

COMMENTARY

Physiology, activity and costs of parental care in birds

Tony D. Williams

ABSTRACT

Parental care is assumed to be costly in that it requires sustained, high-intensity activity sufficient to cause costs of reproduction (decreased survival and future fecundity of parents). Costs of reproduction are, in turn, thought to have a physiological basis where intense activity causes a decrease in parental condition. However, attempts to identify the physiological basis of costs of reproduction have produced mixed results. Here, I argue that in birds, the central idea that parental care represents sustained, high-intensity work might be incorrect. Specifically: (a) the duration of intense activity associated with chick-rearing might be quite limited; (b) flight, the most obvious sustained, high-intensity activity, might only represent a small component of an individual's overall activity budget; (c) some (high-quality) individuals might be able to tolerate costs of intense activity, either owing to their physiological state or because they have access to more resources, without perturbation of physiological homeostasis; and (d) individuals might utilise other mechanisms to modulate costs of activity, for example, mass loss, again avoiding more substantial physiological costs. Furthermore, I highlight the important fact that life-history theory predicts that reproductive trade-offs should only be expected under food stress. Most birds breed in spring and early summer precisely because of seasonal increases in food abundance, and so it is unclear how often parents are food stressed. Consequently, I argue that there are many reasons why costs of reproduction, and any physiological signature of these costs, might be quite rare, both temporally (in different years) and among individuals.

KEY WORDS: Parental care, Costs of reproduction, Activity, Foraging, Physiological costs, Flight

Introduction

Physiology contributes to life-history evolution the analysis of the trade-offs that constrain adaptation

Stearns (1992)

Parental care can be defined as any parental trait (behavioural or non-behavioural, e.g. physiological) that enhances the fitness of a parent's offspring (Clutton-Brock, 1991; Royle et al., 2012). This involves parental expenditure – the expenditure of parental resources (time, energy, physiological capacity) on care of offspring. Parental investment is any investment by the parent that increases offspring fitness at the cost to the parent's ability to invest in other offspring (the cost of reproduction, see Glossary; Williams, 1966). Finally, parental effort is the combined fitness costs a parent

incurs owing to production and care of all offspring 'in a given biologically relevant period', such as a breeding attempt (Smiseth et al., 2012). Theoretically, resources that parents can allocate to offspring are limited (but see below) and cannot then be allocated to parent self-maintenance, and so it is commonly assumed that caring for offspring reduces parental survival. This trade-off between current reproduction and residual fitness is central to life-history theory (see Glossary) (Clutton-Brock, 1991; Stearns, 1992) even though empirical data to support this concept are surprisingly limited (Santos and Nakagawa, 2012; Williams, 2012). As the opening quote by Stearns (1992) highlights, physiology should be able to contribute a detailed analysis of the mechanisms underpinning costs or trade-offs and, thus, contribute to a broader, deeper understanding of life-history variation.

From a physiological perspective, when characterising the mechanism(s) underpinning costs, the most relevant components of parental care are the concepts of parental expenditure and parental investment. If parents invest resources in rearing offspring that are not available for other physiological functions (self-maintenance), we should be able to identify the specific physiological mechanisms that directly generate or lead to fitness costs of reproduction. Parental care is probably the most well-studied phase of the avian life cycle – so what progress has been made? An (admittedly unrefined) search for 'parental care' and 'birds' in Web of Science using 'Topic' generates 1132 hits for the period 2008–2017. Adding the word 'physiology' to this search reduces this number of hits to 40 (3.5%)! Several recent, and otherwise authoritative, reviews of parental care (e.g. Royle et al., 2012) and foraging more generally (e.g. Stephens et al., 2007) contain virtually nothing on physiological mechanisms. Our knowledge of the physiological basis of variation in foraging – a key component of parental care – appears not to have improved much since Maurer's (1996) review. So, there appears to be golden opportunity here for physiologists to contribute to a major, unresolved component of life-history and behavioural ecology – the basis of costs of reproduction. Although several studies have attempted to identify the physiological basis of costs associated with parental care in birds (though not an overwhelming number of studies given the centrality of the topic), results have been mixed (reviewed in Williams, 2012; Williams and Fowler, 2015), with most studies measuring single physiological traits rather than complex suites of traits (but see Hegemann et al., 2013; Fowler and Williams, 2017). For example, in studies where costs of parental care were experimentally increased, there was no effect on several measures of immune function in parents rearing first broods (Tieleman et al., 2008; Hegemann et al., 2013). Similarly, some correlational studies found some evidence that birds with higher levels of parental investment have higher levels of oxidative stress (Norte et al., 2010; Guindre-Parker et al., 2013) but other experimental studies found no relationship (e.g. Wegmann et al., 2015).

