in resource availability (green lines) between individuals (blue shaded area), then survival and reproduction will trade-off across those individuals, as expected.

Hypotheses	Survival	Reproduction
CORT-Tradeoff:	↑	↓
CORT-Adaptation:	-	↑
CORT-Fitness:	↓	↓

Fig. 1 Three hypotheses of CORT-fitness relationships.

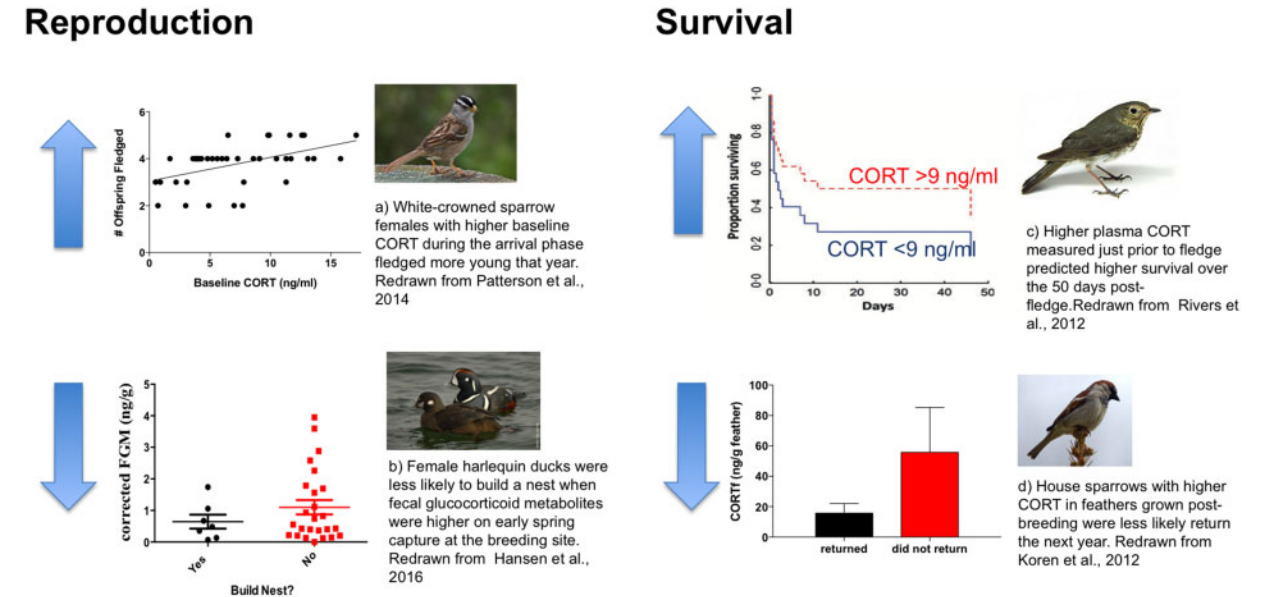


Fig. 2 Recent examples of GC-fitness relationships.

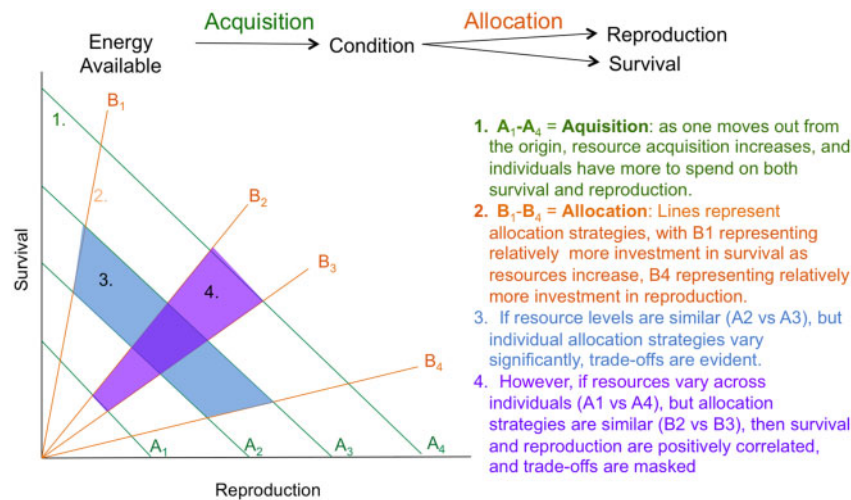


Fig. 3 Both acquisition and allocation determine investment in life-history traits; energy acquisition can mask allocation tradeoffs. The vN and dJ model incorporates resource acquisition to explain why tradeoffs are not always evident among individuals in a population.

