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Running Title:

Heritability of resting metabolic rate in a bird

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Abstract:

Predicting the impact of climate change on biodiversity requires understanding the adaptation potential of wild organisms. Evolutionary responses depend on the additive genetic variation associated with the phenotypic traits targeted by selection. We combine 5 years of cross-fostering experiments, measurements of resting metabolic rate (RMR) on nearly 200 wild collared flycatcher (*Ficedula albicollis*) nestlings and animal models using a 17-year pedigree to evaluate the potential for an evolutionary response to changing environmental conditions. Contrary to other avian studies, we find no significant heritability of either whole-organism, mass-independent or mass-specific RMR, but report a strong effect of nest environment instead. We therefore conclude that variation in

nestling RMR is explained by variation in the early-life environment provided by the parents. We discuss possible underlying specific parental effects and the importance of taking different mechanisms into account to understand how animals phenotypically adapt (or fails to adapt) to climate change.

Introduction:

Phenotypic adaptation to changing environments can either be mediated by plastic changes or, with sufficient additive genetic variation, via evolutionary changes (Lynch and Walsh 1998). A key step towards predicting a population's ability to evolve in response to climate change (i.e. evolutionary rescue; (Carlson et al. 2014) is to estimate the degree of additive genetic variation and/or heritability associated with the relevant phenotypic traits. Resting metabolic rate (RMR), or the amount of energy needed for self-maintenance (Burton et al. 2011), mechanistically links thermoregulation to life history theory (Kersten and Piersma 1987; Nilsson 2002), as it mediates energy allocation-acquisition strategies. The literature describes three types of RMR (Tieleman et al. 2009): whole-organism RMR (a measure of RMR without accounting for mass), mass-independent RMR (the residual of the log RMR as explained by the log of body mass) and mass-specific RMR, where the response variable is RMR divided by mass (reviewed in Table 1 for endothermic vertebrates). It should be noted that mass-specific metabolic rate has been criticized, as this method is unlikely to eliminate the effect of body size on metabolic rate, and introduces statistical biases (Packard and Boardman 1999). We have nevertheless included this measure in the present work for comparison purposes. These different metrics account for the relationship between RMR and mass, given the expectation of an allometric relationship (McNab 2002). Changes to metabolic rate allow endotherms to mediate heat production, leading to thermal adaptation (Klaassen et al. 2004; Naya et al. 2013). Empirically, metabolic rate has been shown to be highly correlated with minimum thermal conductance in 127 rodent species (Naya et al. 2013), solidifying the conceptual link between RMR and thermal regulation. Further, metabolic rate plays an important role in mediating environmental effects on physiological performance, and has been repeatedly linked to key life-history traits, including survival, lifetime reproductive success, growth, immunity and social dominance (Pettersen et al. 2018; White et al. 2019). However, regardless of the selection pressures, RMR cannot evolve without a heritable component (Lynch and Walsh 1998).

RMR is typically a plastic trait (Scholander et al. 1950; Norin and Metcalfe 2019), changing both seasonally and in response to changes in ambient temperature (McKechnie 2008) and diet (Criscuolo et al. 2008). It can be affected by early life experiences as shown by brood

size manipulations in tree swallows (Burness et al. 2000), zebra finches (Verhulst et al. 2006) and pied flycatchers (McFarlane et al. 2018). However, in addition to this plasticity, RMR is typically repeatable (Nespolo and Franco 2007) and heritable (Pettersen et al. 2018). In passerines, the narrow sense heritability of RMR varies from 0.20±0.35 in stone chats to 0.587±0.23 in blue tit nestlings (see Table 1 for a summary of previous findings in endothermic vertebrates, ± is followed by standard errors (SE)). However, many of these studies, including ours, have used nestlings cross fostered a few days post hatching, making it difficult to differentiate between early life effects, specifically those before hatching and just post hatching, and heritable effects (Nilsson et al. 2009). In contrast, early maternal effects are important for the metabolic rate of some mammals, including leaf eared mice (Nespolo and Franco 2007). Fitting effects of both heritability and early life (such as nest of origin) in a model aiming at parsing out the sources of variation in RMR is required to detect maternal effects (McAdam et al. 2014). To our knowledge, this has not yet been done in wild birds.