Here, I discuss why it might be difficult to detect a physiological signature of cost of reproduction (sensu Williams and Fowler, 2015) and I will argue that, in fact, we should not expect to see costs of parental care most of the time. In particular, I will first question the

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Glossary**Altricial**

Hatching of chicks as very dependent young, often blind, naked and unable to thermoregulate.

Asymptotic mass

Maximum mass of developing chicks prior to fledging.

Basal metabolic rate (BMR)

Energy expenditure for a bird that is non-active, post-absorptive and in its thermoneutral zone.

Brood division

Splitting of a brood into smaller family units fed exclusively by one parent after fledging.

Central-place foraging

Parents returning to a central place, most commonly a nest, between foraging bouts.

Cost of reproduction

Negative effects of investment in the current reproductive attempt on future fecundity and/or survival.

Daily energy expenditure (DEE)

Total energy expended on all activities and functions over a 24 h period.

Life-history theory

Theory that attempts to explain the major features of life cycles, e.g. reproductive rates, lifespan, offspring size and number.

Metabolic scope

Daily, or maximum, energy expenditure expressed as a multiple of BMR.

Provisioning rate

Number of nest visits per unit time for parents returning with food to feed chicks.

Wing loading

Ratio of body weight to wing area.

Wing morphing

Changes in wing shape owing to movement of individual feathers in the wing.

central idea that parental care represents sustained, high-intensity work [throughout this Commentary, the terms ‘hard work’ or ‘work load’ capture the idea that parental care involves an elevated level of activity or increased resource expenditure, sufficient to generate negative physiological effects, that might ultimately lead to decreased future fecundity and/or survival]; then consider which specific activities or behaviours associated with parental care might, or might not, generate physiological costs (e.g. flight, foraging, self-feeding); and finally highlight the fact that most of the time, in many ecological contexts, and in some (high-quality) individuals, we should not expect to see trade-offs between parental care and self-maintenance; therefore we should not see costs of reproduction, or physiological signatures of costs. In this Commentary, I do not focus on the specific nature or mechanism of physiological costs (for which see Harshman and Zera, 2007; Williams, 2012; Williams and Fowler, 2015); however, a central requirement for defining costs is that high levels of parental care activity have negative (and documented) effects on physiological state that are directly, causally associated with decreased future fecundity and survival. Here, I focus on parental care in small birds, because: (a) they are classic central-place foragers (see Glossary), with high chick feeding rates; (b) small body size is associated with high mass-specific metabolic rates, i.e. high overall energy demand; and (c) parents generally have continuous access to resources (food) to meet any costs of parental care (cf. seabirds for example, where breeding can involve prolonged fasting, e.g. Green et al., 2009). However, many of my points will be generally applicable to other avian species, I include citations from a wide range of species and, conversely, any framework underpinning life-history theory, costs of reproduction and work load should embrace all birds (even passerines).

Should variation in parental investment and physiological state be related, and how?

Physiological costs should be incurred when individuals engage in sustained, high-intensity activity (Piersma and van Gils, 2011). The idea that parental care is costly owing to the high level of activity required, and in fact that it is the costliest phase of reproduction, can be traced back to seminal papers by Royama (1966) and Drent and Daan (1980). These argued that there is an optimal working capacity or maximal sustained working level beyond which animals would ‘lose condition’ and ‘suffer physical fatigue’, leading ultimately to increased mortality. Drent and Daan (1980) explicitly identified this maximum sustained level at approximately $4\times$ BMR, which they suggested represented the working level of heavy labour in humans. Daan et al. (1996) suggested that the increased mortality they documented in parents rearing experimentally enlarged broods was due to ‘temporary suppression of vitality’ and an increased ‘risk of death by exhaustion’. This idea is still routinely and widely, but uncritically, repeated in many papers today. For example, Caro et al. (2016) state that, ‘the production of offspring represents the most energetically demanding stage of an animal’s life. Raising a brood successfully puts a metabolic demand on breeding birds that is the equivalent to a human cycling the Tour de France’. Similarly, Riechert and Becker (2017) repeated the assertion that ‘chick rearing is often assumed to be the most demanding phase of reproduction’. Piersma and van Gils (2011) concluded that a metabolic scope (see Glossary) of $4\text{--}5.9\times$ basal metabolic rate (BMR; see Glossary) in birds taking care of nestlings reflects animals ‘highly motivated to work’ and that this might represent ‘a reasonable first guess at a maximum physiological working level of seriously challenged animals’.

