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REVIEW

Individual variation in workload during parental care: can we detect a physiological signature of quality or cost of reproduction?

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Abstract How hard do birds work during parental care, chick rearing, or provisioning of their nestlings? And if birds do work hard, can we detect a physiological signature of individual variation in workload ability (perhaps related to 'quality') or costs associated with high workload? Here, we provide a broad conceptual perspective on these questions. Life-history theory predicts (or requires) that (1) parental care is hard work, (2) individuals that invest more in parental care benefit in terms of rearing more, larger, fitter offspring, but that (3) increased investment in parental care comes at a cost: decreased future fecundity and/or survival. However, we start by highlighting studies that are inconsistent with this conventional view, e.g., (1) females often do not pay a survival cost of increased workload (though males do), (2) some (high quality?) individuals appear to maximise numerous life-history traits, and (3) workload during parental care often does not predict productivity. We suggest that an "exercise physiology" perspective on parental care might be informative, but highlight the fact that existing models of exercise often involve conditions very different from that free-living animals experience while foraging (e.g., using forced exercise) and are often divorced from the critical relationship in free-living animals between exercise and acquisition of resources. We briefly review studies looking at physiological effects of workload during parental care in free-living birds, but again highlight our surprising lack of knowledge in this area especially where experimental manipulation of workload is coupled with comprehensive, physiological analysis. Finally, we make three recommendations for how can we advance the study of physiology of parental care in chick-rearing birds: (1) experimental manipulation of workload, (2) obtaining better measures of workload, for large numbers of known-individuals, and (3) better assessment of physiology of individual quality, and identification of specific metrics of workload-induced 'wear and tear'.

Keywords Parental care · Exercise physiology · Workload · *Sturnus vulgaris* · Cost of reproduction · Physiological costs

Introduction

How hard do birds work during parental care, chick rearing or provisioning of their nestlings? This is a deceptively simple, yet fundamental question to answer if we are to identify the physiological basis of individual variation in workload, and potential 'costs of reproduction' arising from high levels of work, associated with chick-rearing (Harshman and Zera 2007; Stearns 1992). It is widely assumed that chick-rearing is hard work, but this is often based primarily on the view that this is a logical necessity. If rearing chicks is 'easy' why do not all individuals rear large numbers of chicks at no cost: the Darwinian demon? Therefore, life-history theory predicts (or requires) that (1) parental care is hard work (we use the terms "hard work" or "high levels of workload", throughout this review to capture the idea that parental care involves an elevated level of exercise or increased energy expenditure, sufficient to generate negative physiological effects, that might

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ultimately lead to decreased survival or future fecundity), (2) individuals that invest more in parental care benefit in terms of rearing more offspring, or larger, fitter offspring, but that (3) increased investment in parental care might come at a cost: decreased future fecundity and/or survival. In fact, life-history theory predicts that individuals should rarely work sufficiently hard to kill themselves (e.g., Daan et al. 1996) if they have significant residual reproductive value, i.e., they should trade-off current reproduction for self-maintenance and future reproduction. Nevertheless, the concept of a cost of reproduction associated with parental effort remains a central tenet of life-history theory.

Much of the current literature reiterates the assumption that parental care in birds is hard work. For example, (parental) feeding rate is thought to require “highly energetically demanding allocation” (Horváthová et al. 2012), and females “are perhaps working close to their maximum provisioning capacity” (Low et al. 2012). Piesrma and van Gils (2011) concluded that a metabolic scope of 4–5 × BMR in birds taking care of nestlings reflects animals “highly motivated to work” and suggested that this might represent “a reasonable first guess at a maximum physiological level of seriously challenged animals that still maintain energy balance” (p. 59), i.e., income breeders that feed while working. Furthermore, Piersma and van Gils (2011) stated that “Any kind of hard work … does come with wear and tear”, which clearly links to the concept of a cost of reproduction. However, an alternative view can be found, albeit less often, in the literature. Speakman (1997) suggested that small mammals and birds “routinely live their lives at well below their physiological capacity”, and Tinbergen and Dietz (1994) argued that natural rates of energy expenditure should reflect an optimization process rather than a physiological maximum, dependent on the evolutionary costs and benefits associated with a certain level of workload (see also Piersma and van Gils 2011, p. 57). Thus, the rate at which animals do perform work during natural activities (e.g., chick rearing) might be a better predictor of fitness than the maximum rate at which they can perform (Husak 2006), an idea called “ecological performance” (Irschick 2003). This dichotomy of opinion has important implications for identifying the physiological basis of individual variation in workload during parental care and the potential costs associated with this, as discussed below.

