Commentary

The role of power versus energy in courtship: what is the 'energetic cost' of a courtship display?

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WHAT IS AN 'ENERGETIC COST'?

'Energetic' courtship displays are prevalent in nature. Male frogs and cicadas sing loudly, swordtail fish swim vigorously, and spiders vibrate before a potential mate. Birds are especially well known for elaborate performances. Among them, hummingbird displays would seem to be the epitome of 'energetic' displays, in which the male aerobatically dives at high speed and/or performs rapid, agile close-range flight manoeuvres to a female. These displays are certainly physically demanding: courting male hummingbirds appear to be near flight performance limits (Clark 2009) and will often perch and pant between bouts of displays (Feo & Clark 2010). Given that hummingbirds have among the highest metabolic rates during flight (Lasiewski 1963; Bartholomew & Lighton 1986; Welch et al. 2007; Clark & Dudley 2009), it might seem obvious that these courtship displays are energetically costly. But as I outline here, although they are certainly impressive athletic performances, the energetic cost of these displays is less clear.

The ambiguity lies in the meaning of the term 'energetic costs' (or metabolic expense, metabolic cost, etc.), which are often

invoked without specificity in the animal behaviour literature. This suggests that the nature of an 'energetic cost' is self-evident or well known. But consider: which human behaviour has the higher energetic cost, walking for an hour or sprinting hard for a minute? The answer depends on the definition of 'energetic cost'.

Energetics (or bioenergetics) is the study of energy and its flow (McArdle et al. 2007, page 122). It is a broad term, and both energy and power (energy per unit time) fall under its umbrella. There are minimally two specific definitions of an 'energetic cost' used in the literature, and although related, they are not synonymous. The first definition of energetic cost is: a quantity of chemical energy (i.e. ATP and its metabolic precursors) that is expended to perform a behaviour. Under this definition the energetic cost of a courtship display is the energy (measured in joules, J, or calories) expended to perform that behaviour. Hereafter I refer to this as the 'joule cost' of a behaviour. The second definition of energetic cost is: a quantity of energy per unit time that is expended on a behaviour. It is the animal's metabolic power input (e.g. its metabolic rate) during performance of the behaviour, measured in watts (W or J/s); or a correlate such as oxygen consumption rate (McArdle et al. 2007). This is the 'power limits' definition, which I use hereafter, and discuss further below (see Costs). Moreover, metabolic energy (ATP and precursors) is the input to a behaviour; muscles convert a fraction of it into mechanical strain energy, which is the output (Alexander 2003; Biewener 2003). For purposes of comparison, the

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mechanical energy and power output of a display may serve as a proxy for metabolic inputs, as they may be more easily measured or estimated than the input.

To answer the previously raised question, and as anyone trying to control their weight through exercise (i.e. expend stored chemical energy) knows, more joules are expended walking for an hour than sprinting at top speed for a minute, even though the latter involves much higher power input (Fig. 1). According to the joule cost definition, walking for an hour has higher 'energetic cost', whereas according to the power limits definition, sprinting for a minute has higher 'energetic cost'. The duration of the behaviour matters.

Both the joule cost and the power limits definitions of 'energetic cost' are commonly used in the animal behaviour literature. Which definition is used is often implicit rather than explicit (authors may switch back and forth between definitions: e.g. Ryan 1988; Stoddard & Salazar 2011), and they are sometimes explicitly conflated. Examples of empirical studies that primarily use the joule cost definition are shown in Table 1, and examples of studies primarily using the power limits definition are shown in Table 2, although to be fair, some of the studies listed use both definitions. Studies employing the joule cost definition have used a variety of experimental techniques to test or infer how many joules (calories) are expended to display, including the measurement of the field metabolic rate (through the use of doubly labelled water), estimates of fat deposits available, estimates of mass loss, or a measurement of the animal's metabolic power input during the display (e.g. with respirometry) coupled with the animal's time budget (references in Table 1). Studies employing the power limits definition have measured power to display via respirometry, or by monitoring heart rate, but do not provide a time budget for the behaviour, so the energy expended on display cannot be calculated from the available data (see Table 2 for references).
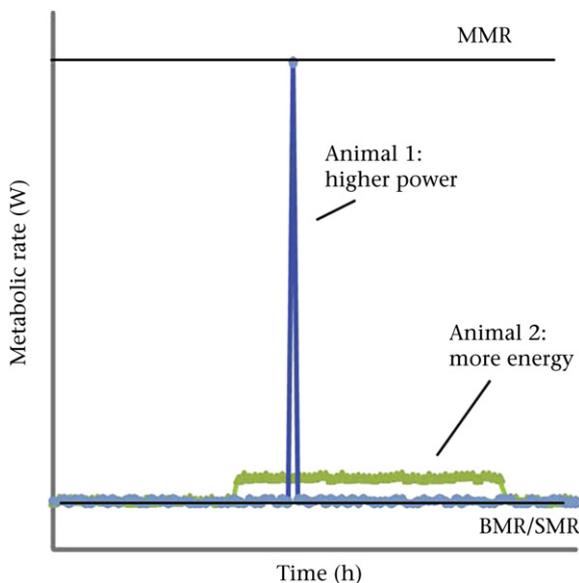
Reviews tend, implicitly or explicitly, to use the power limits definition. In their review of courtship displays, Byers et al. (2010, page 772) define vigour as 'an individual's ability to perform energetically expensive motor acts repeatedly', implying that a single motor act can be energetically expensive. In a review of singing anurans and insects, Prestwich (1994, page 628) defines the energetic cost of sound production as 'the increment in metabolism caused by the muscles used in calling …'. Ryan's (1988) influential paper entitled 'Energy, calling and selection' mostly employs the power limits definition, as do Lailvaux & Irschick (2006).

