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METABOLISM AS A CURRENCY AND CONSTRAINT IN ECOLOGY

# Competition and the density dependence of metabolic rates

**John P. DeLong*†, Torrance C. Hanley and David A. Vasseur**

*Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT, USA*

## Summary

**1.** Although mass and temperature are strong predictors of metabolic rates, there is considerable unexplained variation in metabolic rates both within and across species after body size and temperature are taken into account. Some of this variation may be due to changes in the rate of food intake with population density, as metabolism depends on the throughput of food to fuel biochemical reactions.

**2.** Using data collected from the literature, we show that individual metabolic rates are negatively correlated with population density for a wide range of organisms including primary producers and consumers. Using new data for the zooplankter *Daphnia ambigua*, we also find genotypic variation in the relationship between metabolic rate and population density.

**3.** The relationship between metabolic rate and population density generally follows a power law scaling, and within a population, density-correlated variation in metabolism can span two orders of magnitude. We suggest that density-dependent metabolic rates arise via competitive effects on foraging rates (both exploitation and interference competition), combined with an activity response to accommodate the resource constraint induced by competition. Standard ecological models predict the kind of density-dependent foraging patterns that could give rise to density-dependent metabolic rates, but this has generally not been investigated.

**4.** Our results indicate that after body mass and temperature, population density represents an important third axis that may account for a large amount of unexplained variance in metabolic rates within and among species. The effect of population density on metabolism has implications for the scaling of metabolic rates from individuals to populations and the relative performance of species and genotypes and therefore also for community assembly and evolution.

**Key-words:** *Daphnia*, density dependence, exploitation, interference, metabolic theory of ecology, scaling

## Introduction

Metabolic rate is the rate of energy uptake, transformation and allocation in a body (Brown *et al.* 2004). Variation in metabolic rate within and across species is strongly tied to organism size, as all else being equal, larger organisms require more energy to function (Kleiber 1932). Temperature also contributes substantially to variation in metabolic rate, typically increasing it exponentially up to a point (Robinson, Peters & Zimmermann 1983). The metabolic theory of ecology (MTE; Brown *et al.* 2004) has proposed an integration of these factors by combining the allometric scaling of metabolism with an exponential process that influences the height, but not the slope, of the body size scaling relationship (Gillooly *et al.* 2001). MTE makes the compelling case that metabolism represents a primary constraint on ecological processes because everything an organism does depends on the biochemical processes that are indexed by metabolic rate (Brown *et al.* 2004). In other words, all forms of activity, from foraging to movement to reproduction, contribute to the total energetic flux of an organism, and therefore, nearly all interactions between an organism and its environment are reflected in its metabolic rate.

Metabolism also varies markedly among individuals of a species and through time for any particular individual (Rosa & Seibel 2008; DeLong & Hanson 2009b). This variation is often associated with resource supply and can

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*Correspondence author. E-mail: jpdelong@unl.edu
†Present address: School of Biological Sciences, University of Nebraska, Lincoln, NE 68588 USA.

be quite pronounced, yet MTE explicitly assumes that the metabolic rate of an organism is not dependent on resource supply but is rather tied most directly to demand (Brown *et al.* 2004; Marquet, Labra & Maurer 2004; Price *et al.* 2010). Nonetheless, metabolic rates are known to differ between 'active' and 'endogenous' (basal, resting, or standard) levels when organisms actively acquire resources from the environment vs. use internal reserves to maintain minimal physiological functions, respectively (DeLong *et al.* 2010). Furthermore, metabolic rates are proportional to ingestion rates (Kersting & Leeuw-Leegwater 1976; Verity 1985; Schmoker & Hernández-León 2007), indicating a strong dependence of metabolism on food intake.

It is possible that overlooking resource supply as a source of variation in metabolic rates has contributed to some mismatch between MTE predictions and empirical observations that have led some to reject the MTE. For example, Chalcraft & Resetarits (2004) were unable to predict the rate of fish predation on tadpoles using only predator mass in a MTE framework; it was also necessary to consider predator density. So, while mass and temperature are major drivers of metabolism, variation in resource supply, including variation that is mediated by population density, also may play a role in determining metabolic rates. Indeed, some work has shown that metabolic rates vary continuously with population density, ostensibly in response to variation in per capita resource levels (DeLong & Hanson 2009a; Jaffe 2010), but neither the underlying mechanisms nor the generality of such patterns have been evaluated.