Problems with the conventional view that chick rearing is hard work sufficient to generate costs

A critical reading of the literature highlights some significant problems with the conventional view that parental care in birds is “hard work”, and that individuals that work hard might obtain benefits, but might also pay costs. Santos and Nakagawa (2012) conducted a meta-analysis of experimental data from brood size manipulations to test the generality of the idea that there is a trade-off between parental effort and survival in birds. Although males that experienced increased parental effort were less likely to survive than control males, females that experienced increased effort were just as likely to survive as control females [one caveat here is that brood-size manipulation might not be an effective way to increase parental workload and only 58 % (11/19) of studies in this dataset included data on the effectiveness of the experimental manipulations on parental effort]. Thus, one sex—importantly females—does not appear to show decreased survival in response to increased workload (see Schroeder et al. 2013; Williams 2012 for a broader discussion).

Secondly, individual variation in lifetime fitness is highly skewed in many species, with a relatively small number of “high quality” individuals contributing the majority of offspring to the next generation (Clutton-Brock 1988; Newton 1989). In this paper, we define quality in an evolutionary sense: higher quality individuals have higher fitness, but we also consider “quality” as the product of multiple (yet largely unknown) phenotypic traits (Wilson and Nussey 2010). We acknowledge that “individual quality” remains an elusive concept in ecology (Wilson and Nussey 2010), but in this review we focus on this concept being even more elusive from a mechanistic or physiological perspective (Williams 2012). What physiological component(s) of phenotype define or contribute to “quality” in the context of individual variation in the ability to sustain high levels of workload during parental care or the ability to resist costs associated with hard work. Importantly, some recent studies suggest that some high quality individuals appear to be able to maximise reproductive traits while apparently paying no future fecundity or survival costs (Lescroël et al. 2009; Schroeder et al. 2012; Toïgo et al. 2013). A corollary of this is that we should perhaps be looking for a physiological signature of costs among lower quality individuals and at lower levels of absolute workload.

There is marked individual variation in apparent workload during chick provisioning in birds, but a third problem with the conventional view discussed above is that in many species there is no evidence that individuals that work harder (e.g., with higher provisioning rates) rear more, or better, offspring. In passerines there is typically 5-10 fold variation in hourly or daily provisioning rates, e.g., 300–1500 visits/nest/24 h (by both parents) in blue tits, *Cyanistes caeruleus* (Nur 1984), and 5–45 deliveries per hour in house sparrows, *Passer domesticus* (Schwagmeyer and Mock 2008a). In our study species, the European starling, *Sturnus vulgaris*, provisioning rates of females feeding 6- to 8-day-old nestlings varied from almost tenfold from 1.0 to 9.33 visits/30 min (Fig. 1a). This individual variation is repeatable among consecutive days (2–3 days of 30-min observations), and between first and second broods (M.A. Fowler and T.D Williams, unpublished data). Brood size explained little of this individual variation in provisioning rate: females made between 0.2 and 2.5 visits per chick per 30 min (Fig. 1b). It seems intuitive that females provisioning chicks at the rate of 1 visit per 30 min are working "less hard" than females making 9 visits per 30 min. Furthermore, if females that are working harder benefit in terms of producing more, larger offspring, then females provisioning chicks at the rate of 1 visit per 30 min could be considered "low quality" females and those making 9 visits per 30 min are "high quality" females (see Fig. 1a). However, although there is marked variation in breeding productivity in European starlings (Fig. 2a), this is independent of variation in provisioning rate both for brood size at fledging (Fig. 2a) and chick mass at fledging. Many other studies have reported that chick mass and/or brood size at fledging are independent of inter-individual variation in adult provisioning rate (Dawson and Bortolotti 2003; Garcia-Navas et al. 2012; Mariette et al. 2011; Ringsby et al. 2009; Schwagmeyer and Mock 2008b).

What is interesting about this lack of relationship between parental effort and benefit is that individual variation in provisioning rate is repeatable at least within years, although typically male effort has higher repeatability while female provisioning effort is less repeatable or not repeatable (Dor and Lotem 2010; MacColl and Hatchwell 2003; Nakagawa et al. 2007; Schwagmeyer and Mock 2003). In European starlings, female provisioning rate is repeatable in the short term, across consecutive days, and between first and second broods (where individual accounts for about 40 % of the total variation), but not among years. Thus, we see repeatability of female workload only within a similar ecological context in our study system, i.e., within a single breeding season, not among years.