Some explicitly conflate power with energy. Watson et al. (1998) measured the metabolic power necessary for female water striders (*Aquarius remigis*) to carry courting males, and made statements such as 'females carrying males used 413.9 µW of energy' (page 51). The microwatt (µW) is a unit of power, not energy. Likewise, in their review of the 'energetic costs' of communication, Stoddard & Salazar (2011) refer to signal energy but depict signal power in their Figures 1 and 2.

The conflation of energy with power is not simply a semantic issue. A number of studies have suggested that courtship displays are expensive or costly to perform (Kotiaho et al. 1998; Basolo & Alcaraz 2003; Lailvaux & Irschick 2006; Cummings & Gelineau-Kattner 2009; Barske et al. 2011; Cady et al. 2011) when the data presented are often insufficient to support this conclusion. Rather, the role of power input and output in courtship is underappreciated. For the remainder of this essay, I explore the implication that explicitly distinguishing between a display's energy and power has for understanding why animals perform courtship displays. The ideas expressed here are applicable to the 'energetic costs' of other types of behaviours; this paper focuses on courtship displays because the costs of sexually selected traits remains a topic of vigorous discussion.

ENERGY VERSUS POWER

Behaviours that expend large quantities of energy may not exhibit high power input, and behaviours characterized by high power input do not necessarily result in much expended energy (Fig. 1). Therefore, showing that a behaviour entails a high metabolic rate (or high power input) does not automatically mean that the animal expends a large amount of energy on the behaviour (Reilly et al. 2007; Pelletier et al. 2008; Byrnes et al. 2011). For instance, duck flight requires extremely high metabolic rates (power input), yet relative to their energy budget, common eiders, *Somateria mollissima*, expend little energy on flight because they only spend a few minutes flying per day (Pelletier et al. 2008). Any display that is short, like a spider's ∼1 s drumming display (Kotiaho et al. 1998) will consume relatively small amounts of energy, even if the animal briefly reaches some kind of maximum metabolic rate, because the area under the curve is small (Fig. 1).

The measurement of animal metabolic rates has a long history in physiology (e.g. Kleiber 1961; Blaxter 1989). Perhaps some of the confusion of power and energy in the behaviour literature stems from how metabolic rates are often discussed in the physiology literature. It is common to refer to metabolic rates as 'metabolic costs' (e.g. Alexander 2003; Reilly et al. 2007; Stoddard & Salazar 2011), but this is shorthand. The metabolic rate is the metabolic cost per unit time (i.e. they are time-normalized costs). Implicit normalization can lead to misunderstanding. Two ornithologists might pointlessly argue whether flight is an expensive or cheap mode of locomotion. It is both: flight is costly per unit time but cheap per unit distance (Norberg 1990; Alexander 2003; Biewener 2003). Time normalization allows an investigator to make physiological or biomechanical comparisons of different animals in a laboratory setting, where duration is often just a variable to be controlled. But for anyone wishing to make ecological inferences as

Figure 1. An idealized example of the metabolic rate (W) of two animals that each engage in one behaviour and are otherwise inactive at the basal or standard metabolic rate (BMR/SMR). Animal 1 briefly reaches a maximal metabolic rate (MMR) that is 10× BMR, whereas animal 2 spends a relatively long time at 1.5× BMR. Animal 1 has a far greater peak power, but because animal 2 is active for longer it expends far more energy, where energy is the area under the curve in excess of BMR/SMR. This example is idealized, since animals do not often perform one isolated behaviour. Examples akin to animal 1 are wolf spider drumming displays measured by Kotiaho et al. (1998; see their Figure 1) or manakin jump-snap displays recorded by Barske et al. (2011; see their Figure 4), if their data were plotted on a timescale of hours.

Table 1
Examples of studies of courtship behaviour or morphology that primarily employ the 'joule cost' definition of energetic cost

