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COMMENTARY

Income and capital breeding in males: energetic and physiological limitations on male mating strategies

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ABSTRACT

Income and capital breeding describe two dichotomous breeding strategies that characterise the allocation of resources to reproduction. Capital breeders utilise stored endogenous resources (typically lipids) to finance reproduction, whereas income breeders use exogenous resources (typically carbohydrates). The basis for such characterisation has mainly come from studying females, yet for many species, male and female reproductive success may be determined by substantially different factors. Females allocate resources to offspring production, whereas males typically allocate resources to accessing mating opportunities, e.g. from contests or displays. The primary metabolic fuel (lipids or carbohydrates) in males appears to be dependent on the type of activity being performed (i.e. high versus low intensity or long versus short duration), rather than capital or income breeding strategy per se. Males performing sustained, long-duration effort typically utilise lipids, whereas those undergoing intense activity more often utilise carbohydrates. As a result, either fuel type can be used in either strategy. Breeding season duration can constrain strategy choice; lipids and carbohydrates can be used in short breeding season species, but only lipids provide a viable fuel source for long breeding season capital breeders. Both capital- and income-breeding males must manage their resource use during the breeding season, but capital breeders must also cope with physiological stressors associated with extended fasting. Overall, the capital–income breeding concept applies equally to male reproduction, but compared with females, there are different physical and physiological constraints that shape choice of strategy. This Commentary also highlights some key future areas that need to be investigated to further understand how capital–income breeding strategies shape male mating strategies.

KEY WORDS: Fasting, Sexual selection, Mating system, Male–male competition, Intrasexual selection, Lekking, Polygyny, Oxidative stress

Introduction

Trade-offs in resource allocation by individuals to growth, maintenance and reproduction are a central theme in the study of life history evolution (Stearns, 1992). In particular, the financing of reproduction can occur from two seemingly dichotomous strategies, known as capital and income breeding (see Glossary; Jönsson, 1997). Capital breeders build and/or store reserves that allow them to reproduce at a later time, independent of food availability during breeding, whereas income breeders allocate recently acquired resources directly to reproduction (Stephens et al., 2009). In reality, the strict dichotomy suggested by this terminology masks a

more flexible continuum; individuals can adopt a mixed strategy, either by concurrently using energy reserves and resource income to a greater or lesser extent (Varpe et al., 2009) or by using food intake to supplement existing reserves stored prior to the onset of reproduction (Houston et al., 2007). This flexibility also has a temporal component, as animals may switch between resource types within a breeding season (Wheatley et al., 2008) or switch between tactics depending on factors such as size or age (Mysterud et al., 2008).

Broadly, there are a number of external factors that may favour the use of either capital or income breeding (Stephens et al., 2009, 2014). In particular, the abundance and reliability of food supply is most important; in systems where food is scarce, hard to acquire or spatially separated from breeding sites (Drent and Daan, 1980; Jönsson, 1997), capital breeding is favoured. This would suggest that capital breeding is more common in seasonal environments and where food resources are less predictable (Stephens et al., 2014; Williams et al., 2017).

The original description and concept of capital and income breeding was based on female reproduction (Drent and Daan, 1980) and since then has been predominantly studied from the perspective of female reproductive strategies (Houston et al., 2007; Williams et al., 2017). This is on account of females' high resource investment into offspring production, either directly, via egg production and nutrient transfer, or indirectly, via extended periods of post-natal maternal care (Gittleman and Thompson, 1988). Males instead typically invest in acquiring mating opportunities, and a growing number of studies have shown that energetic costs of male reproduction are typically very high and in mammals can often exceed those of lactating females (Lane et al., 2010). Strategies to manage resource acquisition and energy allocation to reproduction are therefore just as important in males. This Commentary summarises the evidence for capital versus income breeding in males, and compares the key determinants shaping these strategies in males. I discuss key physiological, ecological and physical constraints, before summarising key testable predictions about how physiology and mating behaviour should change relative to differences in capital–income strategy.