This all fits with the general idea we have about parental care – that is, in altricial species (see Glossary), the amount of resources provided to chicks by parents should determine growth rates, body condition at fledging, and subsequent post-fledging survival and recruitment (Naef-Daenzer and Keller, 1999; Schwagmeyer and Mock, 2008). This alone predicts that parents should try to maximise food delivery to the nest and there should be a positive relationship between brood demand (increasing age, size or number of chicks) and parental activity, expenditure or work load (Fig. 1A). If these high levels of activity or workload are physiologically demanding, it seems intuitive to predict linear, or at least positive, relationships between physiological traits and workload (Fig. 1B). The problem with this line of thinking is that, although a metabolic scope of $4\text{--}6\times$ BMR might represent an upper limit for sustained performance – and might be associated with physiological costs – there is abundant evidence for birds, stretching back 30–40 years, that not all individuals operate at, or even close to, this level during chick rearing. Average metabolic scope of daily energy expenditure (DEE; see Glossary) in chick-rearing adults is $\sim 3\times$ BMR in many studies, many individuals operate at only $1.8\text{--}2.3\times$ BMR (Williams and Vezina, 2001), and in widely different species only 16–30% of individuals had measured $DEE \geq 4\times$ BMR (Bryant and Tatner, 1991). The idea that most animals do not operate at maximum levels all, or even most, of the time (‘ecological performance’; Irschick and Higham, 2016) is becoming more broadly appreciated across a range of taxa and fitness-related activities (Irschick and Losos, 1998; Kasumovic and Seebacher, 2018; Wilson et al., 2013). Piersma and van Gils (2011) even termed this ‘the evolution of laziness’. This concept needs to be more widely recognised in relation to costs of activity in general, and costs of reproduction specifically. So, although in theory, DEE or field metabolic rate could provide a measure of overall parental effort, I think this

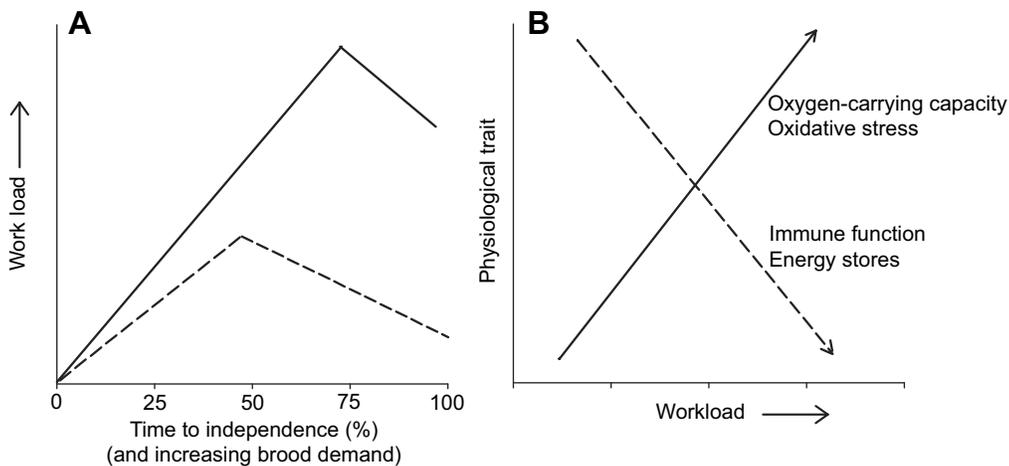


Fig. 1. Predicted relationships between workload and physiology. (A) Predicted relationship between parental workload and brood demand (number, size of chicks) in a species that reaches somatic maturity at fledging (i.e. leaves the nest) before somatic maturity, and (B) predicted relationships between parental workload and different physiological traits. See 'How 'sustained' is parental activity during chick-rearing?' for details.

approach is of limited utility for addressing questions raised in this Commentary. In fact, the majority of studies show no relationship between DEE and various measures of parental effort such as percentage time active, brood size, flight time or provisioning rate (see Glossary) (Williams and Vezina, 2001; Tieleman et al., 2008; Guillemette and Butler, 2012; but see Sanz and Tinbergen, 1999). More importantly, DEE as an integrated measure of energy expenditure over 24 h tells us nothing about the specific mechanisms by which high rates of energy expenditure translate into costs (see Williams, 2012). Furthermore, very few studies have compared variation in DEE with fitness measures, to demonstrate costs, and those that have find either no relationship (Verhulst and Tinbergen, 1997; Welcker et al., 2009; Grémillet et al., 2018) or a positive relationship (Sanz and Tinbergen, 1999). This leaves us with the question of whether sustained activity (or DEE) involving a metabolic scope of only 2–3×BMR is sufficient to cause physiological costs. I would argue that the answer to this question can easily be 'no'; for example, even if energy expenditure of low-intensity activity is twice that of complete inactivity, and therefore requires more energy, it does not follow that this is energy that cannot be spent elsewhere (an actual cost) if individuals have sufficient resources to increase energy intake, for example, owing to seasonal increases in food availability (see below). Similarly, even if low-intensity activity increases absolute production of reactive oxygen species, this will not generate a cost (oxidative damage) if increased reactive oxygen species production can be countered by elevated antioxidant or cell repair mechanisms. At higher levels of activity, it will become increasingly likely that these compensation mechanisms become insufficient; so physiological costs will depend critically on the sustained, high-intensity nature of any activity.