The goals of this study were twofold. First, we sought to determine whether population density is an important source of variation in metabolic rate, and whether different species and/or genotypes within a population show the same qualitative relationship between density and metabolic rate. We did this by collating observations on density-dependent metabolic rates (and net primary production in one case) from the literature and by conducting additional laboratory studies with different genotypes of the zooplankter *Daphnia ambigua*. Second, we attempted to reveal the mechanisms underlying density-dependent metabolic rates by exploring the relationship between foraging rate and density that emerges from a standard model of consumer-resource dynamics. Given the link between foraging and metabolic rates, we asked whether the observed patterns of metabolic rates might mirror those of foraging rates. We conclude by suggesting that population density is a primary source of variation in metabolic rate and that by considering density, the MTE and other frameworks are likely to provide improved predictive and explanatory power.

## Materials and methods

### DATA

To determine whether population density is an important driver of metabolic rates in general, we gathered data from the literature on metabolic rates measured at a range of population densities for a variety of taxa including algae (3 species), protists (3), cladocerans (2), eusocial insects (6) and one spider species. Sources and information on these data are listed in Table 1, and all data sets are included in Appendix S1. In the cases of *Tetrahymena pyriformis* and *Chlamydomonas reinhardtii*, there was more than one data set, so we chose to include the largest set for both species in our analysis. We included the unused data sets in Appendix S1, and note that similar density-dependent metabolic rate patterns were found in each (DeLong & Hanson 2009a, 2011).

We fit a power law function to the relationships between metabolic rate and population density using reduced major axis (RMA) regression on log-transformed data. Log-transformation is appropriate because metabolic scaling data typically have multiplicative error structure (Xiao *et al.* 2011). RMA regression is appropriate for regressions where $x$-axis error is similar in magnitude to $y$-axis error, which is typically the case for estimates of population density and metabolic rates. In the cases of the cladocerans and the spider, however, we used ordinary least squares (OLS) because exact densities were known and experimentally controlled. For both types of regression, we conducted Monte Carlo simulations with 1000 samples drawn with replacement to determine the mean and 95% confidence intervals of the slope of each relationship.

We conducted additional measurements on the metabolism of the cladoceran *D. ambigua*. We used a fluorescent oxygen probe (DO-400, Golden Scientific, Temecula, CA) to measure the change in oxygen partial pressure in liquid media due to the consumption of oxygen. We measured oxygen consumption of 1, 2, 3 and 4 individuals in 0·6-mL microcentrifuge tubes with COMBO medium (Kilham *et al.* 1998). Probes were inserted through a hole punched in the top of the tube, and the entrance was sealed with tacky rubber; headspace was eliminated by slightly overfilling prior to sealing tubes. Individual daphnids were taken from stock cultures maintained in COMBO medium and fed non-limiting concentrations of *Scenedesmus obliquus*, and each one was rinsed in clean COMBO medium prior to measurements. Each individual belonged to one of five different clonal lines (clones C, E, I, J, K). All clones were hatched from sexually-produced ephippia taken from Bride Lake (East Lyme, Connecticut) and reared in the laboratory for at least six months to remove maternal effects (see Walsh *et al.* 2012) for more details). To determine whether there is a genetic component to the density-dependent metabolic rate patterns, we measured the oxygen consumption of each clone separately and analysed differences in slopes and intercepts among clones using ANCOVA.

### MODELLING ANALYSIS

To investigate whether the density-dependent metabolic rate patterns could be linked to the density dependence of foraging, we also extracted the foraging rates from a numerical simulation of a standard consumer-resource model. The goal here was to determine the shape of