Capital and income breeding in males

Both intersexual and intrasexual selection (see Glossary) have led to the evolution of a variety of ways in which males can attain mates (Andersson, 1994). This can be through contests (i.e. fights of agonistic interactions) or acrobatic displays, as well as through the expression of phenotypic traits. Sexual selection is a major evolutionary force driving male phenotype, so it is unsurprising that it may influence the allocation of resources to reproduction. For example, the rate at which males display or the amount of time spent at mating sites can both positively correlate with male mating success (e.g. in anurans: Friedl and Klump, 2005; in birds: Kervinen et al., 2016; in mammals: Apollonio et al., 1989). Male fitness in

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Glossary

Anaplerosis
A series of enzymatic reactions or pathways that replenish the pools of metabolic intermediates in the TCA cycle.

Capital breeding
Reproduction is financed from stored capital resources.

Directional selection
A mode of natural selection where one extreme of a trait is favoured, leading to shifts in the frequency of this trait in one direction.

Disruptive selection
A mode of natural selection where extreme values of traits are favoured over intermediate values.

Income breeding
Reproduction is financed from the current intake of resources.

Intersexual selection
Selection by the opposite sex to reproduce.

Intrasexual selection
Within-sex competition to reproduce.

Lekking
A polygynous mating system where males (or females) form aggregations and the opposite sex attends these aggregations for mating.

Monogamous
A mating system characterised by one mating partnership at a time.

Polyandrous
A mating system where a female mates with more than one male.

Polygynous
A mating system where a male mates with more than one female.

Sexual selection
Intraspecific competition to reproduce.

many of these scenarios is linked to the energetic investment in key activities and/or the ability to sustain these activities over an extended period, and sexual selection can thus select on traits that increase the ability to obtain energy and/or spend it efficiently (Murphy, 1998). These energy investment and expenditure patterns should give rise to differences in the financing of reproductive activities that may fit within the existing income–capital breeding scheme. Indeed, the income–capital breeding strategy in males exists on a continuum (Fig. 1), in the same way it does for females; at the truly capital breeder end of the spectrum, some species rely solely on endogenous reserves and individuals cannot or do not forage. For example, male lesser wax moths (*Achroia grisella*) have atrophied mouthparts and cannot feed or drink, and male elephant seals (*Mirounga angustirostris*) do not forage during the breeding season, for a period much longer than in females. At the opposite end of the continuum are income breeders that may spend considerable time away from breeding sites; species such as the European tree frog (*Hyla arborea*) spend an average of 12 days at breeding ponds out of a 100 day breeding season and the rest of the

time foraging (Meuche and Grafe, 2009). In between these two extremes are species that vary considerably in the amount of time they spend foraging. During the rut, male capital-breeding bighorn sheep (*Ovis canadensis*) and Alpine ibex (*Capra ibex*) can spend respectively ~20% (Pelletier, 2004) and 30–39% (Brivio et al., 2010) of their time foraging, and are closer to the capital-breeding end of the continuum, whereas income-breeding black grouse (*Lyrurus tetrix*) spend 7–9 h away from leks (~50% of time; see Glossary) during the middle of the day.

In males, the capital–income breeding continuum is likely to be used much more flexibly than in females. For females, costs of reproduction in terms of egg production, gestation or lactation are more fixed. Even so, females may switch strategies within a breeding season (e.g. first versus second clutches; Wessels et al., 2010) or use either strategy based on condition (Jaatinen et al., 2016). Males can adjust their reproductive investment even more dynamically, not only across but within a breeding season, in response to any number of short- or long-term factors [e.g. number of competitors (Shine et al., 2003; Nieminen et al., 2016) or age and condition (Mysterud et al., 2008)]. Such flexibility and a greater diversity of potential mating strategies is probably one reason why the study of capital–income breeding in males has been generally neglected, despite such a concept being equally applicable to males and females.

Energetic substrate choice and male mating strategy

Amongst females, a key physiological difference between capital and income breeders stems from the usage of different resources. Capital breeders rely on access to energy in the form of somatic resources, such as stored lipids and sometimes also protein (Warner et al., 2008; Stephens et al., 2009; Plot et al., 2013; Taillon et al., 2013; Jaatinen et al., 2016). In contrast, income breeders typically use income resources such as carbohydrates for energy (Casas et al., 2005). These different sources can be used simultaneously; for example, females can be capital breeders for lipids and/or protein and at the same time income breeders for carbohydrates (Casas et al., 2005).