An exercise perspective on workload during parental care

Exercise and locomotion are essential components of life-histories of free-living animals in their natural environment, for example during reproduction, or migration (Nathan et al. 2008; Sinclair et al. 2014). In a natural context, "exercise" is usually assumed to involve movement that is supported by sustained (not maximal) locomotor performance (Piersma 2011). Even so, sustained performance can represent a high level of activity in some species, e.g., migrating salmon use up to 90 % of their maximal aerobic scope during locomotion (Eliason et al. 2011) and this can lead to death even before spawning (Burnett et al. 2014). Although most free-living animals engage in "exercise"-like activities, the majority of research on physiology of exercise has been conducted in the laboratory on a select number of taxa (e.g., humans, mice, lizards, fish). Furthermore, experiments in exercise physiology can involve "forced exercise" and are often conducted in conditions very different from that which free-

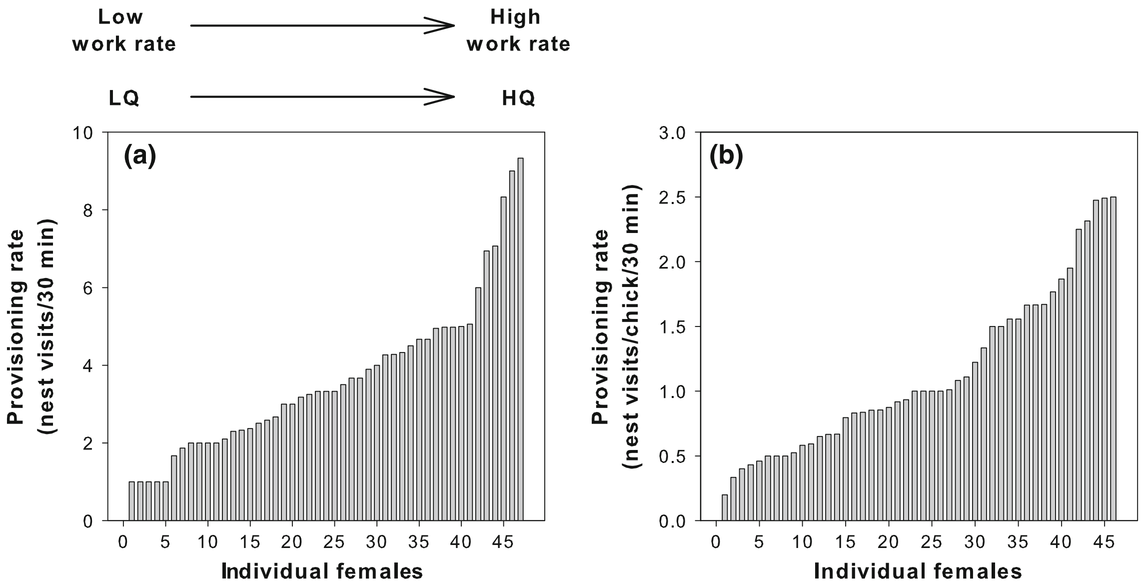

Fig. 1 Individual variation in provisioning rate **a** per nest, and **b** per chick, in female European starlings, *Sturnus vulgaris*, measured during days 6–8 post-hatching

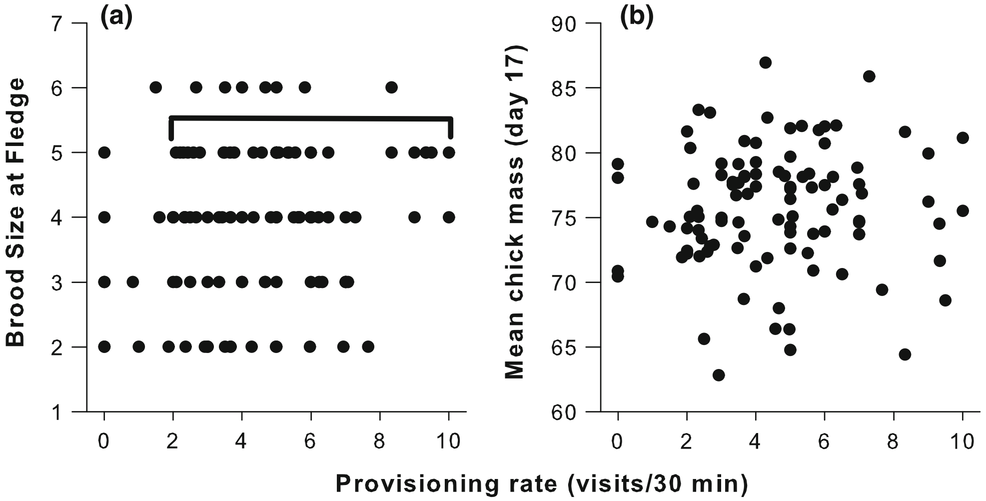

Fig. 2 Lack of relationship between provisioning rate in female European starlings and productivity measured as **a** brood size at fledging, and **b** mean chick mass at day 17 post-hatching. *Bar* in (**a**) demonstrates the 5-fold individual variation in provisioning rate for a brood size of 5 chicks