**Table 1.** Regression results for metabolic rate and net primary productivity vs. population density for 15 species

| Species | Slope (± CI) | $R^2$ | Notes | Reference |
|---|---|---|---|---|
| Algae | | | | |
| *Chlamydomonas reinhardtii* | −0·94 (−1·24 to −0·69) | 0·71 | Density varied through time, resources available | DeLong & Hanson (2011) |
| *Galdieria sulfuraria* | −0·93 (−1·49 to −0·75) | 0·88 | Density manipulated, resources available | DeLong & Hanson (2009a) |
| *Scenedesmus obliquus*, metabolic rate | −0·91 (−1·20 to −0·60) | 0·80 | Density manipulated, resources not available | Walsh *et al.* (2012) |
| *Scenedesmus obliquus*, net primary productivity | −0·86 (−1·10 to −0·62) | | Density manipulated, resources available | Walsh *et al.* (2012) |
| Protists | | | | |
| *Amoeba proteus* | −0·80 (−0·94 to −0·64) | 0·73 | Density manipulated, resources not available | Nässberger & Monti (1984) |
| *Blepharisma* sp. | −0·77 (−1·11 to −0·50) | 0·90 | Density manipulated, resources not available | DeLong & Hanson (2009a) |
| *Tetrahymena pyriformis* | −1·05 (−1·39 to −0·91) | 0·85 | Density varied through time, resources available | DeLong & Hanson (2009b) |
| Eusocial insects | | | | |
| *Odontomachus bauri* | −0·43 (−0·50 to −0·29) | 0·73 | Density manipulated, resources apparently available | Jaffe (2010) |
| *Camponotous rufipes* | −0·43 (−0·55 to −0·37) | 0·87 | Density manipulated, resources apparently available | Jaffe (2010) |
| *Zacryptocerus pusillus* | −3·05 (−3·66 to −2·46) | 0·98 | Density manipulated, resources apparently available | Jaffe (2010) |
| *Pogonomyrmex californicus* | −0·40 (−0·61 to −0·23) | 0·40 | Density varied through time, resources available | Waters *et al.* (2010) |
| *Nasutitermes ephratae* | −0·81 (−1·05 to −0·58) | 0·43 | Natural variation in density among nests, resources available | Muradian, Issa & Jaffe (1999) |
| *Apis mellifera* | −0·49 (−0·59 to −0·41) | 0·61 | Cross-study data set with different methods | Hou *et al.* (2010) |
| Spider | | | | |
| *Latrodectus hasselti* | 0·09 (0·0 to 0·21) | 0·03 | Density manipulated, resources available | Stoltz, Andrade & Kasumovic (2012) |
| Cladocerans | | | | |
| *Simocephalus vetulus* | −0·99 (−1·21 to −0·64) | 0·73 | Density manipulated, resources not available | Hoshi (1957) |
| *Daphnia ambigua* | −0·95 (−1·16 to −0·75) | 0·72 | Density manipulated, resources not available | This study |

All regressions were reduced major axis except for the cladocerans which were ordinary least squares because the number of individuals was experimentally manipulated and known exactly. The 95% confidence intervals are from 1000 bootstrapped samples. None of the negative relationships have confidence intervals that include zero, and only the spider *Latrodectus hasselti* has a positive slope.

density-dependent foraging rates predicted by standard ecological theory and then to compare these patterns to the empirical patterns seen in the density-dependent metabolic rate data.

The model we used has a birth–death framework that is the basis for most of the dynamic population models in ecology:

$$\frac{dR}{dt} = g(R) - Cf(R)$$
$$\frac{dC}{dt} = C(ef(R) - \mu) \qquad \text{eqn 1}$$

This model has an equation for the dynamics of a resource, $R$, and a consumer species, $C$. The resource increases via some function, $g$, and declines according to the foraging rate of the consumer, $f$, which is dependent on resource density. The consumer species grows by converting ingested resources into new consumers at efficiency, $e$, and dies at a natural mortality rate, $\mu$.

There are two relevant observations to make about Equation 1. First, there is a specific per capita foraging rate, $\hat{f} = \frac{\mu}{e}$, that occurs when the consumer population is at equilibrium. As the population grows monotonically from low densities, $f$ will converge to $\hat{f}$ from initially larger values (DeLong 2011). Second, the parameter $e$ is a combined parameter that describes the net production of offspring after resources are *ingested, assimilated and allocated* (DeLong 2011). This process is the very definition of metabolic rate (Brown *et al.* 2004), and therefore, this model predicts that metabolic rates will be proportional to ingestion rates, at least at time scales that exceed the capacity of the organism to use stored fuel to maintain metabolic rates at relatively high levels (Verity 1985; Hood & Sterner 2010). Given this proportionality, density-dependent metabolic rates are predicted to parallel density-dependent foraging rates. Note that biomass-based consumer-resource models view the loss term in Equation 1 as 'metabolic' because in those models, biomass (carbon) is lost from the population due to both mortality and respiration (Yodzis & Innes 1992). In contrast, we emphasize that metabolic rate is fuelled by ingested food, similar to dynamic energy budget theory (Kooijman 2009), and interpret the loss term in the model to be losses of individuals rather than metabolic losses.