Source	Organism	Method of estimating/measuring expended energy	Behaviour	Joule cost
Plaistow et al. 2003	Amphipod, *Gammarus pulex*	Measured lipid stores of males	Mate guarding	Mate-guarding males have higher lipid and glycogen stores
Woods et al. 2007	Fireflies, *Photinus* sp.	Respirometry combined with time budget	Bioluminescent flashing	Flashing increases MR by 37%; accounts for <3.4% of daily energy budget
Reinhold et al. 1998	Waxmoth, *Achroia grisella*	Respirometry combined with partial time budget; mass loss	Ultrasonic singing	Singing increases MR by up to 4× SMR and results in daily loss of 5% of body mass
Mappes et al. 1996; Kotiaho 2000	Wolf spider, *Hygrolycosa rubrofasciata*	Mass loss	Display motions	Males induced to display at high rates lost mass over a series of days
Salazar & Stoddard 2008	Electric fish, *Brachyhypopomus pinnicaudatus*	Respirometry combined with daily energy budget	Electrocommunication signals	Electrogenesis made up 11–22% of males' energy budget
Bennett & Houck 1983	Salamander, *Desmognathus ochrophaeus*	Respirometry combined with energy budget	Entire courtship	Courtship consumes ~2.7 J, which is <1% of daily energy budget
Vehrencamp et al. 1989	Sage grouse, *Centrocercus urophasianus*	Doubly labelled water; mass loss	Display motions	Active displayers expend up to 2524 kJ/day; inactive males expend ~1218 kJ daily
Dearborn et al. 2005	Great frigatebirds, *Fregata minor*	Doubly labelled water	Display motions	Negligible (no correlation between display rate and FMR)
Usherwood 2008	Collared doves, *Streptopelia decaocto*	Kinematics analysis; time budget	Display flights	Displays performed over 1 h expend ~5% of BMR
Höglund et al. 1992	Great snipe, *Gallinago media*	Doubly labelled water and mass loss	Display motions	Males with high display rates expend ~4× BMR daily, while nondisplaying males expend ~2.6× BMR daily
Clark & Dudley 2009	Streamertail, *Trochilus polytmus*	Respirometry combined with time budget	Carrying an ornamental tail	Long tail increases power needed for fast flight; estimated to increase daily energy budget by <3%
Eberhardt 1994	Carolina wren, *Thryothorus ludovicianus*	Respirometry combined with time budget	Singing	Singing increases MR by 2.7–8.7× BMR; accounts for 9.4–25% of daily energy budget
Thomas 2002	Nightingale, *Luscinia megarhynchos*	Mass loss	Singing	Rate of singing positively correlated with mass lost
Ward et al. 2004	Pied flycatcher, *Ficedula hypoleuca*	Respirometry combined with time budget	Singing	Singing increases daily energy expenditure by 0.4%

BMR: basal metabolic rate; FMR: field metabolic rate; MR: metabolic rate; SMR: standard metabolic rate.

to why wild animals perform behaviours such as courtship displays, the duration of time spent performing the behaviour is a crucial variable of interest (Reilly et al. 2007).

What this means is that any type of courtship display that is performed infrequently or briefly has a low joule cost, no matter how impressive. Consider hummingbird courtship displays mentioned above. The Anna's hummingbird, *Calypte anna*, has been a model for studying flight metabolism (Welch & Suarez 2007), flight capabilities (Altshuler et al. 2010b), energetics (Powers & Nagy 1988; Powers 1991) and courtship displays (Clark & Feo 2008; Clark 2009). Its most distinctive courtship display is a dive, in which, over the span of about 13 s, a male ascends about 35 m above the female and then swoops by her, reaching speeds of about 100 km/h (Clark 2009). The metabolic energy expended to perform this display falls in the range of 12–25.5 J per dive (calculations in Appendix). Given a daily energy budget of about 32 kJ (Powers & Nagy 1988), one dive increases the daily energy budget by roughly 0.04–0.08%. Males perform multiple dives in a display bout, and for the occasional female that lingers on a male's territory, these bouts can include up to 40 dives. Yet a bout of 40 dives only increases daily energetic needs of a male by 1.5–3%, and bouts of 40 dives are rare, most likely occurring less than once per day. This is a small increase; a male expends relatively few joules of energy to display.

By contrast, the power expended by the muscles during a dive is substantial. Ascending vertically against gravity requires elevated metabolic power input; this input results in a muscular power output on the order of roughly 270 W per kg of muscle (calculations in Appendix) when ascending vertically just prior to a dive. This is high, comparable to the maximum power output of roughly 230–310 W/kg that hummingbird flight muscles are estimated to attain in experiments designed to elicit maximum hovering flight performance (Chai et al. 1997; Chai & Millard 1997; Altshuler et al. 2010a). These data suggest that when they ascend for a dive, the male Anna's hummingbird's motor is racing, and may be near its maximum power input. It is like running a 100 m dash: the animal's power input is potentially at or near a physiological limit, yet little energy is burned because the behaviour is brief. Similarly, Usherwood (2008) showed that collared dove, *Streptopelia dacaocto*, displays, in which an individual ascends vertically and then glides down to a perch, entail high power output but relatively low energy expenditure. Such displays are impressive in terms of power, not energy.

THE POWER LIMITS HYPOTHESIS

Individual behaviours will entail high joule costs, high power input, both, or neither. In this section, I sketch the properties that behaviours with high joule cost and high power input are predicted to have. I then propose the power limits hypothesis as an explanation for vigorous displays: females may prefer extreme displays,

Table 2
Examples of studies of courtship behaviour or morphology that primarily define 'energetic costs' in terms of metabolic rate (metabolic power input) during display