living animals experience and are often divorced from the critical relationship in free-living animals between exercise and acquisition of resources (Fonseca et al. 2014), i.e., foraging or provisioning in an ecological context. Clearly, therefore, more studies of exercise physiology of free-living birds are warranted, but to what extent can existing model systems inform the objective of identifying the physiological basis of individual variation in workload capacity? For example, can these studies highlight the most promising physiological metrics we should measure in field studies?

In part, we think the answer to this depends on what form, intensity, and duration of exercise is involved in specific model systems relative to that associated with provisioning in birds. In humans, exercise can lead to clear "training effects" with top athletes having very different physiologies compared with less well-trained or sedentary individuals (Joyner and Coyle 2008; Murray and Costa 2012; Neufer 1989), but this typically involves prolonged, high intensity and/or frequent exercise, seemingly very different from chick-rearing birds. However, interestingly, in humans, there is also the well-known syndrome of ''over-reaching'' and ''over-training'' associated with long-term performance decrements due to intense exercise (Borer 2003; Duclos 2008; Hug et al. 2003), which as any amateur athlete knows can lead to ''exhaustion and temporary suppression of vitality'' (to use Daan et al.'s 1996 words). Selection studies of voluntary wheel running in house mice, *Mus domesticus*, have provided a powerful system for identifying the physiological basis of elevated activity levels (Garland et al. 2011b; Malisch et al. 2007; Swallow et al. 1998). After 43 generations of selection, four replicate high runner lines averaged 2.85-fold more revolutions per day than non-selected control lines, and this involved selection on increased speed in females, and increased speed but also time spent running in males (Garland et al. 2011a). Interestingly, in terms of 'costs' of this clearly elevated activity level, although increased wheel-running activity from a young age resulted in decreased body mass at maturity (Swallow et al. 1999), selection for elevated activity levels had few correlated (negative) effects on reproduction, e.g., males from selected lines had larger testis mass (Klomberg et al. 2002), and although females from selection lines had smaller body mass at first parturition litter, neither litter size or nor litter mass at birth or at weaning differed between selected and control lines (Girard et al. 2002). Focusing on avian systems, studies of long-distance migrating birds in wind tunnels or during natural flights suggest that this activity can involve prolonged exercise (days) at a high factorial scope (8–9 × BMR), with no food intake (Piersma et al. 2011 and references therein). In contrast, although parental care during chick-rearing is considered to represent sustained work load (Drent 2006; Drent and Daan 1980), birds 'only' operate at 3–4 × BMR, short flights are interspersed with bouts of foraging, and birds have constant access to food through self-feeding. Thus, activity during chick provisioning is probably best described as voluntary, sustained (sub-maximal) exercise (although this work load is still considered sufficient to generate 'costs of reproduction'; e.g., Daan et al. 1996). Moreover, exercise specifically associated with central-place provisioning is relatively short-term (cf. human training effects), lasting only 2–3 weeks and birds transition rapidly at hatching from a relatively sedentary lifestyle during incubation, to an active lifestyle during chick-rearing. Therefore, while consideration of other model systems for exercise physiology might be informative, we suggest that development of tractable, laboratory-based models of foraging and parental care that better match the context of exercise in free-living birds would be valuable (e.g., see Koetsier and Verhulst 2011; Simons et al. 2014).

What do we know about physiological effects of workload during parental care in free-living birds?

Energy is widely considered to be the currency of life-histories, but energy expenditure per se is only one component of the complex physiology of free-living animals. Elliott et al. (2014) conducted a meta-analysis of studies that added loads, clipped wings or attached recorders to chick-rearing birds feeding chicks at the nest and then measured daily energy expenditure (DEE). Overall DEE did not differ significantly between handicapped and non-handicapped birds ($p = 0.25$). Elliott et al. (2014) suggested that handicapped birds either reduced investment in themselves or they reduced investment in their offspring to remain below an energy ceiling (although among species whether a handicapped individual reduced investment in its own energy stores or its offspring's growth was independent of that species life-history). This raises the question (discussed at the start of this paper) of why, if birds ensure their activity costs are below an energy "ceiling" or maximum, some individuals appear to pay costs of high levels of energy expenditure (e.g., Daan et al. 1996). However, this meta-analysis of a considerable number of studies also suggests that further studies focusing only on energy expenditure and parental care might not be that useful (see Williams 2012), so what do we know about other physiological correlates of workload in chick-rearing birds?