The two main energy sources (carbohydrates and lipids) differ in their properties. Maximal rates of ATP production from glycogen (a stored form of glucose) are higher than those from lipids, and therefore glycogen provides greater power output especially for anaerobic activities. In contrast, lipids carry more energy per gram than other fuels and specifically ~10 times more energy than carbohydrate per gram wet mass, but support lower rates of aerobic activity (Weber, 2011). For males, this means that the type of activity (aerobic or anaerobic activity), the intensity and the overall duration of physical activity play a crucial role in the selection of an appropriate energetic substrate (Clark, 2012).

This can be seen most clearly amongst males showing the same breeding system. For example, amongst lek-breeding species, wood
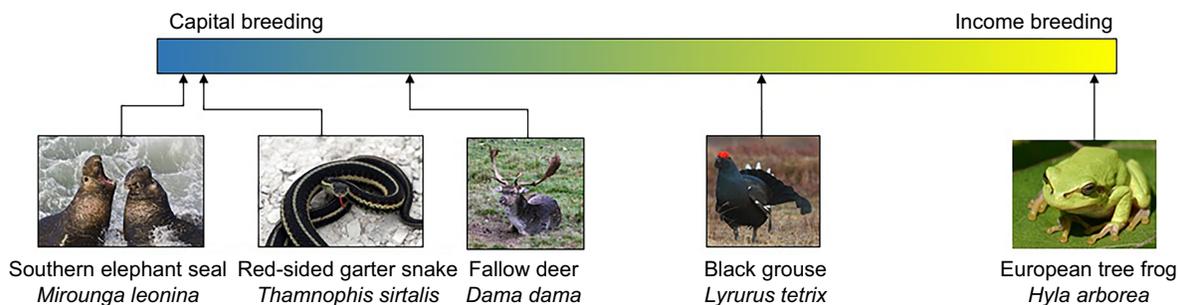

| Capital breeding | | | | Income breeding |

Southern elephant seal
Mirounga leonina

Red-sided garter snake
Thamnophis sirtalis

Fallow deer
Dama dama

Black grouse
Lyrurus tetrix

European tree frog
Hyla arborea

Fig. 1. Example of male breeding strategies and where they sit on the capital–income breeding continuum.

frogs (*Lithobates sylvaticus*) use stored glycogen as a resource in a capital-breeding strategy, whereas spring peepers (*Pseudacris crucfer*) use stored lipids also as capital breeders (Well, 2001). In contrast, European frogs (*Hyla arborea*) use glycogen as an energy source (Grafe and Thein, 2001) and gray tree frogs (*Hyla versicolor*) predominantly use lipids, both in an income-breeding strategy (Wells, 2001). Similarly, in income-breeding male sage grouse (*Centrocercus urophasianus*), most energy comes from exogenous sources, but lipids are used to support lekking and mating during the breeding season (Hupp and Braun, 1989; Vehrencamp et al., 1989), whereas capital-breeding bot flies (*Cuterebra austeni*) mainly use lipid resources (Kemp and Alcock, 2003). Thus, even amongst the same breeding system, different species use different metabolic fuels; fuel use is independent of capital–income breeding strategy. Males showing sustained, long-duration effort typically utilise lipids, whereas those undergoing intense activity more often utilise carbohydrates (Carvalho et al., 2008; Desprat et al., 2017). It is important to remember that male activities are typically a mixture of activity types – intense activities may be carried out infrequently and contribute little to total energetic demand (Clark, 2012), whereas low-intensity activities are likely to be carried out more frequently and for longer duration (McElligott et al., 1998). Species may show a mixture of activity types *sensu* multimodal signalling (Bro-Jørgensen, 2010; Patricelli et al., 2016), which may come with differing energetic requirements (Hack, 1997; Cady et al., 2011).

There may be one final constraint acting on male resource choice: breeding season duration. Lipids can be stored in a dehydrated reduced state (Weber, 2011), meaning that to contain comparable amounts of energy in the form of lipids and carbohydrates would require massively different volumes of resources. As a consequence, for capital breeders, lipids (and possibly proteins) are the only possible energy sources for species with extended breeding seasons (e.g. Irvine et al., 2017). However, where breeding seasons are short, capital breeders can have no appreciable fat stores (e.g. red-sided garter snakes: Shine and Mason, 2005; wood frogs: Wells and Bevier, 1997). By contrast, income breeders can use lipids or carbohydrates to support activity, irrespective of the breeding season length.