Source	Organism	Method of estimating/measuring power input	Behaviour	Metabolic rate
Allen & Levinton 2007	Fiddler crab, *Uca pugilator*	Respirometry	Carrying an ornamental claw	Claw increases MR by 8% of SMR
Bailey et al. 1993	Bushcricket, *Requena verticalis*	Respirometry	Singing	Singing increases MR by ~1.6× SMR
Kavanagh 1987	Two species of crickets (Orthoptera)	Respirometry	Singing	Singing increases MR 4 and 13× SMR
White et al. 2008	Australian mole cricket, *Gryllotalpa monanka*	Respirometry	Singing	Singing increases MR by 13.5× SMR
Watson et al. 1998	Water strider, *Aquarius remigis*	Respirometry	Mate carrying	Mate carrying increases MR by 24% relative to unladen locomotion
Kotiaho et al. 1998	Wolf spider, *Hygrolycosa rubrofaciata*	Respirometry	Display motions	Drumming momentarily spikes MR to 22× RMR
Cady et al. 2011	Wolf spiders, *Schizocosa* sp.	Respirometry	Display motions	Courtship display increases metabolic rate by up to 2.2× RMR
Watson & Lighton 1994	Sierra dome spider, *Linyphia litigiosa*	Respirometry	Courtship sequence	Courtship and copulation increases metabolic rate 1.2–4.5× RMR
Cummings & Gelineau-Kattner 2009	Swordtail, *Xiphophorus nigrensis*	Respirometry	Display motions	Display increases MR by 2–200% over RMR
Basolo & Alcaraz 2003	Swordtail, *X. montexumae*	Respirometry	Display motions, long tail	Display with long tail increases MR by 19% relative to short tail
Grafe et al. 1992	African reed frog, *Hyperolius* sp	Respirometry	Singing	Singing increases MR ~3× SMR
Bucher et al. 1982	Frog, *Physalaemus pustulosus*	Respirometry	Singing	Singing increases MR ~4× SMR
Taigen & Wells 1985	Treefrog, *Hyla versicolor*	Respirometry combined with a partial time budget	Singing	Singing increases MR by up to 22× SMR
Ward et al. 2003	Canary, *Serinus canaria*	Respirometry	Singing	Singing increases MR by 2.4× BMR
Horn et al. 1995	Rooster, *Gallus domesticus*	Respirometry	Singing	Singing increases MR by 1.15× BMR
Oberweger & Goller 2001	Three species of birds	Respirometry	Singing	Singing increases MR by 1.02–1.16× BMR
Barske et al. 2011	Golden-collared manakin, *Manacus vitellinus*	Heart rate telemetry	Acrobatic courtship display	During display, heart rate reaches ~2× RMR

BMR: basal metabolic rate; FMR: field metabolic rate; MR: metabolic rate; RMR: resting metabolic rate; SMR: standard metabolic rate.

such that males are limited in their ability to perform the display by the power capacity of their 'motor'.

Behaviours with high joule cost have one unifying characteristic: they are endurance behaviours, meaning they take a relatively long time to perform. They may be behaviours that elevate the animal's metabolic rate for a relatively long time, and thus result in a significant number of additional calories (joules) expended. Or, they could be behaviours that prevent normal foraging and therefore impact the intake side of the animal's daily energy budget (Ward et al. 2004). Animals preparing to engage in behaviours with high joule cost often gain weight (e.g. fat) prior to the behaviour, as birds do before migration, or before a prolonged incubation (Spée et al. 2010). And they lose weight during these behaviours. Either of these attributes is expected for males that perform courtship displays with high joule cost.

There are numerous examples of endurance mating behaviours in the literature. A frog calling for much of the night expends considerable energy (Ryan 1988); the same is true for lekking birds that deplete stored fat over the course of the breeding season (Vehrencamp et al. 1989; Höglund et al. 1992; Barske et al. 2011). Wolf spiders experimentally induced to display for several days lose body mass, indicating a significant number of expended joules of energy (Mappes et al. 1996). Sage grouse with high display rates were shown (with doubly labelled water) to expend a greater number of joules on display (Vehrencamp et al. 1989). A single sage grouse display requires few joules, but in contrast with the hummingbird example above, during the peak of the breeding season, male sage grouse leks are continually visited by many females (Schroeder et al. 1999), such that a male spends a significant fraction of the day in display. It is not sufficient to measure a male's metabolic rate during display to show that the behaviour costs much energy; it must also be established that the behaviour lasts a long time, in order to determine its impacts on the daily energy budget.

By contrast, high-power behaviours are not necessarily endurance behaviours: they can be very brief. These are 'burst' or 'sprint' performances. Burst behaviours are common in human athletics, such as the 100 m dash, which depends on the mass-specific power output (W/kg of body mass) the performer can muster (Helene & Yamashita 2010). An animal's ability to produce such behaviours is limited or constrained by its motor (its muscles, metabolic physiology and functional morphology). Behaviours derive from muscle contractions, and all muscle contraction entails some degree of power input. Any given muscle has a maximum mechanical power output that it can achieve, set by a broad range of anatomical and physiological variables such as overall size, fibre type, fibre geometry, contraction rate and ATP available (Alexander 2003; Biewener 2003).

I propose the power limits hypothesis as an explanation for 'burst' courtship displays. If females hold directional preferences for male behaviours that are extreme in some way, performance of the behaviour may elaborate until it is limited by the maximum power output the male can muster with the relevant portion of his functional morphology. Such preferences are analogous to female preferences that drive the evolution of extreme morphological ornaments such as a greatly elongated tail. Such behaviours could be extreme in a variety of ways, characterized by high velocities, accelerations, loudness, or other modes of energy dissipation. Since the male's motor only has a certain power capacity, female preference pushes these displays to this performance limit. Limitations on power output are as diverse as animal morphology and physiology; the decibels a frog can put into its song are limited by its laryngeal morphology (Prestwich et al. 1989), just as the power that a hummingbird can put into a dive is limited by its flight morphology or the power that a sprinter can put into a 100 m dash is limited by her legs as well as everything that supports it, cardiovascular and respiratory physiology, etc. This includes tiring (or stamina), which in one view is a physiological limitation on sustained power output, as in Kotiaho et al.'s (1998) wolf spiders.