We estimated the heritability of whole-organism, mass-independent and mass-specific RMR in the collared flycatcher (*Ficedula albicollis*), a model system for ecological and evolutionary studies. It is a small, migratory passerine bird that mainly breeds in Central and Eastern Europe but is expected to expand its breeding range further north in response to climate change (Huntley et al. 2008). We studied this species at the Northern-most edge of its range, on the Swedish island of Öland, which was colonized by this species about 60 years ago. Collared flycatchers have since displaced pied flycatchers (*Ficedula hypoleuca*) from the preferred breeding sites (Rybinski et al. 2016) but face stronger selection to breed earlier (Sirkiä et al. 2017). Pied flycatchers are less sensitive to phenological mis-match, with an advancing peak in caterpillar larvae abundance due to on-going climate change (Sirkiä et al. 2017). A possible explanation to this difference between the two otherwise very similar species is that pied flycatcher nestlings´ RMR exhibit an adaptive plastic response to current food availability, which we did not observe in collared flycatcher nestlings (McFarlane et al. 2018). Thus, variation in RMR may be linked to fitness effects of climate chance both directly in terms of thermal adaptation but also indirectly through

abilities to deal with phenological mismatches with prey species, as suggested from our previous work on the flycatchers.

The apparent lack of adaptive plastic changes in nestling RMR in response to varying temperatures and food availability across years in collared flycatchers (McFarlane et al. 2018) means that nestlings could suffer important fitness consequences of future environmental variation in the absence of evolution in these traits. We thus ask if nestling RMR, measured as whole-organism, mass-independent and mass-specific RMR, is heritable in collared flycatchers. To address this question, we capitalized on partial reciprocal cross fostering experiments combined with quantitative genetic 'animal models' statistical methods to estimate variance components. These variance components include additive genetic variance (V_a), maternal effects associated with the nest of origin (V_m), foster nest effects (V_e), and residual effects (V_r). By placing siblings in different nests before hatching (i.e. as eggs) or when they were three days old we could estimate variance components and differentiate between three often confounded effects, namely additive genetic effects, early life maternal effects and foster nest effects on resting metabolic rate. If early life maternal effects or foster nest effects explain variation in nestling RMR rather than additive genetic variance, adaptive changes in this phenotypic trait would need to occur through evolutionary changes in parental traits that influence the early (e.g. yolk content) and/or late (e.g. offspring feeding patterns) rearing environment.

Methods:

We collected data on breeding collared flycatchers on the Swedish island of Öland as part of a long-term survey (Qvarnström et al. 2010). Briefly, between 2002 and 2018, we monitored over 2000 nestboxes and caught, ringed and measured all breeding birds and their nestlings. All nestlings were weighed at six and 12 days of age, and additionally when eight days old for experimental nestlings (see below). For quantitative genetic analyses based on animal model approaches (Kruuk 2004), we built a pedigree using a total of 25131 collared flycatchers. This is a social pedigree, where the attending adults are assumed to be the parents of the nestlings. There is approximately 17% extra pair paternity in our population (Cramer et al. 2016), but the 'animal model' (see below for further description) is fairly

resilient to extra pair paternity (Firth et al. 2015). All experiments were approved by the Linköping Animal Care Board, (Dnr 10-13), and performed in accordance with all relevant guidelines and regulations.

Partitioning genetic and environmental effects on resting metabolic rate

To partition environmental and genetic effects on nestling RMR, we took advantage of several years of large-scale cross-fostering experiments performed between 2013 and 2018, in addition to our long-term pedigree. While these three experiments differ slightly in their design as they were originally used to answer different questions (plasticity in RMR, (McFarlane et al. 2018) and parental effects on plasticity, on-going experiment), they all enable us to compare full siblings raised either by their own or by foster parents, across multiple years and environmental conditions. We are reporting measurements of morphology and metabolic rate on nestlings that were raised either with their biological parents or with foster parents from three days of age, in nests of either similar brood sizes as the ones they were born in (58 nests, 2013-15, Figure S1A) or reduced (-2) or increased (+2) brood sizes compared to the ones they were born in (19 nests, 2014-15, Figure S1B, see also McFarlane et al. 2018). Additionally, we include measurements on nestlings that were incubated by a different female than their biological mother and raised by a second set of foster parents from three days of age (15 nests, 2017-2018, Figure S1C). In some cases, this female was a closely related pied flycatcher female (Supplementary Methods). For nests where eggs were swapped during incubation, we removed eggs from their original nest approximately two days after the biological mother started incubating, and the entire clutch was transferred to a foster nest for incubation. For all cross-fostering of three days old nestlings, we did partial brood swaps, where two to four nestlings were exchanged between pairs of nests (2 against 2 for equal brood sizes, 2 against 4 for brood size manipulations, and two halves of each clutch split between two separate secondary foster nests for eggs that had been swapped before incubation, see supplementary methods for more details). Nests were paired by laying date, brood size (± 2 nestling) and average nestling mass, to ensure that nestling growth would not be affected by fostering *per se* (Hadfield et al. 2013). All nestlings were individually marked using toenail clipping at three days of age (Qvarnström et al. 2009), and received standard alphanumeric metal rings when six days old, which allowed us

to determine the nest of origin and keep track of each individual through the different cross-fostering events.