We conducted numerical solutions of Equation 1 in Matlab © using standard ODE solvers, and we used the solutions to show how foraging rates vary with population density. We set the growth function g = D(S–R), where $D$ is the dilution rate and $S$ is the supply rate, as in a chemostat model. We set

$$f = \frac{aRC^m}{1 + ahRC^m},$$

which is a standard Hassell-Varley-Holling functional response model (Hassell & Varley 1969; Arditi & Akçakaya 1990; DeLong & Vasseur 2011), with area of capture, $a$, handling time, $h$, and mutual interference, $m$. We used this functional response because both interference and exploitation competition jointly affect foraging rates, and we were interested in determining whether one or the other was more likely to generate density-dependent metabolic rates given the foraging patterns that emerge. With the HVH functional response, exploitation is always present above a certain population density, but interference can be included by setting $m < 0$. By solving the model both with and without interference, we were able to compare how each form of competition influences the relationship between foraging rates and population density. In this simulation, we varied $m$ from 0 to −1, and for the remaining parameters, we used the following values: $D = 50$, $S = 100$, $a = 0{\cdot}2$, $h = 0{\cdot}02$, $e = 0{\cdot}3$, $\mu = 0{\cdot}05$. Similar results were obtained for a wide range of parameters.

## Results

Nearly all species, including heterotrophic protists, algae, cladocerans and eusocial insects, showed density-dependent metabolic rates that were well described by a power law function (Table 1, Fig. 1). Variation in density caused up to two orders of magnitude variation in metabolic rates (Fig. 1). Fourteen of the 15 regressions revealed exponents that were significantly negative, indicating that observed metabolic rates are density-dependent in nearly all of the data available to date. The exponents of the negative relationships ranged from −0·43 to −3·05, with only one value more negative than −1·05 (Fig. 1, Table 1). The mean slope was −0·85. The one positive relationship was slight, with a slope of 0·09. The algae *S. obliquus* also showed density-dependent net primary production (i.e. net oxygen change measured in the light; Fig. 2). For *S. obliquus*, the exponents for dark and light measurements were very similar (−0·91 and −0·86, respectively; Table 1).

Metabolic rates for *D. ambigua* were density-dependent ($F = 105{\cdot}0$, $P < 0{\cdot}001$), but they also varied among genotypes ($F = 2{\cdot}8$, $P = 0{\cdot}054$; Fig. 3). Although clones K, I and J were not statistically different from each other, the intercept of E was higher ($P = 0{\cdot}03$; −22·92 vs. −23·26) and that of C was lower ($P = 0{\cdot}01$; −23·67 vs. −23·26) than the overall (mean for all clones) intercept, and the slope of clone E was steeper than the overall slope ($P = 0{\cdot}01$; −1·47 vs. −0·94).

Numerical solutions of Equation 1 showed that foraging rates declined with population density towards the equilibrium value $\hat{f}$ (Fig. 4). When there was no interfer-

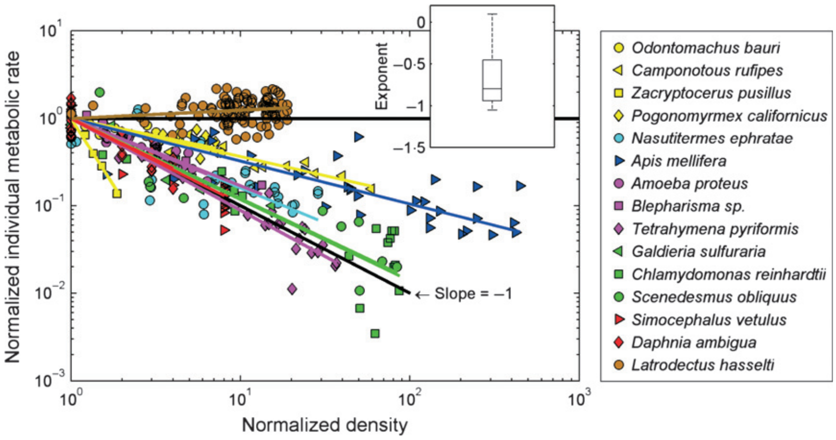

**Fig. 1.** Density-dependent metabolic rates. Rates are normalized to 1 at a population density of 1 to facilitate slope comparisons and grouped by colour (yellow = ants, cyan = termites, blue = bees, pink = protists, green = algae, red = crustaceans, and brown = spider). The solid black lines indicate a slope of −1 (labelled) or 0 (horizontal line). See Table 1 for sources and regression fits. The inset shows a box-plot of displayed slopes (exponents), excluding the −3 value for *Zacryptocerus pusillus* for clarity.