Physiological limitations on income and capital breeders
For many capital and income breeders, reproductive success is generally tied to the ability to occupy a territory or monopolise females. Such behaviour, particularly in capital breeders, can often require extended fasting or certainly reduced time spent foraging. Both capital and, to a lesser extent, income breeders must manage the speed

at which they utilise energy stores. Unsurprisingly, capital-breeding males generally lose more total body mass across the breeding season (Table 1) than income breeders, with a negative relationship between per day mass loss and length of breeding season (Fig. 2). Income breeders also lose mass across the breeding season (Table 1), with some individual males losing considerable mass (Wells, 1978). However, mass loss in general seems to be at a slower rate than in capital breeders (Fig. 2). This pattern of mass loss is consistent across a range of taxa (e.g. territorial insects: Kemp and Alcock, 2003).

Income breeders may lose less mass across a breeding season, but have to cope with significant short-term, even within-day resource depletion. For example, *H. arborea* males use ~63% of carbohydrate reserves after 3 h of calling activity (Grafe and Thein, 2001). In the lekking great snipe (*Gallinago media*), males lose around 7% of body mass in a single night, but replenish this daily; total mass loss across the whole breeding season is only 6% (Höglund et al., 1992). Such high within-day mass loss means that being an efficient forager and being able to replenish energy reserves are likely to be important features under selection in males. Indeed, there can be a link between energy expenditure and foraging efficiency in income breeders (e.g. Vehrencamp et al., 1989), where high-quality males are better at accessing and assimilating resources to replenish energy reserves. Alternatively, income-breeding males may feed continuously throughout the day, albeit at low levels (e.g. Calder et al., 1990).

Across male mating strategies, but especially in polygynous and lekking mating systems, males engage in vigorous physical activity that increases their metabolic rate substantially (Lane et al., 2010). Thus, large volumes of long-duration or intense physical activity will probably lead to increased production of reactive nitrogen and oxygen species (Soulsbury and Halsey, 2018). Extended fasting is also associated with increased oxidative stress and, in particular, with the depletion of dietary-based antioxidant defences (Pascual et al., 2003; Schull et al., 2016). As yet, there are not enough comparative data available to allow us to understand how the capital–income breeding continuum may impact oxidative stress and DNA damage, or specifically the sources of these stressors, but both are increased in capital breeders (oxidative stress in male and female elephant seals: Sharick et al., 2015; oxidative stress in male king penguins, *Apteodytes patagonicus*: Schull et al., 2016; telomere length in male red-sided garter snakes: Rollings et al., 2017). For capital breeders, the resources available for somatic maintenance or for reproduction are more fixed at the start of the breeding season. As has been shown in females, substances such as dietary-derived

Table 1. Variation in total mass loss across the season and daily mass loss of capital- and income-breeding males

Species	Type of breeding	Mating system	Total mass loss (%)	Mass loss per day (%)	Mating season duration (days)	Reference
Red-sided garter snake *Thamnophis sirtalis parietalis*	Capital	Polygyny	11	2.3	13	Shine and Mason, 2005
Big horn sheep *Ovis canadensis*	Capital	Polygyny	11.4	0.25–1.1	15–16	Pelletier, 2004
Fallow deer *Dama dama*	Capital	Lek	25.5±0.5	1.2	~21	McElligott et al., 1998
Northern elephant seal *Mirounga angustirostris*	Capital	Polygyny	35.6	0.4	~100	Deutsch et al., 1990
Common frog *Rana temporaria*	Capital	Polygyny	27	0.47–0.61	46–56	Ryser, 1989
Lesser wax moth *Achroia grisella*	Capital	Lek	64.4	4.6	14	N. Gillingham, P. Eady and C.S., unpublished data
Grey headed flying fox *Pteropus poliocephalus*	Capital	Polygyny	21	0.23	70	Welbergen, 2011
Great snipe *Gallinago media*	Income	Lek	6	0.54	11	Höglund et al., 1992
Black grouse *Lyrurus tetrix*	Income	Lek	3.8	0.24	14	Lebigre et al., 2013
Sage grouse *Centrocercus urophasianus*	Income	Lek	4.6	0.11	42	Beck and Braun, 1978
Common tree frog *Hyla arborea*	Income	Lek	2.12	0.12–0.53	58	Meuche and Grafe, 2009; Friedl and Klump, 2005
Green frog *Rana clamitans*	Income	Polygyny	11.25	0.28	40	Wells, 1978
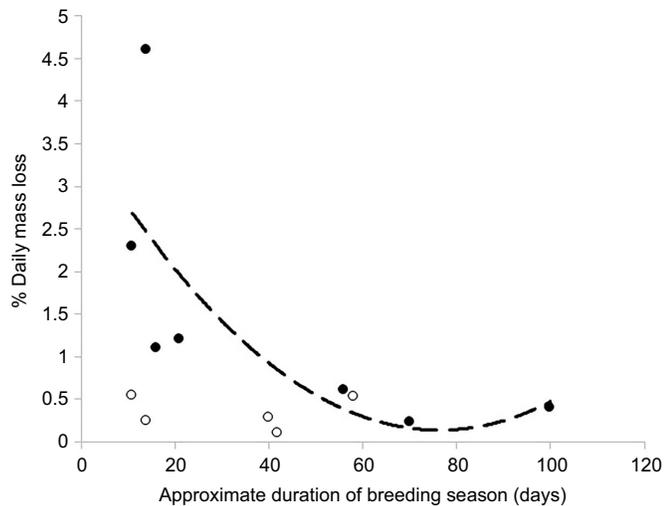
Fig. 2. Daily mass loss for capital (filled circles) and income breeders (open circles) in relation to the duration of the breeding season. A non-linear best fit line for capital-breeding data is shown. Source data are taken from Table 1.