Although there have been a large number of experiments where the goal was to make provisioning birds work harder (e.g., using brood size manipulation, wing-clipping, adding weights; see below) surprisingly, few studies have coupled this with physiological measurements. These studies were recently reviewed in Williams (2012), so here we highlight specific examples to illustrate key concepts important for the current review. First, most studies to date tend to have focused mainly on one component of physiology, e.g., immune function (Hegemann et al. 2013; Tieleman et al. 2008), oxidative stress (no studies where reproductive effort was manipulated; reviewed in Metcalfe and Monaghan 2013), or nutritional profiling of intermediate (plasma) metabolites (Horak et al. 1999; Kern et al. 2005). Correlational studies suggest that single physiological measures can be systematically related to workload or aerobic capacity. For example, birds rearing larger broods, or with higher provisioning rate, have been reported to have higher levels of oxidative stress, as indicated by increased reactive oxygen metabolites (Guindre-Parker et al. 2013) or higher glutathione peroxidase activity (GSH-Px) activity (Norte et al. 2010), and Burness et al. (1998) found a positive correlation between VO_2 max. (the maximum rate of oxygen consumption) and hematocrit in provisioning tree swallows, *Tachycineta bicolor*. In contrast, Tieleman et al. (2008) clipped primary feathers in tropical house wrens such that work effort for flapping flight would be increased by at least 7.5 %. However, there was no effect of treatment on FMR, BMR or several measures of innate immune function, perhaps because handicapped parents decreased their nestling feeding frequency by 23–31 %.

While it is a good sign that studies increasingly assay multiple physiological metrics, albeit still typically within a single physiological system, it is notable that this often generates inconsistent, or at least complex, results among different metrics assayed within each physiological system, and often report many non-significant results. As an example, Hegemann et al. (2013) handicapped adult skylarks, *Alauda arvensis*, by attaching weights equalling c.10 % of body mass during breeding, but found no effect of treatment on several measures of immune function (lysis, agglutination, haptoglobin, proportions of white blood cells or heterophils:lymphocyte, H:L, ratio) in parents rearing first broods. However, there were treatment effects or treatment × brood interactions in parents rearing second broods, but with complex patterns, e.g., agglutination titres decreased between first and second broods in control birds and increased in experimental birds in 1 year, while this pattern was reversed in a second year. Furthermore, in females, haptoglobin concentrations decreased more strongly in control birds than in experimental birds, while concentrations in control males increased and in experimental males decreased, and there was no treatment effect on body mass, leukocyte proportions, or H/L ratio. This highlights two important points: (1) physiological costs of increased workload to the parents might not be manifest in the first, manipulated breeding attempt, but are often only seen in subsequent breeding attempts, and (2) there is not necessarily co-variation among physiological traits, even when these traits are components of the same physiological system (e.g., immune function), suggesting that birds are able to adjust individual components of their physiology independently (Buehler et al. 2012; Tieleman et al. 2010) either seasonally or in different ecological contexts (e.g., Versteegh et al. 2014). Thus, measuring multiple physiological traits is essential in future studies (see below)—at least allowing for detection of possible co-variation or trade-offs among different traits—though this will complicate the analytical task, but it is equally important that we know the ecological context for interpreting the more comprehensive physiological data. In short, however, the study of physiology of parental care in chick-rearing birds (and of foraging more generally) represents a more or less wide open field and one of considerable significance in uniting mechanism and evolutionary theory; so how should we proceed?

How can we advance the study of physiology of parental care in chick-rearing birds?

We suggest that three things should be considered in future studies that will help expedite our understanding of the physiological basis of individual variation in workload during parental care in birds, and associated costs of reproduction. We illustrate these using preliminary data from our on-going studies of parental care in European starlings, *Sturnus vulgaris*.