How 'sustained' is parental activity during chick-rearing?

Assuming that chick-rearing birds might undertake some activity at a maximum sustained level ($\geq 4 \times \text{BMR}$ sensu Drent and Daan, 1980; Piersma and van Gils, 2011) sufficient to incur physiological and life-history costs, how sustained or prolonged is any such activity during parental care? The mean nestling period for a sample of $n=118$ species with body masses <100 g (mean female mass 28.4 g, range 7.9–97.5 g) is 14.4 ± 3.9 days [range 8.5–29 days; data from HormoneBase (Vitousek et al., 2018)]. Although parental workload should generally increase through parental care in altricial species, the duration and slope of this positive relationship will depend on the developmental mode of the chicks. In many species (e.g.

European starlings, *Sturnus vulgaris*; Cornell et al., 2017), asymptotic mass (see Glossary) or size of chicks (somatic maturity) is attained at, or close to, fledging age (Starck and Ricklefs, 1998), i.e. chick growth continues throughout the nestling phase. Thus, brood demand, parental workload and potential physiological costs should increase while chicks remain in the nest, potentially for 2–4 weeks. In these species, parents will be central-place foragers for a longer period of time, making more, potentially costly, flights between the nest and foraging areas (but see below), with a longer rate of increase in sustained workload (Fig. 1A, solid line). However, even in these species, parental workload should decrease at fledging because chicks are then able to follow their parents around during the post-fledging period, reducing foraging distances. In other altricial species, chicks leave the nest well before they are somatically (or physiologically) mature (Yackel Adams et al., 2001; reviewed in Remeš and Matysioková, 2016) and the duration of parental care requiring central-place foraging might actually represent a very small component of the total period of parental care. Chick mobility post-fledging should greatly reduce parental foraging distances and, thus, parental expenditure or workload (Fig. 1A, dashed line; McLaughlin and Montgomerie, 1989). Brood division (see Glossary), defined as the splitting of a brood into smaller family units fed exclusively by one parent after fledging, can further reduce parental expenditure during the post-fledging period (Byle, 1990; Harper, 1985). So, in many species, parental care requiring sustained activity associated with central-place foraging might only last 1–2 weeks; now, how intense is parental care activity over this period?

How 'intense' is activity during chick rearing?

It is a widely held view that physiological costs of reproduction should be associated with sustained, high-intensity activity (see above; Piersma and van Gils, 2011). So, which specific behaviours or activities associated with parental care are most likely to contribute to physiological costs? The obvious answer is flapping flight associated with central-place foraging, with a minimum energetic cost of $9.2 \times \text{BMR}$ (Butler, 2016; admittedly derived from birds in wind tunnels). Many papers explicitly link the high cost of parental care to flight and foraging. For example, Schifferli et al. (2014) state, 'parents may spend a large part of their time and energy collecting food for their offspring [and] the high energetic costs that parents incur while provisioning young are largely due to increases in foraging time' (see Schultner et al., 2013 for a similar example). So, how much time do birds spend flying during parental care? Our

data for female European starlings suggest that flight is only a small component of overall parental activity. In an hour of daylight, female starlings spend ~ 3 min at the nest feeding chicks (8 visits $h^{-1} \times 20$ s). Modal foraging distance is 400 m so birds spend ~ 11 min flying (8×800 m round trip at 10 m s^{-1}). Although some European starling females make longer foraging trips (up to 1600 m), many forage much closer to, or even just below, their nest boxes (< 50 m). Thus, flight is only a small component of daily activity (18%), leaving most of the time (77%) available for foraging or other activities (these numbers agree very well with other studies of European starling activity budgets and foraging distances: Heldbjerg et al., 2016; Tinbergen, 1981). This result should not actually be that surprising because many early studies reported low percentage flight activity during parental care in birds (13%, $n=7$ passerine species; data in Pelletier et al., 2008). Thus, the physiology of sustained, flapping flight that might place demands on the respiratory, cardiovascular (energetic) and muscular systems of birds is not synonymous with the physiology of foraging, or the physiology of investment in parental care. Some authors have even suggested that reduced flight activity during breeding might actually lead to atrophy of the main flight muscles, at least relative to sustained flight during migration (Bishop and Butler, 2015), giving a very different perspective on costs of reproduction (and see below).