antioxidants may decline through usage during the breeding season (Stier et al., 2017). As a consequence, capital breeders may suffer higher oxidative stress or DNA damage than income breeders, unless they can counter this potential physiological cost. Possible mechanisms for limiting oxidative stress during the breeding season could include having higher pre-breeding season levels of circulating antioxidants (Vázquez-Medina et al., 2012) or storing antioxidants (e.g. carotenoids stored in adipose tissue; Negro et al., 2001). Alternatively, during the breeding season, there may be an increased reliance on antioxidant enzyme responses (Sharick et al., 2015) to counteract reactive species production.

Antioxidants are not the only component that may become depleted during the breeding season in capital breeders. Fasting capital breeders must also rely on lipid mobilization and catabolism, resulting in large amounts of acetyl-CoA production (Quijano et al., 2016). This acetyl-CoA enters the TCA cycle (also known as the Krebs cycle), leading to the aerobic production of CO_2, H_2O and ATP. However, TCA cycle intermediates are needed (especially citric acid), otherwise acetyl-CoA molecules are converted into ketones, which, at high levels, may lead to metabolic ketoacidosis. Hence, capital breeders must have physiological mechanisms to replenish depleted TCA cycle intermediates or to prevent their depletion [e.g. via anaplerotic pathways (see Glossary; Owen et al., 2002) or by consuming small amounts of food]. Income breeders, by contrast, can continuously replenish TCA intermediates.

A range of other aspects of an animal's physiology are potentially at risk during the extended fasting that may occur during capital breeding. For example, extended fasting in capital-breeding male king penguins is associated with decreased immunoglobulin and higher corticosterone concentrations (Bourgeon et al., 2007). Hormonal changes are expected when there are extended periods of fasting (Secor and Carey, 2016); these may include those specifically related to metabolism regulation, e.g. thyroxine (Cherel et al., 1988), or osmoregulation, e.g. angiotensin II (Ortiz et al., 2006). Capital breeders may also need to cope with increased amounts of circulating urea/uric acid waste as a result of some level of dehydration (Cherel et al., 1988).

Finally, capital breeders are required to build up sufficient stores of capital prior to the breeding season. Thus, energy-regulating

hormones such as baseline glucocorticoids, ghrelin, insulin and thyroxine can directly activate lipogenesis at the liver or directly bind to adipocytes, increasing fat reserves in subcutaneous and visceral adipose tissue. These hormones have been found to increase in pre-breeding capital-breeding females (Hennin et al., 2016) and males (Girard-Buttoz et al., 2009), and to facilitate energy regulation. In addition, modification of resting metabolic rate (RMR) may be an important factor determining the efficiency of building this capital; a lower RMR would facilitate capital deposition. Capital breeders may be expected to have lower RMR overall or a seasonal strategy of lowered RMR (e.g. female grey seals, *Halichoerus grypus*: Sparling et al., 2006). Currently there are no studies comparing RMR between capital- or income-breeding strategies, though there is potential to do this using existing datasets (e.g. Genoud et al., 2018). Energy storage also requires the maintenance of supportive tissues as well as that of the storage compounds themselves (Sheridan, 1994). Consequently, metabolic rate often increases with body mass, and there is evidence of a metabolic cost associated with capital energy storage (Griffen, 2017).