1. Experimental manipulation of workload in free-living birds: Piersma (2011) suggested that free-living animals might be resistant to experimental manipulations to increase their instantaneous work levels if, for example, "a precipitous increase in the likelihood of organ or performance failure, and mortality" is associated with increases in energy expenditure (sic). We agree with this point in relation to the simplest, and most widely used manipulation for increasing parental effort: brood size manipulation. This is often an ineffective way to manipulate parental workload because parents have the 'option' of maintaining investment in self-maintenance and passing the cost onto their offspring. In general, although average feeding rate per nest increases in experimentally-enlarged broods feeding rate per chick decreases (Nur 1984; Wright et al. 1998), and although parents can rear more offspring to fledging in enlarged broods, these offspring are in poorer condition (Dijkstra et al. 1990). In contrast, direct manipulation of parents, using feather clipping/removal or addition of weights, means that birds cannot escape the biomechanical effects of these manipulations, i.e., increased wing loading. So here, if parents 'choose' to maintain provisioning effort, this must come at some increased biomechanical, physiological or energetic cost. The "ideal" manipulation would actually be one where there are clearly predictable biomechanical or flight costs (e.g., due to reduced wing area) but no effects on mean provisioning rate, i.e., parents maintain their workload despite the extra cost. In fact, responses to wing-clipping are highly variable. In some studies, handicapped birds often reduce their provisioning rate and have lower productivity (Jacobs et al. 2013; Slagsvold and Lifjeld 1988; Tremblay et al. 2003), but, perhaps as a consequence, do not have different return rates than non-manipulated birds (Bijleveld and Mullers 2009; Wright and Cuthill 1989). However, in other studies, even though wing-clipped birds reduced provisioning rates, they had lower return rates either with no difference in productivity (Winkler and Allen 1995) or even with a decrease in current productivity [Love and Williams (2008); see Fig. 3]. This suggests that wing-clipping can, in some situations, push birds into a zone where physiological costs of reproduction are incurred representing a valuable form of experimental manipulation.
2. Better measures of workload, for large numbers of known-individuals: over 15 years ago, Wright et al. (1998) highlighted the fact that individual birds can adjust their workload during provisioning by not only varying nest visit rate but also by varying load size, prey type, size, and nutritional content, foraging distance, travel time to and from the nest, and even costs of specific activities during foraging in food patches (see also Stodola et al. 2010). Nevertheless, the simplest and most commonly used measure of parental effort continues to be the number of visits/unit time to the nest or per chick (correcting for brood size) as discussed above. It is generally difficult to collect large amounts of data for many individuals on these other components of provisioning effort, but this is becoming easier with developments in nest cameras (García-Navas and Sanz 2010; Stodola et al. 2010), RFID tags (Mariette et al. 2011), automated radio-tracking systems that can cover relatively large areas of habitat (Mitchell et al. 2012; Ryder et al. 2012), or accelerometers (Elliott et al. 2013; Spivey and Bishop 2013). Thus, the goal should be to take a multivariate approach to obtain an integrated measurement of individual variation in parental workload coupled with physiological analysis of these same individuals. However, there might be an additional advantage of focusing on energetic or physiological costs of different components of provisioning behavior (e.g., foraging vs. flight costs): this might identify the specific source of activity-related costs, as has been demonstrated in other systems. For example, perhaps counterintuitively, songbirds expend double the amount of energy during stopovers that they spend on flight over their entire migration (Wikelski et al. 2003). Similarly, in large predatory mammals, travel while seeking prey can be more energetically costly than the subsequent chasing of prey (Scantlebury et al. 2014; Williams et al. 2014). Preliminary data for Europeans starlings suggests there will be marked individual variation in