The power limits hypothesis of a display behaviour can be tested through understanding the functional morphology, physiology or

biomechanics of the signal in question. Physiological experiments are predicted to show that displays males produce are near the limits of power expenditure for the morphology used to display, which is not necessarily the same as the whole animal's maximum metabolic rate. Behavioural experiments are predicted to find that females have preferences for aspects of the signal that contains high power. There is already some support for this hypothesis: female preferences for song loudness are in effect preferences for maximum acoustic power (Ryan 1988; Prestwich 1994), and female golden-collared manakin, *Manacus vitellinus*, preferences for faster male displays may be preferences for maximum metabolic power (Barske et al. 2011).

There are many displays that cost little energy to produce and that also do not appear to be power limited. The courtship of the salamander *Desmognathus ochrophaeus* neither entails many joules expended nor involves maximum power output (Bennett & Houck 1983). Swordtail courtship swimming may not push a performance limit in *Xiphophorus* sp. (Basolo & Alcaraz 2003; Cummings & Gelineau-Kattner 2009), and similarly, many birds such as cock-of-the-rock (Trail 1985), birds of paradise, or peafowl perform elaborate behavioural displays that do not seem power limited. In such displays, female preferences may instead target other, more poorly understood aspects of motor performance, such as coordination, repeatability or control (Byers et al. 2010). Such displays seem akin to figure skating or some gymnastics events, in which superior performers do not necessarily have the highest mechanical power output, rather quality hinges on other, less well-understood performance attributes.

COSTS

What constitutes the cost of a display? A cost is the price paid for something in the form of some sort of currency. A currency is any expendable resource, such as time, money, energy or fitness, such that the allocation of the currency to one use renders it unavailable for another. Hence there are trade-offs associated with use of a currency, and currencies have budgets. The costs of displays are of interest because all sexual selection models posit that, when pushed away from a naturally selected optima by female preference, sexually selected characters have fitness costs, expressed as reduced survival and/or future mating opportunities (Andersson 1994; Kotiaho 2001; Bradbury & Vehrencamp 2011). In fitness currency, both the energy and power involved in production of a display could have costs. Moreover, energy is also a currency in its own right whereas power is not, meaning it is crucial to differentiate between fitness costs and energy costs.

Chemical energy available is a currency; therefore, use of energy entails a joule cost. Animals have energy budgets, and they eat to replenish expended energy (Kleiber 1961). A crucial feature is the connection, if any, between the joule cost and the fitness cost of a given behaviour. The joule cost of a behaviour will result in a fitness cost only if the expenditure of energy on a display reduces survival or future mating opportunities (Kotiaho 2001). Only when energy intake is limited do animals face cost/benefit trade-offs and the need to strategically allocate energy. To conclude that the energy costs of a courtship display have meaningful fitness costs, two things must be demonstrated: the joules expended to display are a significant fraction of the daily energy budget, and that these joules are not simply replaced through increased foraging.

Energy-based theory has successfully explained behaviours of long duration (i.e. behaviours that last hours, days, or longer). Examples include optimal migration theory (Alerstam & Hedenström 1998) and optimal foraging theory (Pyke 1984). Likewise, the energy budget must balance over the long term, not the short term. The timescale for 'long-term' is typically longer than a day (and can be much longer for behaviours such as hibernation). Physiologists measure the energetic budget by the day or longer, not the hour or minute, because most animals exhibit pronounced diel cycles in energy intake and expenditure. By contrast, power tends to be important for brief, extreme behaviours, such as a fight or escape from a predator, that often last only seconds, in which absolute performance trumps energy economy. Successful performance of such behaviours often hinges on maximal performance (e.g. mechanical power output), and large fitness stakes may rest on small differences in ability. Many courtship displays appear to fit these criteria.

Power is not a fuel or a currency. It does not get used up, so power production is not costly in the same way that energy is. The capacity for power input or output is a rating of the 'motor', like a car's horsepower. An animal's motor is its functional morphology: muscles, appendages, etc. The morphology associated with a given courtship display is predicted to have fitness costs if it has shifted a male away from a naturally selected optimum. This shift may occur because any given morphology and physiological state has a maximum power input or output that the animal can produce for a given behaviour. If females prefer a more extreme display, males will be sexually selected to acquire the functional morphology or physiology to produce it (Oufiero & Garland 2007). For example, male manakins have hypertrophied muscles for increased force production during wing-snapping displays (Schultz et al. 2001). In this case, the wing muscle (the motor) is a sexually selected physiological ornament.