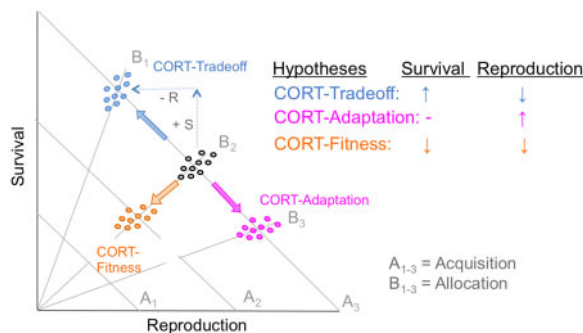


Fig. 4 The GC-fitness hypotheses can be placed within the vN and dJ framework.

However, if allocation strategies are relatively similar, but resource availability is very different (purple shaded area), that trade-off is masked, and there is a positive relationship between the survival and reproduction. This visual heuristic simplifies the math underlying the relationships (units of measure will influence outcomes, see below and Roff and Fairbairn 2007), but is a useful tool to communicate the importance of acquisition when estimating allocation between survival and reproduction. To understand the allocation decisions regulated by GCs, it is necessary to incorporate resource availability into tests across the CORT-Tradeoff, CORT-Adaptation, and CORT-Fitness hypotheses.

In fact, the van Noordwijk and de Jong (vN and dJ) framework is an ideal conceptual model to visualize different predictions among the GC-fitness hypotheses (Fig. 4). It allows us to predict the direction of trait movements given variation in resource availability. Elevated GCs will create variance in allocation strategies (moving animals between lines B1–3), but

resource level will determine whether we see a positive, negative, or no correlation between survival and reproduction. For example, if we have a group of individuals with high resource availability (represented by the black circles in Fig. 3), we can elevate GCs in those animals and measure trait movement. If GC-elevated animals enhance energy spent on survival (blue circles), they must decrease energy spent on reproduction (because resources are held constant, animals must move along the A_3 resource line). This change in allocation decision supports the CORT-Tradeoff hypothesis. However, if GC-elevated animals increase investment in reproduction instead (pink circles), this supports the CORT-Adaptation hypothesis. Support for the CORT-Fitness hypothesis is only possible if resources are reduced, or overall energy expenditure is increased, as a reduction in both survival and reproduction requires movement toward the origin (orange circles).

Placing the GC-fitness hypotheses within the vN and dJ Y-model allows for testing among the predictions for each hypothesis, as each prediction holds a different space in the graph. While the model cannot account for every factor involved in resource acquisition, or expect to incorporate the hierarchical nature of resource allocation, it is good to remember that all models are wrong, but some are more useful than others (Box 1976). Our expectation is that the Y-model will be useful in sorting among the GC-fitness hypotheses.

Measuring acquisition

Resource acquisition is a general term representing a multitude of processes. The amount of food available

in the environment can differ across habitats, but individuals can also vary in their foraging effort, foraging efficiency, assimilation efficiency (movement of nutrients from the gut into the blood), or production efficiency (the metabolic cost of producing tissue). vN and dJ recommend moving all variables into units of energy (e.g., kJ), but how detailed can we get in estimating kJ available for allocation?

To start simply, one can measure food intake in a laboratory setting and estimate amount of energy assimilated. However, we are not prescribing this as the only way forward. Our aim here is to encourage environmental endocrinologists to consider resource availability as they test for GC effects on fitness. Different types of expertise will allow for different estimations of resource availability/acquisition/assimilation. The Y-model breaks the fewest assumptions when all measures (resources, survival, and reproductive metrics) can be translated to a common currency, such as kJ. This, however, can be difficult given the types of measures we can take as field endocrinologists. Hence, our goal is to familiarize the field with caveats intrinsic to the Y-model, and promote accounting for resources whenever and however possible.