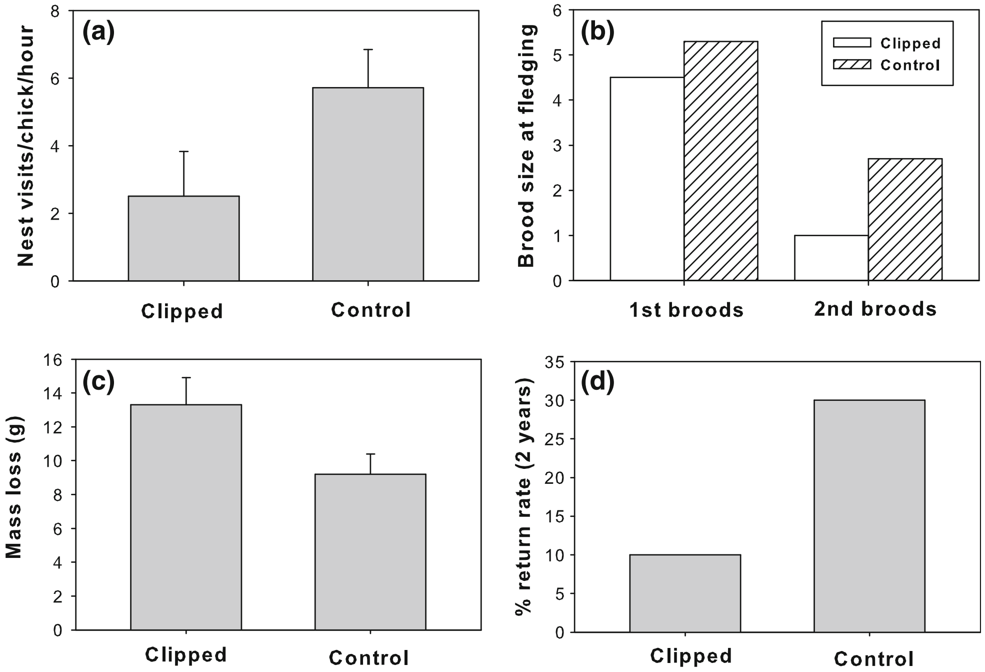

Fig. 3 Effects of wing-clipping in female European starlings on **a** provisioning rate of 1st broods, **b** brood size at fledging for 1st and 2nd broods, **c** mass loss (g) and **d** local return rate over 2 years following the manipulation. Re-drawn from data in Love and Williams (2008)

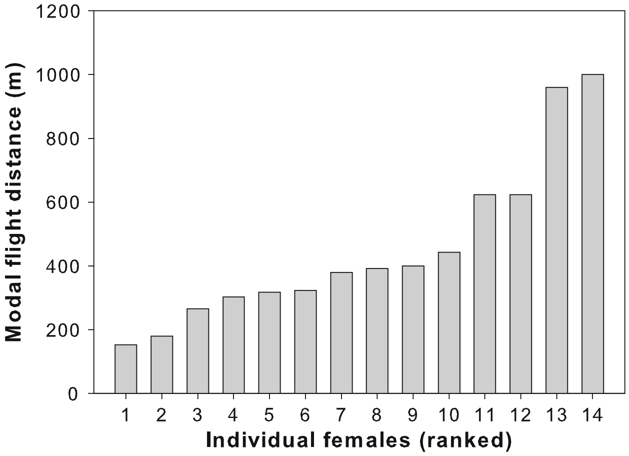

Fig. 4 Individual variation in modal flight distance per foraging trip in female European starlings (estimated based on radio-telemetry data of birds between days 1–19 post-hatching)

many components of provisioning, e.g., individual birds commonly bring back load sizes with either 1, 2, 3, or 4 tipulids, *Tipula paludosa* larvae, individual tipulid larvae vary from 0.08 to 0.45 g, and modal flight distance of foraging trips by individual females varies 5-fold from <200 to 1000 m (Fig. 4).

3. Better assessment of physiology of individual quality, and identification of specific metrics of workload-induced ‘wear and tear’: Animals are complex organisms and a whole suite of physiological systems must function in an integrated and coordinated manner to determine fitness. Almost by necessity, most studies reduce this complexity by studying just one physiological system, but it is still common for studies to measure only one or two specific traits even in a single physiological system. Many authors have cautioned against making generalizations about physiological costs based on results from single measurements (Adamo 2004; Metcalfe and Monaghan 2013; Monaghan et al. 2009; Norris and Evans 2000) and in assuming that fitness costs will be associated with putative “negative” changes in single measured physiological traits (Williams 2012). For example, a decline in a single measured component of immune function cannot be interpreted as “immunosuppression” unless it is demonstrated that there is no compensatory up-regulation of unmeasured traits of the same (e.g., cell-mediated) or different (e.g., humoral) components of the immune system (Keil et al. 2001; Salvante 2006). Similarly, oxidative stress measured as an imbalance between reactive oxygen species and antioxidants cannot be assumed to have negative effects unless measures of oxidative damage and repair mechanisms are also obtained (Monaghan et al. 2009). Furthermore, if birds are able to adjust individual components of their physiology independently (Buehler et al. 2012; Tieleman et al. 2010; Versteegh et al. 2014), we will only capture this level of complexity (e.g., trade-offs) if we measure multiple traits in multiple physiological systems (see Travers