Other than flight, what else do parents get up to during parental care? Might other activities be sufficiently sustained and intense to generate physiological costs? Foraging is a major component of time–activity budgets, but the cost of this will depend on the mode of foraging. In aerial insectivores, which feed on the wing, foraging is closely linked to flapping or soaring flight, flight makes up a much greater proportion of parental activity (~ 50 – 60%), and these species likely operate for longer at maximum sustained metabolic rates. Many arboreal species forage by frequently hopping or flying very short distances between branches, so although flapping flight is a small proportion of time/activity, this form of foraging might (Nudds and Bryant, 2000; Tinbergen and Dietz, 1994) or might not (Chin and Lentink, 2017; Yap et al., 2017) generate high physiological costs. In contrast, for ground-feeding birds (such as starlings, thrushes, shorebirds, etc.), foraging per se is almost entirely uncoupled from flight (other than that to and from foraging areas) and mainly consists of walking, turning, capturing and handling prey. Even if sustained, this would appear to be relatively low-intensity activity unlikely to incur physiological costs (as described above). This latter assumption might be premature because recent work suggests substantial costs of turning during locomotion (at least in humans; Halsey, 2016b), but this highlights the fact that we need to focus on the specific details of parental behaviour during chick rearing rather than simply assuming that any and all activity will contribute to physiological costs of reproduction.

Variation in workload during parental care is still most commonly measured as nest visit rate or provisioning rate. However, this excludes a key activity, parental self-feeding, that captures the essence of any trade-off underpinning costs of reproduction. Early studies suggested that: (a) among individuals, adults consume an average $\sim 30\%$ of all prey captured, but this varies from 10 to 60%; (b) adult self-feeding varies with prey size or quality; (c) considerable variance in foraging use of patches can be explained by variation in parental self-feeding; and (d) frequency of nest visits might be influenced more by time devoted to self-feeding than by time spent loading prey for chicks (Carlson, 1985; Kacelnik, 1984; Swihart and Johnson, 1986). In some species, self-feeding might

involve very different diets, and therefore potentially different foraging areas or foraging activities, than foraging for prey returned to chicks (Markman, 2014). Given all this potential variability, it is surprising that few, if any, recent studies have focused on this component of parental care, especially when the issue has been well highlighted previously: ‘provisioning the young is only one of the feeding considerations that must be dealt with by an adult’ (Swihart and Johnson, 1986).

Will all individuals incur the same cost of any sustained, intense activity?

In an age of ‘individual variation’, this is clearly a silly question to ask; this would be like taking a random group of amateur cyclists and expecting them to all do equally well, or equally badly, when entered in the Tour de France (sensu Caro et al., 2016). Obviously, we would predict that some individuals would perform better, and some worse, most likely because they possess different physiological attributes that ‘pre-adapt’ them to either (a) support sustained intense activity, e.g. higher hematocrit (Fig. 1B), higher energy stores or more efficient fuel use, or (b) better tolerate negative effects of this activity, e.g. with lower rates of increase in oxidative stress or of decrease in immune function for any given activity (Fig. 1B). To my knowledge, few studies have approached the issue of costs of reproduction from this perspective – does an individual’s physiological state either before reproduction or during early breeding stages influence its subsequent reproductive effort, workload ability or fitness (but see Merklings et al., 2017; Montoya et al., 2016; below)? This contrasts with the standard view that reproductive effort itself influences an individual’s physiological state at the end of the breeding season. Can we predict ‘winners’ and ‘losers’ based on their physiological state ahead of time?

We measured 13 different physiological traits across four different physiological systems during mid-incubation in female European starlings (M. F. Fowler and T.D.W., unpublished data). We then related this to individual ‘quality’ based on total number of offspring reared over a 2-year period and up to four potential breeding attempts (combining future fecundity and survival). Although total breeding productivity varied 2.5-fold (3.9 to 10.3 chicks), even among ‘successful’ birds, this was independent of variation in all physiological traits, including traits that might support higher aerobic performance [e.g. hematocrit (Fig. 2A), hemoglobin, glucose, triglycerides]. Breeding performance was also independent of the suite of traits associated with an experimentally induced ‘cost of reproduction’ (Fowler and Williams, 2017) based on principal components analysis (Fig. 2B, and see Fig. 3). By contrast, Merklings et al. (2017) suggested that individual physiological state before laying does modulate upcoming reproductive effort: individuals with higher pre-laying baseline corticosterone and lower antioxidant (superoxide dismutase) activity ‘invested more in reproduction’. This was based on the cumulative number of days spent rearing chicks, which is a somewhat strange measure of reproductive effort, and other measures of the oxidative stress system (malondialdehydes, glutathione ratio) were unrelated to reproductive effort. Nevertheless, Merklings et al. (2017) concluded that ‘only individuals that could afford to invest heavily in reproduction did so’. Montoya et al. (2016) reported that reactive oxygen species levels during courtship were not associated with subsequent provisioning effort, time attending offspring, or chick growth, but mothers with higher pre-laying lipid peroxidation spent less time attending their chicks even though they provisioned chicks at the same rate. These studies provide very limited support for the idea