In summary, capital breeding as a strategy will induce strong selective pressure on an organism's physiology because it requires an organism to balance somatic maintenance with investment in reproduction during periods of little or no food intake. Evidence from both males and females shows strong effects on individual physiology at this time, but as yet more work is needed to examine both the physiological costs of capital breeding and potential strategies to reduce or mitigate these costs.

Ecological and physical correlates of income and capital breeding males

There are a number of important ecological correlates that can determine capital- or income-breeding strategies in females. These generally relate to resource distribution: capital breeding is favoured where resources are hard to acquire, less predictable or spatially separated from breeding sites (Drent and Daan, 1980; Jönsson, 1997; Stephens et al., 2014; Williams et al., 2017). Resource distribution will also play a similar role for males. For example, there is spatial separation between breeding and feeding sites in capital-breeding humpback whales (*Megaptera novaeangliae*), but not in sperm whales (*Physeter microcephalus*; Irvine et al., 2017). Similarly, spring peepers start to breed early in the year, before insect prey is available; spring peepers therefore need to build capital stores of energy before they overwinter (Wells and Bevier, 1997). Hence, capital and income breeding as a life history in males will be tied to some extent to the ecological conditions in the same way as it is in females.

Energy storage can impact locomotion and impede certain types of movement, such as flying (Witter and Cuthill, 1993), as has been found in female capital breeders (Kullberg et al., 2005). Specifically, being fat can reduce take-off velocity and angle of ascent, which may impair predator evasion (Kullberg et al., 1996). In other scenarios, lipid stores may provide insulative protection in cold climates and act as buoyancy aids (Adachi et al., 2014). Hence, trade-offs between resource storage and effective movement may also directly impact the use of capital–income strategies.

Sexual selection may also place physical restrictions on capital or income breeding. For example, selection for agility or manoeuvrability has selected against larger males in some species, leading to reduced or even reversed sexual size dimorphism (Székely et al., 2004, 2007). Consequently, sexual selection for smaller, more agile size limits a male's capacity to act as a capital breeder. Being agile or manoeuvrable specifically requires males to not carry excess

fat, so therefore an income-based strategy will be favoured. In broad-tailed hummingbirds (*Selasphorus platycercus*), for example, males keep their body mass lower during the daytime as this may impact flight agility, only feeding minimally until evening, when displays have finished (Calder et al., 1990). Conversely, mating systems that include contest behaviour typically select for larger male size (Soulsbury et al., 2014), and this could increase the likelihood of a capital-breeding strategy. Thus, the relative importance of different types of behaviours and the number and type of sexually selected traits are likely to be important drivers of capital- or income-breeding strategy in males.

Strong sexual selection can also lead to the evolution of alternative reproductive tactics, that manifest as bimodal or multimodal distributions of behavioural, physiological and sometimes morphological traits within same-sex conspecifics (Taborsky et al., 2008; Taborsky and Brockmann, 2010). There is increasing evidence that these strategies may be underpinned by variation along a capital–income breeding continuum. For example, in a cichlid (*Lamprologus callipterus*) with two distinct male phenotypes, the larger, nest-building males can be classed as capital breeders, whereas dwarf sneaker males follow an income-breeding strategy (Schütz et al., 2010; von Kuerthy et al., 2015). Alternative reproductive tactics may also lead to age-specific differences; males can follow an income-breeding strategy in younger age groups and a capital-breeding strategy when older (Mysterud et al., 2008). Overall, capital and income breeding can require very different phenotypes. Selection pressures on male phenotype via sexual selection (directional or disruptive; see Glossary) and natural selection may therefore act to constrain one particular breeding strategy.

Capital and income breeding in males: future directions

This Commentary has summarised the capital–income breeding strategy as a key concept that, although traditionally applied to females, can equally apply to males. However, it is clear that considerable gaps remain in our understanding of male mating strategies. We know that metabolic substrate usage by males should be primarily adapted to the type, duration and frequency of physical activity in the breeding season, i.e. high-intensity versus long-duration activities, rather than the capital–income breeding strategy itself (Table 2). In females, techniques such using isotopic tracers have allowed researchers to track the use of endogenous and exogenous resources and their allocation to reproduction (Casas et al., 2005; Warner et al., 2008). Similar studies in males would be ideal to begin to piece together a more detailed understanding of how resources are allocated and where males fit on the capital–income breeding continuum.