Measuring Resting Metabolic Rate

We measured the RMR of eight-day old nestlings from nests involved in the cross foster experiment. Briefly, nestlings were taken from their nest in the evening, brought to the field laboratory, and measured for O_2, CO_2 and water vapour pressure using a respirometer (Sable Systems, Henderson NV, USA) while asleep. Nestlings were returned to their nest within two hours of sunrise, to disrupt the parental feeding regime as little as possible. See Supplementary Methods for details on the equipment we used, calibration, flow rate, and the calculation of RMR from the raw gas measurements.

Statistical Methods

Mixed effect 'animal models' decompose variance using the phenotypes of related individuals to determine how much related individuals resemble each other, as this resemblance can be attributed to additive genetic variance (Kruuk 2004). We used a pedigree that began with 25131 individuals, and we pruned this to 405 informative individuals using 'prunePed' in MCMCglmm (Hadfield 2010). We fit animal models to three different RMR measures: whole-organism RMR (mL/min of oxygen), mass-independent RMR, where we used log RMR as the response variable and log mass as a covariate, and mass-specific RMR, where the response variable is RMR divided by mass. For all models, we included experimental treatment as a fixed effect, and four random effects, namely, the 'animal' effect of the pedigree, which is an estimate of additive genetic variance, a nest of origin effect, which estimates early life factors, including maternal effects, incubation and parental effects up until 3 days of age, nest of rearing and year. In all cases, we used parameter expanded prior probabilities as we wanted to have non informative priors (Hadfield 2010), and have reported the posterior modes and 95% confidence interval of all estimated variance components. All animal models were run for at least 500 000 iterations, with 100 000 iteration burn in, with thinning as needed to sample 1000 points. Some models were run for longer (up to 15 000 000 iterations) to achieve convergence, which

was tested by assessing the autocorrelation, as well as Heidelberger and Welch (Heidelberger and Welch 1983) and Geweke (Geweke 1991) convergence diagnostics.

Results:

We found an average whole-organism RMR in 184 collared flycatcher nestlings of 1.68±0.9 (SD) mL/min. This is consistent with what was previously reported in this population (1.54± 0.7 mL/min; (McFarlane et al. 2018)). The average mass of eight-day old collared flycatchers was 13.0±1.5 grams, and their average mass-specific RMR 0.127±0.06 mL/min/g.

Experimentally increasing clutch size or cross-fostering to different females during incubation (Experiments B &C, see Supplementary Material) did not affect either whole-organism or mass-independent RMR (Supplementary Table 1). However, nestling collared flycatchers that we incubated by pied flycatcher females had a lower mass-independent RMR than those incubated by females of their own species (Supplementary Table 1).

We found extremely low heritabilities of whole-organism, mass independent and mass specific RMR respectively (Table 2, Figure 1). However, both nest of origin effects and foster nest effects were moderate for whole-organism and mass-independent RMR, but lower for mass-specific RMR (Table 2, Figure 1). Generally, the lower estimates of variance explaining mass-specific RMR could be due to a large year effect on this trait (Table 2 and Supplementary Table 2).

Since we found substantial early life effects on RMR, we used a trait-based method to explore if there are specific maternal traits that explain this plasticity (Supplementary Material). We re-ran our animal models ad hoc with maternal phenotypic traits (age, tarsus, wing length) included as fixed effects. We still found extremely low heritabilities, and relatively high effects of both biological and foster nests. However, none of the included maternal traits significantly explained variation in nestling RMR. When an environmental variable, habitat quality, was included, the estimate of early nest effect was slightly lower, although not significantly so (Supplementary Table 2).

Discussion:

We did not find significant heritable variation for whole-organism, mass-independent or mass-specific RMR of eight-day old collared flycatcher nestlings. We did, however, find strong nest of origin effects on nestling RMR, particularly on whole-organism and mass-independent RMR (Table 2). Since these nestlings were cross-fostered as eggs or when three days old, we conclude that nestling RMR is strongly influenced by the early environment provided by the mother, possibly mediated through egg yolk composition, incubation and brooding behaviour.