Strengths and weaknesses of the vN and dJ approach

Using the vN and dJ approach allows the incorporation of resource acquisition into tests of the GC-fitness hypotheses. If resource intake is widely different between individuals, the amount allocated between reproduction and survival may not reflect differential strategies between those individuals, only a change in strategy within an individual given the amount of resource available.

To account for resources in GC studies, previous studies have altered food availability in captivity (Adams and Lovern 2008; Cornelius et al. 2010; Cote et al. 2010; Lyons and Roby 2011; Will et al. 2014; Robart et al. 2019), accounted for resource levels across territories or habitats (Kitaysky et al. 2010; Escribano-Avila et al. 2013; Lodjak et al. 2015; Madliger and Love 2016), limited resource availability in the field (usually done by making foraging more energetically expensive through feather clipping or increase in weight; Harding et al. 2009; Beaulieu et al. 2010; Patterson et al. 2011; Harris et al. 2017; Rivers et al. 2017; Casagrande and Hau 2018), or compared allocation decisions within individuals across treatments (Berk et al. in review; Vitousek et al. 2018). While these approaches do not come close to estimating kJs assimilated, they can reduce noise in the reproduction and survival

measures we are taking; this will make it more likely we will identify trait movement in response to increased GCs. The vN and dJ model also allows mapping of the three hypotheses into visual space, creating testable predictions that distinguish between hypotheses. Another benefit intrinsic to this approach is the need to measure both survival and reproductive-related processes at the same time. If we are only measuring survival or reproduction, we have much less power to assess effects on overall fitness. If we have measures of both reproduction and survival, we can gain estimates of Λ across different GC levels.

However, there are several drawbacks to this approach. First, it is easiest to control food availability in a lab setting, taking our metrics out of ecological context. One of the strengths of the field of Environmental Endocrinology is that we can test physiology and behavior within natural settings. Another weakness of the lab setting is that we are limiting our measures back to aspects of reproduction and survival, instead of overall reproductive output or annual survival that we can measure in the field. One of the main tenants of Breuner et al. (2008) and Bonier et al. (2009a) was the need to incorporate both the “intermediate performance measure” effects of GCs (e.g., territoriality, song production, and parental care) and more direct measures of fitness. There was too much hand-waving saying that a decline in territoriality, for example, represented a decline in reproduction to benefit survival. If vertebrates can breed in captivity, though, it would be possible to measure many different aspects of reproduction (e.g., in birds: feeding rates, incubation patterns, and nestling growth rates) and survival (e.g., weight change, immune function, and telomerase activity), and combine those multiple metrics into evaluations of reproduction and survival within the same individuals.

If one wants to take the Y model from a visual heuristic to the mathematical assessment of traits, there are further considerations. The vN and dJ model is not without drawbacks. One of the principal issues comes from the assumption that absolute variation in allocation must be larger than absolute variation in acquisition to see a trade-off between reproduction and survival metrics. This is an oversimplification and can lead to spurious conclusions; primarily because the units of reproduction and survival are usually not monotonic (a unit change in one trait equals the energy represented by a unit change in the other trait). vN and dJ state several times that measures need to be converted to equal units of energy, or at least be monotonic in nature.

However, this expectation has been widely ignored in studies using this model. Roff and Fairbairn (2007) elegantly illustrate that it is the coefficient of variation (CV, dividing the variation into the mean) that is important if metrics are not monotonic; hence, it is not just the variance among individuals on each axis (reproduction and survival metrics), but also the mean that variance surrounds that will affect the covariation of the two traits. They also propose a simpler way to evaluate whether and how traits covary: if the variance in acquisition exceeds the sum of the trait variances, then the traits will positively covary; however, if the sum of the trait variances exceeds the variance in acquisition then the traits will trade-off.

However, we are proposing the Y model primarily as a conceptual tool, a heuristic model used to demonstrate the importance of resource acquisition in allocation measures. In addition, we propose that initial investigations into differential allocation between reproduction and survival, and the subsequent effect of GCs on that allocation, be done under known resource availability (lab settings), which avoids several of the problems spelled out by Roff and Fairbairn.