Such physiological ornaments probably have fitness costs to grow, maintain or carry, which are expressed either by interfering with naturally selected functions, or by incurring additional growth and maintenance costs. While the diverse ways that ornaments can incur fitness costs are too numerous to list here, I want to emphasize that the relationship between ornaments and joule costs is variable. Some ornaments will incur secondary joule costs by elevating the resting metabolic rate. For instance, Allen & Levinton (2007) showed that the ornamental claw of male fiddler crabs increases resting metabolic power by 8%. If we assume that fiddler crabs spend the entire day resting, then the joule costs of the claw would also be 8% of the daily energy budget, which could be significant in the context of their foraging ecology. By contrast, ornaments that hinder locomotion may incur relatively low joule costs if the hindrance is rarely expressed. For example, Clark & Dudley (2009) found that greatly elongated, ornamental tail feathers increase the metabolic power for hummingbird flight by about 10%, but only at high flight speeds. Hummingbirds spend only a small fraction of the day flying at high speed, so the joule costs of this large ornament are estimated to be less than 3% of the daily energy budget (Clark & Dudley 2009). Morphological ornaments such as an elongated tail may affect an animal's power margin (the power available for burst behaviours such as manoeuvres; Altshuler 2006), which could have deleterious effects during behaviours requiring maximum power output such as escape from predators, attacks on prey or fights with conspecifics. The point is that a physiological ornament evolved for a display may impose fitness costs through a variety of mechanisms, and joule costs are not necessarily included.

FEMALE PREFERENCES

Female preferences are widely accepted as the underlying evolutionary reason why males have evolved complex courtship displays (Darwin 1871; Andersson 1994; Bradbury & Vehrencamp 2011). It has been argued that females have preferences for

displays in which males incur high 'metabolic costs' because these costs reveal a male's quality to a female (e.g. Mappes et al. 1996; Barske et al. 2011). What type of information might a display with high power contain? First I consider adaptive mate choice hypotheses (i.e. females derive direct or indirect benefits from picking the best male). Recent authors have distinguished between 'handicap' signals and 'index signals' of male quality (Maynard Smith & Harper 2003; Bradbury & Vehrencamp 2011; Számadó 2011). Handicap signals are strategic, meaning that all signallers can choose the intensity of the signal, but cheating is not advantageous for low-quality signallers because there is a signal fitness cost differential that covaries with signaller quality. Index signals, on the other hand, contain information because their form is physically constrained or limited, such that signallers intrinsically vary in their ability to produce the signal (Maynard Smith & Harper 2003; Bradbury & Vehrencamp 2011; Számadó 2011).

Put in this light, power-limited aspects of displays are by their nature well suited to be index signals, as power output is intrinsically limited (see Costs). For instance, female manakins prefer faster male performances (Barske et al. 2011), and it seems unlikely that slow males could fake being fast, rather they are intrinsically limited by their capacity to perform, just as humans that lose a 100 m dash are not being slow for strategic reasons; they are slow, period. Displays often involve many aspects of the phenotype (e.g. morphology, neural capability, respiratory physiology, etc.) and so may be suited to be index signals of condition (e.g. Rowe & Houle 1996).

Applying the handicap hypothesis to power-limited displays is more complex. Power-limited displays could function as condition-dependent handicaps if there are strategic fitness costs associated with producing the physiological ornament (motor) underlying the display. It appears this hypothesis would be difficult to test. To support it, a strategic fitness cost differential associated with production of the physiological ornament (the motor) must be demonstrated. Such fitness costs are most likely subtle and could be expressed at any stage of ontogeny or life history. For instance, like a training athlete, suppose that a 'good' performance requires extensive practice. (In birds, there are abundant anecdotal stories of birds apparently 'practising' displays, a topic that seems understudied). What are the fitness costs, if any, of practising a display, and how could they be shown? It seems strategic fitness costs associated with practising a display may be hard to demonstrate at all, let alone the strategic cost differential required to support the handicap hypothesis.

With respect to the energy expended during a display, there is some scope for handicaps in conjunction with the energy costs of display, as energy is a strategically allocated currency. And as mentioned above (The Power Limits Hypothesis), there is evidence that courtship behaviour in general (e.g. lek attendance) incurs energy costs (e.g. Höglund et al. 1992; Barske et al. 2011), meaning that breeding behaviour may be an endurance behaviour, from the perspective of a male. But, females are unlikely to use displays to measure energy directly. The reason is, a female that encounters a male in the middle of a display (such as singing to attract her) has no direct indication of how long the male has been performing the display prior to her arrival, and thus she has little information regarding the cumulative number of joules he has expended. The simplest way for a female to measure how many joules a male has expended on a display would be to assess the duration of an endurance behaviour (observing a display for hours or days to sample one male). According to this hypothesis, display evaluation should take a long time. But in many mating systems, females encounter males during mid-display, and assess the male in the span of minutes, not hours or days. Lek attendance (or other general aspects of being in breeding condition) might be endurance behaviours for the male, but this does not automatically mean that

the courtship displays a male performs when the female arrives are a signal to the female of his energy status.

The alternate to these adaptive hypotheses is the null that female preferences are arbitrary and that displays evolve through the runaway process (e.g. Prum 2010). Arbitrary directional female preferences could also generate extreme male displays, just as arbitrary preferences can generate elaborate morphology via the Fisher runaway process (Kirkpatrick & Ryan 1991).