The RMR estimates that we report here are higher than previous RMR estimates in birds of this size (Stager et al. 2015), and adult collared flycatchers (McFarlane et al. 2016) and adult or nearly grown pied flycatchers (Bushuev et al. 2011). A possible explanation is that eight-day old nestlings are in a period of exponential growth, which is expected to be very energetically expensive, and thus our estimates of RMR ought to be considered "RMR plus the cost of growth" (McFarlane et al. 2018). Further, as we did not fast our nestlings prior to measurement of RMR, some nestlings with a particularly high RMR may have been digesting their last meal, leading to an increased estimate. While this may also have affected our heritability estimate, by increasing the residual variance component, it is a standard practice not to fast individuals in studies of wild bird RMR (Nilsson et al. 2009; Bushuev et al. 2011).

The lack of significant heritable variation in nestling collared flycatcher RMR contrasts with previous studies on captive zebra finches (Rønning et al. 2007) and wild blue tit nestlings (Nilsson et al. 2009) that reported significant heritability estimates (Table 1). These estimates may have been inflated by early maternal effects, since such effects were not specifically tested for in these previous studies on sources of variation in avian nestling metabolic rate. It is difficult to know if maternal effects would be found without explicitly estimating them; although maternal effects can decrease over ontology in some traits, physiological traits show no difference in maternal effects depending on life stage (Moore et al. 2019). Since our sample sizes are relatively small for a quantitative genetic study, we lack precision in detecting low but significant estimates of heritability. However, we have a

similar sample size (n = 184) to other studies of RMR in wild birds, where Nilsson (et al. 2009) used 122 nestlings, and Bushuev used 210 nestlings to estimate the heritability of RMR. As both of these studies used partial, reciprocal cross fostering, as we did, to ensure a strong pedigree with links between related individuals (Wilson et al. 2010), we can be confident that we would have detected a similar high heritability (between 0.4 and 0.6; Table 1) if it had been present in this system.

While early-life effects on RMR have rarely been quantified in birds, there are often substantial maternal effects found in mammalian RMR. Such effects explain 13.8% of the variation of bank vole mass-independent RMR (Sadowska et al. 2009) and 28% of the mass-independent RMR in house mice (Dohm et al. 2001). Our estimates, with 4.8% - 23% of the variation explained by early-life effects, are well in line with these previous estimates. Further, when prenatal effects were not included in the model, the heritability of mass-independent RMR in house mice was estimated to be 0.09, but significant heritability was not found when maternal effects were modelled (Dohm et al. 2001). Similarly, Nespolo (Nespolo et al. 2003) report significant maternal effects on whole-organism RMR in leaf eared mice, but report the result of a model without maternal effects, inflating the estimate of heritability. In contrast, maternal effects were not found in deer mouse mass-independent RMR (Careau et al. 2011).

We found a similar pattern of early-life environmental effects on offspring RMR in collared flycatchers as has been demonstrated in mammals. However, we found no evidence supporting that maternal age, morphology, or the habitat quality of the breeding territory act as major underlying drivers of the detected early-life effects (Figure 1, Supplementary Table 2). We can therefore only speculate about the specific underlying mechanism. Incubation behaviour (Koski et al. 2020), thyroid hormones (Hsu et al. 2019) and yolk androgens (Rice et al. 2013) are all important early-life maternal effects that have previously been shown to have long-lasting effects on offspring performance in studies of collared flycatchers. We therefore consider these maternal effects as likely candidate drivers to the observed early-life (i.e. before day 3) effect on nestling RMR that can be targeted by future studies. Incubation behaviour might be particularly interesting given the

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effect of incubating species that we found on mass independent RMR in a comparison between collared flycatchers and the closely related pied flycatcher, and will continue to be explored as part of our on-going research (Supplementary Table S1). Additionally, we found strong year effects on all types of metabolic rate, but particularly on mass-specific RMR. The large year effects and treatment effects on mass (McFarlane et al. 2018), would be difficult to account for without using a bivariate model, and estimating the genetic covariance between RMR and mass. We did not embark on such analyses for two reasons; firstly, we were committed to reporting comparable heritabilities to other avian studies which have primarily used univariate animal models to estimate heritability (Table 1). Secondly, we likely lack power to estimate a genetic covariance, as bivariate models require more data than univariate models to be resolved (Wilson et al. 2010). Thus, it is difficult to separate the treatment effects on RMR from those on mass, given the strong relationship between the two.