Many studies use measures of 'condition' to compare differences between males and relate these to measures of fitness, such as mating success. More specifically, measures of 'condition' are based on a relationship between mass and some measure of physical size, e.g. length, where greater body mass for a given body size is linked to some component of condition, e.g. size of energy reserves (Peig and Green, 2010). Energy storage is central to the dichotomy in capital and income breeding, and measures that rely on overall size and mass can be predicted to be more important in capital breeders. In capital breeders, there are many examples of strong relationships between male 'condition' and mating success, but the link between body 'condition' and mating success may be weaker or absent in income breeders. Studies can show positive relationships between 'condition' and reproductive success (goshawk: Pérez-Camacho et al., 2015), but not in all years studied (white-bearded manakin, *Manacus manacus*: Shorey, 2002) or not at all (buff-breasted sandpiper, *Tryngites subruficollis*: Lanctot et al., 1998). Similarly, Friedl and Klump (2005) used a different metric of condition in green tree frogs, because mass–length residuals only reflect short-term physiological state. Thus, quantifying 'condition' is probably harder in income breeders, and any such relationship between condition and reproduction will be weaker or even absent (Table 2). Studies of male income breeders need to carefully assess the applicability of the metric chosen.

In comparison to females, there is a poorer characterisation of the physiological adaptations to capital–income breeding males. In particular, it is not clear how males build and store capital (Table 2), and then manage these resources and important nutrients (e.g. antioxidants, TCA intermediates) over time. So far, our insights stem from studies with extreme fasting and low sexual selection (e.g. Schull et al., 2016), whereas studies comparing short and long periods of fasting across different mating systems are needed.

This Commentary has mainly used evidence from species that are polygynous (including lekking); information on a diversity of mating systems is currently missing from the literature. The differences in the strength of sexual selection between mating systems may lead to different selective pressures on male physiology and phenotype. For example, males and females in monogamous species (see Glossary) are more likely to have similar capital–income breeding strategies, because some parental roles and fitness are more similar than in other mating systems. In contrast, males and females of polygynous or polyandrous mating systems (see Glossary) may have differing capital–income breeding strategies; for example, roe deer (*Capreolus capreolus*) are seen as a 'classic' income-breeding species, though females follow an income-breeding strategy and males a capital-breeding strategy (Hewison et al., 2011). As a consequence, selection on shared fitness traits in each sex may lead to displacement from the phenotypic or physiological optima in the opposing sex (i.e. intralocus sexual conflict). This may drive or constrain

Table 2. Predictions for male capital- and income-breeding strategies

Theme	Prediction
Metabolism	Carbohydrates will be utilised as a fuel source where males carry out intense physical activity in both capital and income breeders.
	Lipids will be utilised as a fuel source where males carry out sustained, low-intensity activity in both income and capital breeders.
	Capital breeding males will have lower overall or lower pre-breeding RMR to facilitate building capital storage.
Physiological adaptations	Male capital breeders will have higher pre-breeding antioxidants either in circulation or in storage.
	Capital breeders will have higher levels of pre-breeding energy-regulating hormones that will facilitate lipid deposition.
Physical adaptations	Species with agile displays and reduced sexual size dimorphism are more likely to be income breeders.
	Positive associations between amount of stored resources and male 'quality' or 'condition' will be significantly stronger in capital breeders than income breeders.
Sexual conflict	In species where capital and income breeding is different between males and females, differing fitness optima between sexes may lead to sexual conflict.

RMR, resting metabolic rate.

physiological and/or behavioural adaptations and their underlying genetic variation (Bonduriansky and Chenoweth, 2009). Hence, sex differences in income- and capital-breeding strategies within a species may plausibly create differential selection on physiological or physical traits, leading to sexual conflict (Table 2).

Conclusions

In conclusion, capital–income breeding is an important concept to apply to males, and considering this concept helps to frame questions about key physical and physiological traits that shape males and male reproductive investment. Compared with information available for females, this topic is relatively unexplored in males; hopefully this Commentary will help to bring into focus some potential areas of investigation to begin to extend our knowledge in this area and provide a better framework for characterising and comparing males' investment in mating strategies.

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