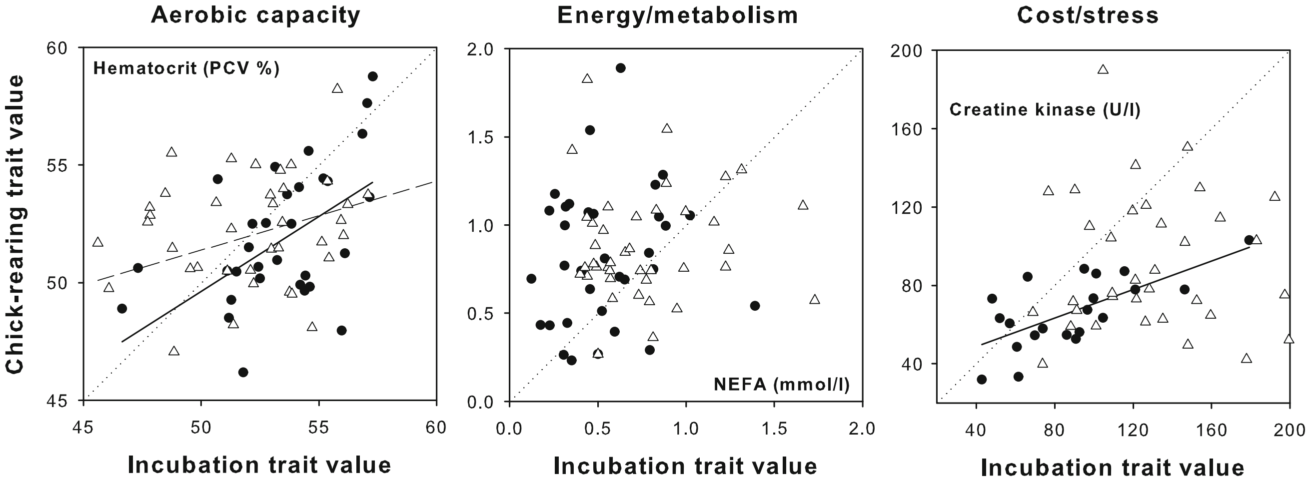

Fig. 5 Examples of individual, breeding stage, and year variation in three physiological traits as putative indicators of aerobic capacity (hematocrit), energy or metabolic state (non-esterified fatty acids) and physiological costs/stress of muscle damage (creatine kinase); data are for individual female European starlings sampled during incubation and at days 10–12 of chick-rearing for 1st broods in 2013 and 2014 (see text for more details)

et al. 2010). The selection of a suite of traits encompassing multiple physiological systems will inevitably involve some compromises due, for example, to small plasma volumes (in birds <100 g body mass), or because some assays are not (yet) compatible with sample collection from free-living birds in the field (Monaghan et al. 2009). However, in European starlings (90 g body mass), we can obtain data on 14 physiological traits using only 100 µl plasma and 15 µl whole blood. This includes measures of oxidative stress and muscle damage (total antioxidant capacity, oxidative damage, creatine kinase), metabolic regulators (corticosterone), immune function (haptoglobin, lysis, agglutination), aerobic capacity (hematocrit, hemoglobin, reticulocytes), and intermediary metabolism or nutritional profiling (free fatty acids, triglycerides, glucose, uric acid).

We obtain repeated measurements from individual, banded females sampled during the peak of provisioning effort in first and second broods (days 8–10 post-hatching) to capture the idea that physiological costs of increased workload to the parents might not be manifest in the first (manipulated) breeding attempt, but are often only seen in subsequent breeding attempts (e.g., Hegemann et al. 2013). In addition, we can anchor analysis of changes in physiological state to a "baseline" level by sampling the same individuals during incubation (again the choice of a true "baseline" state will require compromise: in our study of workload during chick-rearing we assume, at least, that overall activity is lower during incubation). Thus, we can not only ask if multivariate physiological state at incubation predicts exercise capacity but also whether individual variation in the physiological "training" response, i.e., the change in physiological state from incubation to peak chick-rearing, or the change between first and second broods, predicts individual variation in workload or productivity. Preliminary analysis of this more comprehensive (and complicated!) physiological dataset suggests that there are systematic, but variable, patterns of change in physiological state with change in workload between incubation and chick-rearing (Fig. 5). For example, hematocrit (a measure of aerobic capacity?) was on average lower in individual females in 1 of 2 years during chick-rearing birds compared to during incubation, non-esterified fatty acids (a measure of energy or metabolism) was higher during chick-rearing in both years, whereas creatine kinase (a measure of muscle damage?) was lower during chick-rearing in both years. However, what is most notable in Fig. 5 is the large individual variation in the change in trait values, as well as the mixed evidence for repeatability among traits or among years (solid and dashed lines for hematocrit and creatine kinase but not non-esterified fatty acids). Clearly, the analysis of complex, multivariate physiological data will require the application of more complex multivariate statistical approaches (Frost et al. 2014; Williams 2008) common in ecology, development of novel indices of 'quality', e.g., physiological dysregulation (Travers et al. 2010), and approaches borrowed from evolutionary biology, e.g., physiological reaction norm analysis (Williams 2008). Despite the challenges, this clearly represents an almost untouched area where physiological studies could significantly contribute to a mechanistic understanding of individual variation in parental care that has been the focus of so much research from an ecological and evolutionary biology perspective.

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