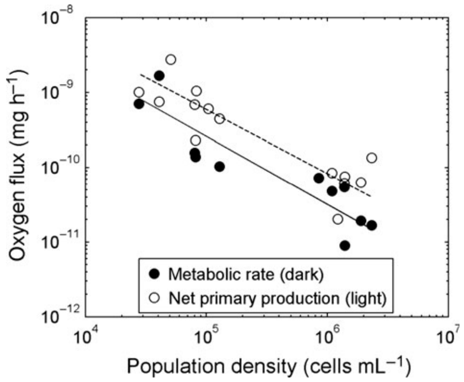

**Fig. 2.** Density-dependent metabolic rates and net primary production for the algae *Scenedesmus obliquus*. See Table 1 for regression details.

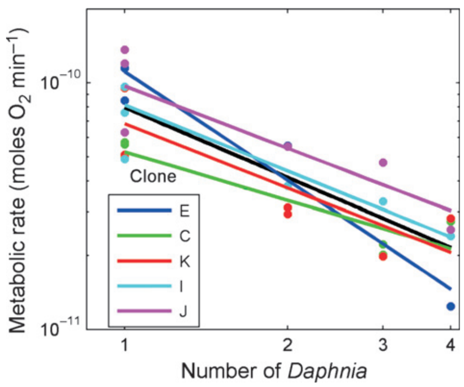

**Fig. 3.** Density-dependent metabolic rates of *Daphnia ambigua*. Each colour represents a different clonal line drawn from the same population at Bride Lake in East Lyme, CT, USA. The black line is the overall fit to all the data.

ence competition, that is $m = 0$, foraging rates were at their maximum at low densities and then began to decline at higher densities, resulting in a two-phase relationship between foraging rate and density. (This two-phase relationship depends upon initial conditions being such that resource availability exceeds maximum per capita foraging rates.) When interference competition was added, that is $m < 0$, the two-phase relationship became less pronounced and moved towards a power law relationship as $m$ approaches $-1$. Thus, the pattern of density-dependent foraging rates produced in the simulations was very similar to the patterns of density-dependent metabolic rates, as long as intermediate to high levels of interference were included (Fig. 1).

## Discussion

Density-dependent population processes such as growth rate are widespread (Sibly *et al*. 2005), so it is reasonable to suggest that individual energetics would be as well. Our analysis of published data on metabolic rates indicates that nearly all species tested to date do indeed show density-dependent metabolic rates. Despite the variety of

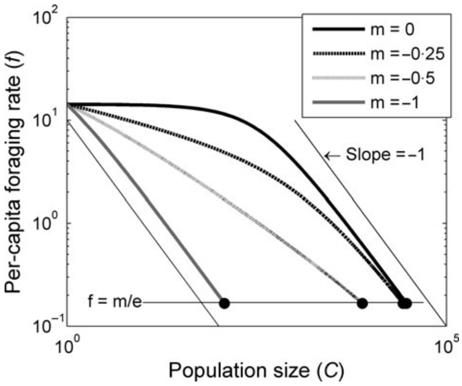

**Fig. 4.** The relationship between per capita foraging rate and population density that emerges from the solution of a simple consumer-resource model. As population density increases (through population growth), foraging rate declines towards the equilibrium foraging rate $\hat{f}$. When there is no interference competition ($m = 0$), a two-phase relationship may emerge, but with typical levels of interference ($m = -0{\cdot}5$ to $-1$), power law like relationships between foraging rate and population density emerge. These patterns are strongly reminiscent of the pattern between metabolic rate and population density, and the dependence of metabolic rate upon food intake suggests that density-dependent metabolic rates may emerge from this pattern. See Methods for simulation details.

taxa (including unicellular and multicellular, aquatic and terrestrial, and colonial and unitary organisms), all but one showed a common pattern of a power law like decline in metabolic rate with population density. The declines in metabolic rate commonly spanned an order of magnitude, but in some cases, the variation ranged up to two orders of magnitude (Fig. 1), indicating that population density has a large effect on observed metabolic rates. This much variation is frequently seen in the scatter around temperature-normalized plots of metabolic rates vs. body size (Sieg *et al*. 2009; DeLong *et al*. 2010), some of which could be due to variation in population density.