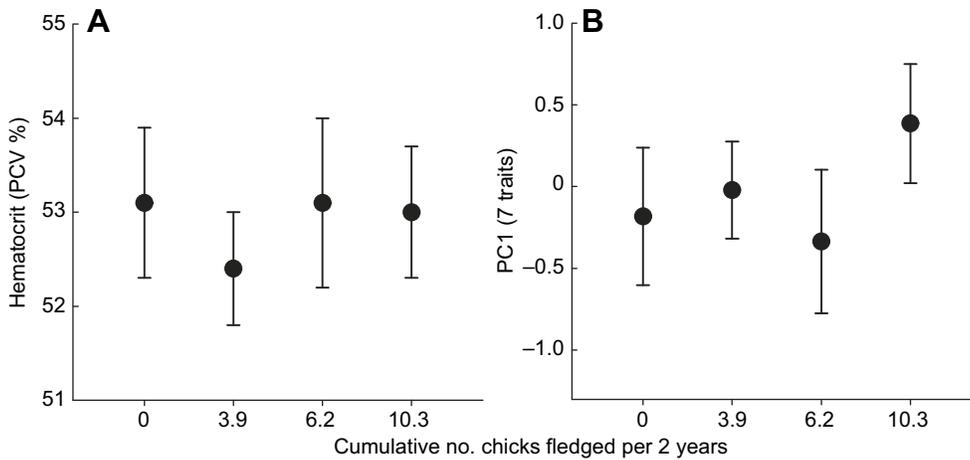


Fig. 2. Physiology and cumulative productivity. Physiological state during incubation does not predict subsequent cumulative two-year breeding productivity either for (A) individual traits such as hematocrit or (B) for 'PC1' for a suite of traits associated with an experimentally induced 'cost of reproduction' (hematocrit, hemoglobin, non-esterified fatty acid, triglyceride, haptoglobin, reactive oxygen metabolites, uric acid; see Fowler and Williams, 2017).

that baseline physiological state, measured at a time when parents are not involved in intense, demanding activity (e.g. pre-laying or during incubation), is informative in predicting subsequent reproductive effort, workload ability or fitness, but further studies (with more comprehensive measurement of physiological traits and hopefully better standardisation of measured traits) would be useful.

An alternative idea is that, independent of initial 'baseline' physiological state, individuals differ in their physiological response to rapid onset of more-intense activity (at hatching of their young), or the gradual increase in intensity of workload as the chick-rearing period progresses. Some (high-quality) individuals might cope with increasing activity more efficiently without incurring negative changes in physiological state that would otherwise be associated with decreased fitness. Again, to my knowledge, there are no data available to address this point. However, importantly, all studies that report physiological data for chick-rearing birds sampled individuals late in chick rearing – that is, they only sampled 'successful' birds, and these might be the very individuals that can work hard without paying costs. Blood sampling of birds closer to, or during, transitions in workload (e.g. soon after hatching) might capture those individuals in which increased workload does lead to physiological perturbations that subsequently cause breeding failure and/or longer-term costs. A related, and intriguing, idea here is that some individuals might be able to increase their performance capacity or their tolerance of costs

of gradually intensifying activity via exercise or training effects (physiological plasticity), for example, by maintaining higher activity prior to hatching or by undertaking 'voluntary' activity to maintain physiological state in anticipation of increased workload. This possibility has been virtually unexplored, especially in free-living animals (Halsey, 2016a; Killen et al., 2017), and is a rich area for future research.

Individuals might also be able to mitigate costs of parental care in other, simpler ways. A universal response to handicapping of parents (addition of weights or radio-transmitters, or via wing clipping) appears to be mass loss, typically between incubation and chick rearing (see Fig. 3C). Mass loss (and other adjustments, e.g. changes in take-off velocity) can completely compensate for any mass loading, or changes in wing loading, imposed by the experimenter through handicapping (Nudds and Bryant, 2002). However, mass loss also occurs in non-manipulated parents, and varies from year to year (T.D.W., unpublished data; Fig. 3C), suggesting that this might provide a general mechanism to deal with natural variation in potential costs of parental care in different ecological contexts, avoiding broader physiological costs. In other words, mass loss reflects a strategic 'decision' by parents, decreasing wing loading (see Glossary) and costs of flight. Again, this is not a new idea (Freed, 1981), and Norberg (1981) actually predicted energy savings and the gain in number of chicks that parents could realise for a given decrease in body mass. Despite this,