Based on data from nearly two decades of long term monitoring we have previously revealed that collared flycatchers face strong selection to breed earlier as Swedish springs become warmer (Sirkiä et al. 2017). Late breeding individuals experience high nestling mortality (Qvarnström et al. 2009), likely because their nestlings are unable to fully adjust their resting metabolic rate through plastic responses to variation in environmental conditions (e.g. food availability) experienced during growth (McFarlane et al. 2018). The results of this study, highlighting a lack of significant heritability in collared flycatcher nestling resting metabolic rate, suggest that the alternative "evolutionary rescue" scenario also is unlikely for this trait in our study population. It is thus possible that phenotypic responses to changes in environmental conditions during the breeding season (including temperature, precipitations and food availability) will mainly happen through changes in breeding behaviour (e.g. timing) in adults in this species. The plasticity or heritability of female incubation and maternal investment behaviour may also facilitate adaptation to future changes in climate, provided that mothers are able to respond to reliable environmental cues. A recent analysis of multiple natural long-term datasets showed that plasticity can at least partly facilitate phenotypic tracking of an optimum phenotype that is moving through time, especially in birds (de Villemereuil et al. 2020). Similarly, there are a number of

instances of phenological traits responding to changing climate, via plasticity or genetic changes (Franks et al. 2014), including maternal traits that affect offspring fitness (Bonnet et al. 2019). The extent to which different traits may phenotypically adapt through plastic or genetic changes in response to selection across species or populations facing similar changes in climate deserves further attention. While previous reports of heritability of RMR suggest some species may be able to adapt to novel environmental pressures, the potential for early parental effects to contribute to these reported patterns should certainly not be ignored. Further detailed studies of long-term datasets collected under natural conditions are needed to help us better predict the consequences of, and opportunities of natural populations to adapt to environmental changes on a global scale.

Statement of Authorship: SEM and AQ conceptualized the project, SEM, MÅ and PS collected the data, MÅ and AQ oversaw the long-term data collection, SEM did statistical analyses, SEM and MÅ wrote the original draft of the manuscript, all authors contributed to the review and editing of the final manuscript.

Data and Code accessibility: All data and code for this project are available at https://figshare.com/projects/Low_heritability_but_significant_early_environmental_effects_on_resting_metabolic_rate_in_a_wild_passerine/90371. DOIs: https://doi.org/10.6084/m9.figshare.14531679.v1, https://doi.org/10.6084/m9.figshare.13050821.v1, https://doi.org/10.6084/m9.figshare.13050815.v1, https://doi.org/10.6084/m9.figshare.13050806.v1

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Figures and Tables:

Table 1: Previous studies of the heritability of resting metabolic rate in endothermic vertebrates. The literature describes three types of resting metabolic rate: whole-organism, mass-independent and mass-specific. Different statistical models have been used to decompose the components of variance in RMR depending on the experimental set up of the study. While previous studies of the heritability of RMR in birds have used animal models to estimate V_a, as noted in the 'method' column, but have not accounted for both foster nest (i.e. brood) and nest of origin while estimating V_a, thus confounding V_a with early maternal effects. Heritability estimates are followed by standard errors (SEs).

reference	taxa	study species	lab vs field	h2 estimate	whole or mass standardized?	method	formula
Rønning et al. 2007	bird	zebra finch	lab	0.250 (0.043)	whole-organism	animal model	RMR~Va
Rønning et al. 2007	bird	zebra finch	lab	0.041	mass-independent	animal model	RMR~Va
Nilsson et al. 2009	bird	blue tit	field	0.587 (0.25)	whole-organism	animal model	RMR~Va+brood
Tielman et al. 2009	bird	Stonechat rubicola	lab	0.555 (0.15)	whole-organism	animal model	RMR~Va
Tielman et al. 2009	bird	Stonechat rubicola	lab	0.48±0.16	mass-independent	animal model	RMR~Va
Tielman et al. 2009	bird	Stonechat rubicola	lab	0.401 (0.170)	mass-specific	animal model	RMR~Va
Tielman et al. 2009	bird	Stonechat axillaris	lab	0.202 (0.39)	whole-organism	animal model	RMR~Va
Tielman et al. 2009	bird	Stonechat axillaris	lab	0.20±0.35	mass-independent	animal model	RMR~Va
Tielman et al. 2009	bird	Stonechat axillaris	lab	0.441 (0.34)	mass-specific	animal model	RMR~Va
Tielman et al. 2009	bird	Stonechat maura	lab	0.37±47	mass-specific	animal model	RMR~Va
Bushuev et al. 2012	bird	pied flycatcher	field	0.43 ± 0.17	whole-organism	animal model	RMR~Va+year
Bushuev et al. 2012	bird	pied flycatcher	field	0.55 ±0.18	mass-specific	animal model	RMR~Va+year
Bushuev et al. 2012	bird	pied flycatcher	field	0.52 ±0.18	mass-independent	animal model	RMR~Va+year
Mathot et al. 2013	bird	zebra finch	lab	0.45±0.06	mass-specific	animal model	RMR~Va
Wone et al. 2009	mammal	house mouse	lab	0.26±0.08	whole-organism	animal model	RMR~natalcage+postweaningcage+ maternalgeneticvariance+ maternalenvironmental
Wone et al. 2010	mammal	house mouse	lab	0.19±0.07	mass-independent	animal model	RMR~natalcage+postweaningcage+