Next steps in GC-fitness studies: context dependency and dose

Incorporating resource availability into GC-fitness tests should clarify support across the three hypotheses. However, there are many factors (contexts) that influence GC physiology and may regulate its effects on fitness. Life-history strategy, for example, appears to be a major determinant of GC effects on fitness, with short-lived species favoring a CORT-Adaptation hypothesis, and long-lived species favoring CORT-Tradeoff (Bokony et al. 2009; Breuner 2010; Hau et al. 2010). Schoenle et al. (2018) recently reviewed many of the major context-dependencies regulating GC physiology, focusing primarily on the nature of the stressor, the life-history stage, and the physiological state of the animal. These three broad categories contain most of the aspects previously considered, and could be useful in categorizing context into broader areas to look for patterns across species. We expect that accounting for resource availability will remove one of the large sources of variation confounding measures of resource allocation during challenge, and allow for clearer investigation of how other contexts influence GC effects on fitness.

There is one aspect, though, that has not been closely considered in the literature: dose. Hormone dose can have major effects on organismal function,

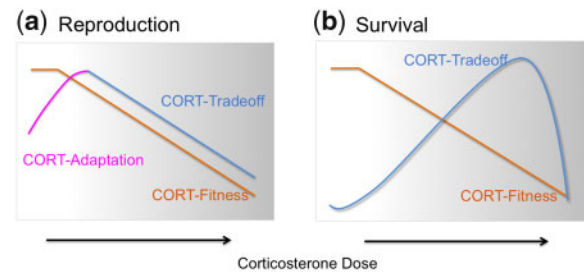


Fig. 5 A prediction for how CORT dose may affect the relationship between CORT, reproduction, and survival. (a) As CORT levels increase, reproductive investment may increase, until levels are high enough that reproduction is suppressed, supporting both the CORT-adaptation and CORT-Tradeoff hypotheses. (b), similarly, increasing CORT may enhance survival (supporting the CORT-Tradeoff hypothesis) until levels become too high, suppressing survival, and providing support for the CORT-Fitness hypothesis.

with evidence for linear and inverted-u-shaped relationships (e.g., Cador et al. 1993; Breuner and Wingfield 2000). For the three primary GC-fitness hypotheses, we believe that dose may account for the major differences between the (1) CORT-Tradeoff and -Adaptation hypotheses and (2) the CORT-Tradeoff and -Fitness hypotheses. (1) The CORT-Adaptation hypothesis states that increases in GCs may enhance reproductive effort (with the idea that this is especially likely when the challenge causing GC increase is related to reproduction—Bonier et al. 2009a). We believe that small elevations in GCs may increase allocation to reproduction up to a point (as discussed in Moore and Jessop 2003). However, when GC levels are well outside of baseline titers—closer to max hormone levels—then GCs will likely follow the CORT-Tradeoff hypothesis and suppress reproduction (Fig. 5a). (2) Under the CORT-Tradeoff hypothesis, GCs will enhance survival; however, there is likely a point at which GC elevation inhibits survival, then matching the CORT-Fitness hypothesis (Fig. 5b). Dose-response studies are some of the hardest studies to complete, given the high variability in GC secretion across individuals, and the lack of precision in hormone dosing techniques. However, we believe that level of GC response to challenge may clarify when situations will follow each of the three GC-fitness hypotheses.

Conclusions

In spite of the phenomenal amount of field data collected regarding GC correlations with, or effects on, fitness in free-living vertebrates, we still do not have a clear understanding of when GCs may enhance reproduction or survival (or neither). However, to understand allocation of resources,

one must account for variation in acquisition. We believe patterns of GC effects will be easier to evaluate when the confound of resource acquisition is recognized and accounted for the best of our ability. Toward this end, we propose using the vN and dJ Y-model to project the three major CORT-fitness hypotheses into graphical space, allowing for incorporation of variation (or constancy) of resources. We propose this primarily as a conceptual model, used to visualize trait movement in space as GCs and resources change. However, it would also be possible to use as an analytical model, calculating covariation between traits.

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