What causes density-dependent metabolic rates? The requirement of mass and energy balance suggests that variation in foraging rates may generate density-dependent metabolic rates. Standard models broadly used in ecology are implicitly energetic, and indeed, a breakdown of the conversion parameter $e$ shows that metabolic rate *per se* is incorporated into all simple consumer-resource models (DeLong 2011). Because the conversion parameter $e$ is a multiplier on foraging rate, ecological theory predicts that metabolic rates will show density dependence that closely follows the density dependence of foraging rates. Indeed, numerical solutions of Equation 1 revealed that foraging rates may be expected to vary with density in a manner that is remarkably similar to the observed density dependence of metabolic rates (Figs 1 and 4). That is, foraging rates and metabolic rates both may vary with population density following a power law like relationship.

Both interference and exploitation competition can produce power law like relationships between foraging rate and population density (Fig. 4). When competition is solely exploitative ($m = 0$), however, a two-phase relationship may emerge. This two-phase pattern has not been seen in density-dependent metabolic rates, perhaps because (i) metabolic rate data are insufficiently precise to detect the transition, especially at very low densities, (ii) resource levels are not usually high enough to generate the transition from maximal metabolic rates to food-constrained rates or (iii) interference competition is at the root of the density-dependent metabolic rate pattern. This latter possibility is supported by the widespread presence of interference competition with values that centre on a mean of $m = -0{\cdot}8$, very close to the mean density-dependent metabolic exponent of $-0{\cdot}8$ to $-0{\cdot}9$ (DeLong & Vasseur 2011). At this time, no study has attempted to pair measurements of density-dependent foraging rates with metabolic rate measurements under the same conditions to determine whether they have the same scaling slopes, so the type of competition that sets the foraging and metabolic rates in any system is unknown. In addition, comparisons among groups such as terrestrial and aquatic organisms cannot be made without additional work.

An alternative hypothesis is that organisms respond to increasing density by lowering their activity levels. Waters *et al.* (2010) found that mean ant velocity decreased with colony size, indicating that activity may account for some of the change in these populations. This explanation is also supported by the observation that some of the density-dependent metabolic rate measurements were conducted without the presence of prey in the measurement chamber (Table 1). Thus, over the time scales of these measurements, organisms at varying densities experienced the same resource conditions (i.e. none) and would have been more likely responding to the density of conspecifics rather than experiencing an immediate food constraint. Some of the other data sets, however, came from studies in which food was available during the measurements, indicating that competition-based constraints may have been operating.

We cannot at this time robustly determine whether the density dependence of metabolic rate arises from competitive interactions, activity adjustments, or both. It is likely that in the face of competitive constraints on food availability, changes in activity levels would be a suitable way of reducing individual demand to match the supply of resources. Thus, reductions in foraging velocity would be a good way of slowing down metabolic requirements in response to competition-based reductions in food availability. Indeed, Houston & McNamara (2013) show how increasing foraging intensity can lead to lower body condition because metabolic costs increase faster with foraging intensity than net energy intake. This process would favour a decrease in foraging activity in the presence of competition, making it likely that activity modifications and resource constraints are both part of the density dependence pattern. In addition, our measurements of oxygen consumption and net oxygen production for *S. obliquus* suggest that these two processes work together (Fig. 2). The same pattern of density dependence was observed in net oxygen production when organisms were measured in the presence of the light resource and in oxygen consumption, when there was no light, and thus, resource levels were nil at all densities. That the same pattern of density dependence emerged suggests that density-dependent metabolic rates reflect both a resource constraint and a response to that constraint.

Of the 15 data sets, only the spider *Latrodectus hasselti* showed a positive relationship between metabolic rate and population density (Stoltz, Andrade & Kasumovic 2012). This deviation from the general trend of negative relationships is perhaps due to an experimental design that prevented competition and promoted developmental differences. In this study, male spiders growing over the course of the experiment were surrounded by a variable number of other male spiders, but each spider was physically separated from the others. This design thus precluded interference or exploitative competition, and therefore, the absence of negative density-dependent metabolic rates may represent an exception that proves the rule. Instead of competitive effects, the spiders displayed developmental plasticity in response to their neighbours, showing an increase in growth rate as the density of neighbours increased. Stoltz, Andrade & Kasumovic (2012) attributed the faster growth rate to a sexual selection process that favoured larger males. Because production and metabolism are tightly linked (Brown & Sibly 2006), it seems likely that these spiders increased their metabolic rates to support faster growth, given the unimpeded availability of resources and the lack of competition.