CONCLUSIONS

In this essay, I have pointed out that authors discussing 'energetic costs' of courtship display behaviours often implicitly use and sometimes conflate two disparate definitions of this cost: the joules expended to display (energy), and the power input (metabolic rate) of the animal during the display. Conflating the two is like confusing a car's gas tank (energy stores) with its motor (horsepower). Nobody buys a sports car specifically because it burns a lot of gas. Sports cars are sexy because their acceleration, top speed and manoeuvrability make them fun to drive, attractive performance attributes related to the car's high horsepower. Two courting males of the same species are analogous to two cars of the same make and model. (The mind naturally turns to the comparison of an economy car with a sports car, but this is akin to comparing an ectotherm such as an insect or lizard to an endotherm such as a mammal or bird.) Any difference in the condition of the motor might lead to detectable differences in performance, allowing females to prefer one over the other. Sports cars also get low gas mileage, but this well-known fact is a distraction. It is similar to laboratory studies of 'metabolic costs' discussed above, in that it is time-normalized cost. The actual amount of gas burned depends on the length of the drive. Taking a quick trip around the neighbourhood to impress a date will burn little gas (Fig. 1). It is the performance that impresses, not the energy consumed.

In this essay I have used the clunky term 'joule costs' of displays because the term 'energetic cost' at present has varying meanings. Going forward, I suggest that the term 'energetic costs' should refer specifically to the energy and not power definitions: the energetic cost is a number of joules or calories expended, relative to the animal's daily energy budget. This means that walking for an hour has higher energetic cost than sprinting for a minute, and that hummingbird courtship displays tend to have low energetic cost. Are courtship displays in general energetically costly? From the studies listed in Table 1, it appears that there is little evidence for energetic costs of many types of displays! Ectotherms that broadcast for extended periods appear to be the biggest exception, such as the signals of electric fish (Stoddard & Salazar 2011) or amphibians that sing for much of the night (Ryan 1988; Prestwich 1994). Even in these courtship systems, energy use may best be viewed as an effect of their mating system; it is not clear that females actually measure energy per se. Another open area worth further scrutiny is how energy costs translate into fitness costs. On this point, Vehrencamp et al.'s (1989) study on sage grouse is especially intriguing; males with the highest display rates had the highest daily energy costs, but also experienced the lowest rate of mass loss over the course of the study. This suggests they were able to compensate for increased expenditure with increased foraging (Vehrencamp et al. 1989). If males vary in their ability for energy compensation (e.g. by varying in their foraging or metabolic efficiency), it could lead to a cost differential.

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Appendix

Estimates of the metabolic energy and the mechanical power of the display dive of Anna's hummingbird, *Calypte anna*.

The Display Dive

Male Anna's hummingbirds perform bouts of courtship dives for females. Prior to a dive, the male flies straight up, rising roughly 30–35 m in the air, over the course of about 7 s (Stiles 1982; C. J. Clark, unpublished data). Next, he dives vertically, pulling up and passing over the female, reaching velocities of 100 km/h near the bottom of the dive. After the dive, he briefly pauses for 2–3 s to sing while hovering about 5 m above the female, before starting another dive or transitioning to another behaviour (Hamilton 1965; Wells et al. 1978; Stiles 1982; Russell 1996; Clark 2009). Males dive repeatedly to females, with consecutive dives occurring every 12–13 s (Stiles 1982; Russell 1996; C. J. Clark, unpublished data). The number of dives in a bout varies, with bouts of 1–40 dives common. Respirometry estimates of the metabolic power input, or in vivo measurements of muscle mechanical power output during the display are unavailable. But from the basic display kinematics just described plus those presented in Clark (2009), it is possible to make crude estimates of the energy and power input and output involved in the display.

Energy expended per dive

Hovering flight requires relatively high metabolic power input (Ellington 1984; Bartholomew & Lighton 1986; Clark & Dudley 2009), simply to produce the aerodynamic forces to remain aloft. Ascending vertically requires additional energy that is transferred to gravitational potential energy. So, one crude approximation of the gross chemical energy to dive (E_{dive}) is

$$E_{dive} = E_{hover} + E_{ascend} \tag{1}$$

E_{hover} is known: in male Anna's hummingbird, hovering flight costs about 45 ml of O_2 per g per h (Bartholomew & Lighton 1986; Clark & Dudley 2009). Males have an average mass (m) of about 0.0045 kg (Clark 2009), and a dive lasts about 12 s, so hovering for 12 s would require 0.67 ml of O_2. As there are approximately 5000 calories per litre of O_2 (Biewener 2003), remaining aloft for this duration (E_{hover}) has a baseline cost of about 14 J.