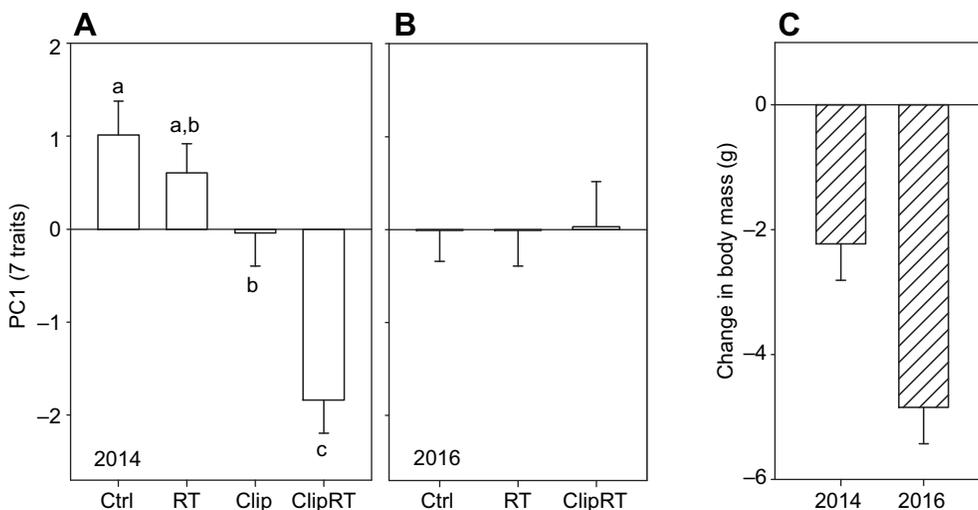


Fig. 3. Handicapping, physiology and body mass. Experimental handicapping of European starlings (radio-attachment, wing-clipping) was associated with a clear physiological signature of costs of reproduction in (A) 2014 (data from Fowler and Williams, 2017), but not in (B) 2016 (T.D.W., unpublished data), and (C) mass loss was greater in 2016 compared with 2014. Clip, clipped wings; ClipRT, clipped wings plus radio tag; Ctrl, control; RT, radio tag.

mass loss continues to be widely viewed only as a cost. Mass loss combined with wing morphing (see Glossary) (Swaddle and Witter, 1997; Hieronymus, 2016), i.e. coordinated movement of feathers within a wing, might even allow birds to mitigate the seemingly direct, negative biomechanical effects of wing clipping: our experimental manipulations might not be as effective as we think!

Finally, individuals will vary in the amount of resource they can acquire to meet the demands of parental care and this will modulate any cost of reproduction trade-off (van Noordwijk and de Jong, 1986), likely interacting with seasonal variation in resource availability (see below). In the human sphere, although millionaires might face the same theoretical trade-offs as those on low incomes, the former still have bigger cars and better houses (Reznick et al., 2000)! Similarly, individual, high-quality birds can have higher breeding productivity and higher survival (e.g. Garant et al., 2007), perhaps because they can acquire more resources, sufficient to avoid any costs of reproduction. This might involve individual differences in efficiency of foraging or something as simple as choosing a nest site in closer proximity to foraging areas, again decreasing the amount of sustained, intense activity associated with parental care.

Will meeting the costs of any 'hard work' be difficult, or equally difficult in all contexts?

'Costs of reproduction' should reflect the energetic/physiological demands of parental care but will be balanced by the resources available to meet these demands. Stearns (1992) – a book that should still be required reading for graduate students – highlighted the fact that trade-offs should only appear under 'food stress', i.e. when food availability is limiting. Most birds breed in spring and early summer for one very simple reason – this is the time when food is most available to support growth of chicks – and unless birds are 'food stressed', we should not expect to see costs of reproduction or physiological signatures of costs. Seasonal increases in food availability might mean that most individuals have ample resources with which to meet any increase in energy expenditure associated with parental care.

This issue of seasonal or annual variation in 'relative' costs of parental care is exemplified by two studies, both of which comprehensively investigated physiological costs using an experimental approach in multiple years. Hegemann et al. (2013) handicapped adult skylarks (*Alauda arvensis*) by attaching weights to both adults of a pair and measured several immune traits (lysis, agglutination, haptoglobin, proportions of different white blood cells, heterophil/lymphocyte ratio), breeding productivity and fitness (return rates, recruitment rates). They concluded that the balance between current reproduction and survival shifted from affecting nestlings to affecting parents as the reproductive season progresses, with physiological costs in adults apparent in second but not first broods, and that immune function is one physiological mechanism involved in this trade-off. However, there were substantial differences in response to the same handicapping manipulation in the two different years: (a) nestlings raised by handicapped parents had higher agglutination titres and haptoglobin concentrations than controls in one year (2007), but this pattern was reversed in the second year (2008); and (b) in adults, agglutination titres decreased through the season in control birds but increased in experimental birds in 2007, and this pattern was reversed in 2008. More importantly, the effect of handicapping on breeding performance varied among years: in 2007, more control nests (78%) were successful compared with experimental nests (25%), but in 2008, 62% of control and 87% of experimental nests were

successful. Similarly, return rates of previously handicapped birds were lower than control birds in 2008 (40.0% versus 85.7%), whereas in 2009, handicapped birds actually had higher return rates (72.7% versus 66.6%; albeit with small sample sizes). Thus, there was substantial annual variation in response to the same standardised handicapping treatment.