The time scale of observation should influence the detection of density-dependent metabolic rates. Many organisms may store resources in their body and use them to maintain homoeostatic physiological processes in the face of temporal variation in food intake (Schmidt-Nielsen 1997). In this way, metabolic rates may be controlled in part by the rate of release of resources from their internal bodily stores (Maino *et al.* 2013). Thus, each organism may have a time scale at which their metabolic rates would respond to a change in the average rate of resource uptake, as well as other time scales where it would not. In this study, the organisms measured are generally quite small, and so, the time scales at which their metabolism would respond to resource availability would be very short, on the order of hours in most cases. Larger organisms, including birds and mammals, are likely to integrate their food levels over days or longer periods, while their metabolic rates generally are not measured at time scales at which population dynamics could alter their population density and resource levels. Thus, it remains an open question whether density-dependent metabolic rates are detectable in larger organisms, but in principle, anything that displays density-dependent population growth rates could be experiencing density-dependent food intake and metabolic rates.

The slope of the density-metabolism relationship may vary with temperature. In the algae *C. reinhardtii*, the slope of the relationship became much shallower at warmer temperatures (−0·4 at 25 °C compared with −0·79 at 20 °C), with a strong effect on the resulting population dynamics (DeLong & Hanson 2011). Such variation is suggestive of a change in interference or activity patterns rather than exploitation effects, as with exploitation we expect the slope to remain close to −1 (Fig. 4). The change in slope in this study was also linked to a change in body size, with *C. reinhardtii* becoming about five times larger in the warmer temperature. At this time, it is unclear how temperature or body size influences interference competition (DeLong & Vasseur 2011), either separately or interactively, but direct changes in interference parameters with temperature have been seen for beetles (Lang, Rall & Brose 2012). Because temperature influences other parameters that drive population dynamics via the functional response (Dell, Pawar & Savage 2013), it is clear that an integrated investigation into the consequences of temperature on both exploitation and interference competition, and therefore of density-dependent metabolic rates, is warranted.

Although the different species showed qualitatively similar responses of metabolic rate to density, measurements on different clones of *D. ambigua* also revealed genotype-specific patterns of density-dependent metabolic rates (i.e. variation in the slope and intercept of the relationship; Fig. 3). These differences could influence how each clone responds to high and low densities, creating opportunities for some clones to thrive at times when others do not. In this way, variation in how metabolic rates vary with density could influence eco-evolutionary dynamics (Bolnick *et al.* 2011; Walsh *et al.* 2012), as individual metabolic rates are tightly linked to demographic rates and thus performance (DeLong & Hanson 2009b, 2011). For *D. ambigua*, clone E could be high performing at low density but low performing at high density, while clone J could be high performing at all densities (Fig. 3), altering the relative population growth rates of each clone through time and influencing the genotypic composition of the population. Much additional work needs to be performed to better understand the link between metabolic rates, demographic rates, and eco-evolutionary dynamics.

In conclusion, the MTE has achieved considerable success in explaining broad-scale patterns by focusing on the role of body size and temperature as metabolic constraints (Allen, Brown & Gillooly 2002; Meehan, Jetz & Brown 2004; Price *et al.* 2010). These successes have come even though short-term metabolic rate measurements are applied to long-term and large spatial scale patterns. Our results suggest that population density may be as important to the real-time energetics of organisms in nature as body size and temperature, where short-term variation in rates may be linked to local-scale dynamics. Density-dependent metabolic rates may be relevant to scaling up energetics from individuals to populations (DeLong & Hanson 2009a), the understanding of population and eco-evolutionary dynamics, the viability of species as invaders, and the susceptibility of rare species to density effects. Nonetheless, even after considering mass, temperature and density, there remains additional variation in metabolic rates, perhaps due to genetic or other individual-level factors, which merit further exploration.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Data sets for density-dependent metabolic rates used in DeLong *et al.*, 'Competition and the density dependence of metabolic rates'.