$E_{ascend} = E_{mech}/k$, where E_{mech} is the mechanical work done against gravity (g) to ascend, and k is the parameter used to convert metabolic power input into mechanical power output. k includes muscular efficiency and any interactions between E_{hover} and E_{ascend}. $E_{mech} = mgh$, where mg is 0.044 N ($g = 9.8$ m/s^2) and h is about 35 m, therefore E_{mech} is 1.5 J. k is unknown, but reasonable values for it can be bracketed with high and low estimates. For a low estimate, I assume that E_{ascend} is paid entirely independently of E_{hover} (i.e. no energy is stored or recovered during the dive, and muscular efficiency is unchanged when the bird ascends). Given that hummingbird flight muscles operate at about 10% efficiency during hovering (Wells 1993a; Evangelista et al. 2010), the assumption that $k = 0.1$ yields the estimate $E_{ascend} = 15$ J of metabolic energy. A high estimate is that all inefficiencies of flight are paid to hover, so that the energy to ascend is paid without any kind of penalty (i.e. $k = 1$); under this assumption, the ascent requires 1.5 additional joules of metabolic energy. The estimate of $k = 0.1$ probably overestimates the true cost; male hummingbirds glide for part of the descent, suggesting that gravitational potential energy may be recovered, and it is highly likely that the cost of ascending is not paid independently of hovering (e.g. muscular efficiency may improve during ascending flight), as adding mass does not result in a linear increase in the cost of flight (Wells 1993b). The low estimate is certain to be an underestimate, as it is highly unlikely that the muscular efficiency of ascending flight is dramatically better than that of hovering flight. Equation (1) with the range $0.1 < k < 1$ brackets the likely true gross energy cost of diving (E_{dive}) somewhere between 15.5 J and 29 J of metabolic energy.

Finally, the above calculations are the gross energy cost of a dive. The bird dives instead of performing another cheaper behaviour such as perching. Perching costs roughly 25% of the metabolic rate of hovering (Pearson 1954), so the bird would have expended roughly 3.5 J of energy to perch for the same duration. Therefore, the net cost of a dive is 12–25.5 J of metabolic energy.

Sugar yields about 4200 calories per gram (Biewener 2003), and there are 4.18 J per calorie. So to balance an expenditure of 12–25.5 J, the male would need to feed on 0.7–1.5 mg of sugar to perform one dive. This is comparable to the nectar available from a single low-yield flower; the average daily nectar produced by 153 hummingbird-pollinated plants was 5.9 ± 8.5 mg of sugar per flower (Ornelas et al. 2007). Given their average daily energy budget of about 32 kJ (Powers & Nagy 1988), one dive represents an 0.04–0.08% increase in daily metabolic rate.

Power expenditure during the dive

An animal's power can be considered at two levels: the metabolic power consumed by the muscles in the form of ATP (chemical power input) and the mechanical (nonheat) power produced by the

muscles (mechanical power output). Hummingbird muscle efficiency is roughly 10% for hovering (Wells 1993a; Evangelista et al. 2010), but is unknown for flight modes such as ascending. Moreover, estimates of whole-animal metabolic power input are error-prone, and comparison with other animals uncertain. These limitations are circumvented by considering just the mechanical power output of the flight muscles (rather than attempting to estimate the whole-animal metabolic power input).

The muscular power needed to dive potentially reaches maxima at two stages of the dive: the ascent, at which time the bird is ascending straight up, against gravity, and during the pull-up of the dive, at which point the bird has its wings spread to produce substantial aerodynamic forces. During the pull-up, centripetal force reaches about 9.5 times gravity and therefore requires large forces from the pectoralis muscles to hold out the wings (Clark 2009). However, during this behaviour the pectoralis muscles do not change in length (isometric contractions), and there are no published estimates for the metabolic power required for isometric contraction of these muscles in hummingbirds, so it is not possible to develop reasonable estimates of the power required for this specific part of the dive.

During the ascent it is possible to calculate muscle power, because the bird must produce a known amount of work against gravity to ascend. For simplicity I assume the bird ascends at a constant rate. According to Newtonian mechanics, the power to ascend (P_{ascend}) = mgh/t, where mgh is 1.5 J (see above), and t is approximately 7 s (Stiles 1982; C. J. Clark, unpublished data), thus $P_{ascend} = 0.2$ W (whole animal). The flight muscles (pectoralis and supracoracoideus) of male Anna's hummingbird weigh about 1.2 g (Clark 2009); thus, 166 W per kg of muscle is expended by the bird to produce the power to ascend (P_{ascend}). This would be the power to ascend if the wings were perfectly aerodynamically efficient (i.e. profile and induced drag on the wings are zero, and elastic energy storage is perfect). The wings are not perfectly efficient (Ellington 1984), so the true power must be higher. Following the logic used for the energy analysis (above), a crude estimate of the total power is $P_{total} = P_{hover} + P_{ascend}$. Using the aerodynamic analysis of Ellington (1984), hummingbirds' power to hover (P_{hover}) is estimated to be roughly 100 W per kg of muscle (Wells 1993a; Chai et al. 1997; Chai & Millard 1997). As a result, a rough estimate that total mechanical power produced by the muscle is on the order of 270 W per kg of muscle during ascent. As in the energy analysis (above) it is possible there are interaction effects between P_{hover} and P_{ascend} that would reduce the total power: the wings could become more efficient when flapped at a higher wing-beat frequency or stroke amplitude, for example. But it is difficult to see how this efficiency improvement could be large, as profile and induced drag seem unlikely to change dramatically when an animal produces greater time-averaged aerodynamic forces with its wings. Therefore, the estimate of 270 W per kg of muscle is a reasonable estimate of muscle power required to perform the behaviour of ascending for a dive. This is comparable to the maximum power output of roughly 230–310 W/kg that hummingbird flight muscles were estimated to attain in experiments designed to elicit maximum hovering flight performance (Chai et al. 1997; Chai & Millard 1997; Altshuler et al. 2010a).