Fowler and Williams (2017) manipulated parental workload of female European starlings by handicapping using radio-transmitter attachment and wing clipping. They reported a widespread decline in physiological function across multiple physiological systems with increased workload (Fig. 3A). Females that paid a cost of reproduction (lower future fecundity and lower return rates) had lower oxygen carrying capacity (lower hematocrit and hemoglobin levels), lower energy reserves (plasma non-esterified fatty acid and triglyceride levels), decreased immune function (lower haptoglobin levels) and elevated levels of oxidative stress (higher levels of reactive oxygen metabolites and lower levels of the endogenous antioxidant uric acid). Perhaps foolishly, I repeated this experiment in a subsequent year (2016) using the same manipulations (radio-transmitters and wing clipping) and measured the same seven physiological traits. In this second year, there was absolutely no relationship between the predicted experimental increase in workload and physiological state (Fig. 3B). Furthermore, as in Hegemann et al.'s (2013) study, wing-clipped birds had lower return rates than radioed birds in 2014, but the opposite was true in 2016 (T.D.W., unpublished data).

These two studies clearly illustrate that both physiological effects of experimentally manipulated work load and 'fitness' outcomes of parental effort can vary by year even with the same standard manipulation depending on the ecological context of the experiment. Hegemann et al. (2013) did not discuss differences in ecological context in their two study years. In our study (Fowler and Williams, 2017), population-level breeding productivity was similar in both years (2016 versus 2014) and there was no treatment effect on provisioning rate for the current breeding attempt in either year. The only potential difference we could identify is that wing-clipped females with radios had far greater mass loss in 2016 compared with 2014 (Fig. 3C). This suggests they were able to utilise the mass loss 'strategy' described above, differently in different years and, in the latter year, this might have been sufficient to completely compensate for any experimental increase in workload (sensu Nudds and Bryant, 2002), without any perturbation of physiological homeostasis – thus, avoiding any costs of reproduction.

Conclusions

There are many reasons why we should not expect to see costs of reproduction associated with parental care (even in small-bodied, short-lived passerines with high mass-specific metabolic rates where activity costs should be high) and hence why we will not detect any physiological signature of costs associated with parental care. (1) The duration of intense physical activity associated with provisioning or chick rearing might be quite limited (in particular, where there is early nest departure, brood division, etc.). (2) Flight, the most obvious sustained, high-intensity activity, might only represent a small component of an individual's overall diurnal time or activity budget. (3) Some (high-quality) individuals might be able to better tolerate any costs of intense activity, without major perturbation of physiological homeostasis (and these are the individuals we will most often sample if we restrict sampling to late in the chick-rearing period, when low-quality birds will already have failed and dropped out of the population). These same individuals might have behavioural attributes (e.g. foraging skills)

that provide them with better access to resources sufficient to avoid physiological costs. (4) Individuals might utilise ‘simple’ mechanisms to modulate costs of activity (for example, mass loss, adjustment of wing loading, wing morphing), again avoiding more substantial perturbation of physiological homeostasis. (5) Reproductive trade-offs should only be expected under ‘food stress’ (Stearns, 1992), otherwise trade-offs between current reproduction, future reproduction and survival will be zero or even positive. Most birds breed in spring and early summer precisely because of seasonal increases in food abundance, and so it is unclear how often parents are ‘food stressed’. Thus, life-history theory (sensu Stearns, 1992) clearly predicts that costs of reproduction might be rare. In addition, phenotypic plasticity (sensu Schlichting and Pigliucci, 1998) clearly predicts that parents should have myriad ways to deal with variation in brood demand, with individuals adopting different ‘strategies’ in different ecological contexts and, perhaps, different physiological states. We should expect complexity of parental care (contra Mathot et al., 2017).

In summary, there are many reasons why costs of reproduction – and any physiological signature of these costs – might be quite rare, both temporally (in different years) and among individuals. Finding no evidence for costs of reproduction in single-year studies where ecological context (e.g. natural food availability) is unknown, or not reported, should not come as a surprise! But does this mean that researchers should abandon the search for the physiological basis of costs of reproduction? Absolutely not. However, as another must-read review article highlighted, when it comes to costs of reproduction, ‘the devil is in the details’ (Harshman and Zera, 2007). We need to adopt a far more detailed, more nuanced understanding of the complexity of behaviour during parental care – something that is now possible with advances in biotelemetry (Killen et al., 2017). Finally, we need to think about ‘cost of reproduction’ correctly in relation to the original formulations of life-history theory.

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Competing interests

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