							maternalgeneticvariance+ maternalenvironmental
Nespolo et al. 2007	mammal	leaf-eared mouse	lab	0.01	whole-organism	animal model	RMR~Va+maternal+Environemtal
Sadowska et al. 2009	mammal	bank vole	lab	0.40 ±0.02	mass-independent	animal model	RMR~VA+dominance+ maternalenvironmental+envrionment
Sadowska et al. 2007	mammal	bank vole	lab	0.4	mass-independent	animal model	RMR~VA+dominance+ maternalenvironmental+envrionment
Careau et al. 2011	mammal	deer mice	lab	0.39±0.20	mass-independent	animal model	RMR~Va +commonenvironment+environment
Dohm et al. 2001	mammal	house mouse	lab	-0.11	mass-independent	animal model	RMR~VA +commonenvironment+prenatal+ environment
Bacigalupe et al. 2004	mammal	leaf-eared mouse	lab	0.21±0.21	mass-independent	animal model	RMR~Va +commonenvironment+environment
Konarzewski et al. 2005	mammal	house mouse	lab	0.38±0.21	mass-independent	p-o regression	
Zub et al. 2012	mammal	weasel	field	0.66±0.19	whole-organism	animal model	RMR~Va+`Vpe

Table 2. Variance components of whole-organism, mass-independent and mass-specific metabolic rate of eight-day old nestling collared flycatchers estimated with quantitative genetic 'animal models' statistical methods. to estimate variance components. Partial reciprocal cross fostering experiments where siblings were placed in different nests before hatching (i.e. as eggs) or when they were three days allow differentiation between three often confounded effects, namely additive genetic effects, early life maternal effects and foster nest effects on resting metabolic rate. Each model includes a pedigree-linked estimate of additive genetic variance, a nest of origin effect, a foster nest effect, a year effect and a residual variance component.

	Va	Nest of Origin	Foster Nest	Year	residual	h2	early shared environment	late shared environment	year
Whole-organism	0.000833 (3.3e-08 - 0.30)	0.127 (0.060 - 0.26)	0.140 (0.056 - 0.27)	0.239 (0.041 - 1.7)	0.421 (0.24 - 0.60)	0.00094 (2.5e-08 - 0.23)	0.117 (0.025 - 0.22)	0.111 (0.031 - 0.25)	0.197 (0.084 - 0.69)
Mass-independent	0.00637 (1.2e-05 -0.74)	0.373 (0.12 - 0.89)	0.325 (0.078 - 0.80)	0.239 (0.069 - 2.05)	0.284 (0.00018 - 0.41)	0.00248 (7.1e-06 - 0.39)	0.233 (.048 - 0.45)	0.168 (0.031 - 0.40)	0.168 (0.031 - 0.40)
Mass-specific	0.0000248 (9.0e-10 - 0.0044)	0.0185 (0.014 - 0.029)	0.0191 (0.014 - 0.028)	0.130 (0.045 - 1.5)	0.00213 (0.00047 - 0.0041)	0.0000622 (2.5 e-9 - 0.015)	0.0478 (0.0043 - 0.16)	0.0273 (0.0057 - 0.15)	0.912 (0.70 - 0.99)

Figure 1: Variance components from animal models, where the response variable is either whole-organism RMR, mass-independent RMR or mass-specific RMR of eight-day old nestling collared flycatchers. Some ad hoc models include an additional fixed effect of a maternal phenotypic trait. It should be noted that the additive genetic variance component (in grey) is difficult to see (at top).