

REVIEW

Variations in cost of transport and their ecological consequences: a review

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ABSTRACT

Movement is essential in the ecology of most animals, and it typically consumes a large proportion of individual energy budgets. Environmental conditions modulate the energetic cost of movement (cost of transport, COT), and there are pronounced differences in COT between individuals within species and across species. Differences in morphology affect COT, but the physiological mechanisms underlying variation in COT remain unresolved. Candidates include mitochondrial efficiency and the efficiency of muscle contraction–relaxation dynamics. Animals can offset increased COT behaviourally by adjusting movement rate and habitat selection. Here, we review the theory underlying COT and the impact of environmental changes on COT. Increasing temperatures, in particular, increase COT and its variability between individuals. Thermal acclimation and exercise can affect COT, but this is not consistent across taxa. Anthropogenic pollutants can increase COT, although few chemical pollutants have been investigated. Ecologically, COT may modify the allocation of energy to different fitness-related functions, and thereby influence fitness of individuals, and the dynamics of animal groups and communities. Future research should consider the effects of multiple stressors on COT, including a broader range of pollutants, the underlying mechanisms of COT and experimental quantifications of potential COT-induced allocation trade-offs.

KEY WORDS: Locomotion, Metabolic rate, Muscle, Mitochondria, Temperature, Exercise, Allocation trade-off

Introduction

Limited resources lead to preferential allocation of resources to biological processes that maximise overall fitness. However, if two or more fitness-related processes compete for the same resource, there will be an allocation trade-off that can potentially reduce fitness (Angilletta et al., 2003). Most fitness-related processes, such as growth, reproduction and locomotion, are thermodynamically unfavourable and require energy (see Glossary) input. However, energy supply is a constraint for most organisms either because of limited environmental availability or because of physiological constraints in the processing capacity to convert food to usable cellular energy (adenosine triphosphate, ATP). Hence, fitness-related processes are likely to compete for the same limited resource, thereby causing an energy allocation trade-off.

One such trade-off may occur between locomotion and other traits (Husak, 2016; Husak et al., 2016). Almost all animals need to move in some way to maintain fitness by obtaining food (e.g. foraging, competition), interacting with conspecifics to increase opportunities

for reproduction (e.g. territoriality, courtship, copulation), or interacting with other species (e.g. escape predation) (Husak and Fox, 2008; Lailvaux and Husak, 2014; Wilson et al., 2015). Movement is expensive energetically and comprises a considerable proportion of the energy budget of individuals (Malishev and Kramer-Schadt, 2021; Di Santo et al., 2017; Thiem et al., 2016). Energy allocation to locomotion is therefore likely to trade off with other fitness-related processes such as reproduction and immunity (Husak et al., 2016; Lailvaux and Husak, 2017).

However, the energetic cost of moving a given distance at a particular speed (cost of transport; COT; see Glossary) is not constant. COT can vary with environmental conditions (Brown et al., 2011; Claireaux et al., 2006; Li et al., 2017) and between individuals (Jahn and Seebacher, 2019; Kraskura et al., 2021; Seebacher et al., 2016a), populations (Fu et al., 2013, 2015; Gamperl et al., 2002; Rodnick et al., 2004) and species (Rubio-Gracia et al., 2020a). Hence, the factors causing variation in COT can be instrumental in determining allocation trade-offs, and thereby ecological success and evolutionary trajectories. Understanding the physiological mechanisms that underlie COT, and the environmental and behavioural contexts that influence COT is instrumental in predicting the impacts of environmental change on animal energetics and hence ecology and evolution (Fenkes et al., 2016; Morales-Marín et al., 2019). The aim of this Review is to summarise existing knowledge of the causes of variation in COT to identify the drivers and contexts of energy allocation trade-offs.

COT denotes the aerobic energy expended per unit body mass for a given distance travelled (Claireaux et al., 2006; Halsey, 2016; Wickler et al., 2000). Energy (ATP) for locomotion is primarily supplied by mitochondria. However, anaerobic metabolism can contribute to extend movement when the intensity of locomotion surpasses the capacity for mitochondrial ATP production (Martin et al., 2015; Zhang et al., 2018). Prolonged movement (exercise) causes a metabolic imbalance that needs to be restored to resting levels after completion of movement; for example, phosphocreatine and glycogen stores need to be replenished, and muscle damage needs to be repaired (Lee et al., 2003; Moxnes and Sandbakk, 2012). These post-exercise adjustments require aerobically produced ATP in mitochondria (Moxnes and Sandbakk, 2012; Zhang et al., 2018). Consequently, metabolic (oxygen consumption) rates remain elevated following exercise (excess post-exercise oxygen consumption, EPOC; see Glossary) (Gaesser and Brooks, 1984). Together, COT and EPOC represent the total energetic cost of locomotion (Fig. 2) (Cordero et al., 2019; Svendsen et al., 2010).

Theory predicts that undisturbed animals should travel at speeds that minimise COT (optimal speed, U_{opt} ; see Glossary) (Claireaux et al., 2006; Weihs, 1973a). Adjusting speeds can therefore improve locomotor performance and efficiency (Weihs, 1973a). Interestingly, animals rarely travel at maximal capacity, but at intermediate realised speeds (Husak and Fox, 2006; Miln et al., 2021; Wilson and Husak, 2015) that can be influenced by

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Glossary

Cost of transport (COT)

Energy expended per unit body mass for a given distance travelled across varying speeds, often measured as the aerobic cost in terms of oxygen consumption.

Critical swimming speed (U_{crit})

The maximum swimming speed achieved in a ramping exercise protocol.

Energy

Here, refers to chemical energy in the form of adenosine triphosphate (ATP) that is produced primarily aerobically in mitochondria, and to a lesser extent anaerobically in glycolysis.

Excessive post-exercise oxygen consumption (EPOC)

Increased oxygen consumption following movement. EPOC is caused by restoring pre-exercise physiological conditions after intense exercise.

Integrated COT

Integral of COT across a range of speeds that provides a single value to compare individuals while incorporating the changes in costs across speeds.

Minimum COT (COT_{min})

The minimum point on the COT_{tot} versus speed curve.

Net COT (COT_{net})

Cost of movement only, where resting metabolic rates are subtracted from the metabolic rate during movement.

Optimum swimming speed (U_{opt})

The speed at which COT_{min} is minimised.

Total COT (COT_{tot})

The total amount of energy required to sustain movement, plus resting metabolic rates.

physical constraints of the environment, behavioural contexts and the energetic cost of movement (Rezende et al., 2006; Seebacher et al., 2016b; Wilson et al., 2015). In aquatic environments, constraints such as temperature (Kraskura et al., 2021), salinity (Nelson et al., 1996; Seebacher et al., 2016b) and oxygen saturation (Oldham et al., 2019) can operate in isolation or interact to influence realised speeds (Kraskura et al., 2021; Oldham et al., 2019; Seebacher et al., 2016b). Therefore, it is not advantageous to always travel at maximal speed, and it is not always possible to travel at speeds that minimise COT (Han et al., 2017).

Here, we review the literature to establish the current state of knowledge of COT in animals, with a particular focus on identifying drivers of potential energy allocation trade-offs and particular conditions under which these may occur (Fig. 1). We focus on animals other than humans and therefore exclude medical or sport studies, which have a different focus to our aim here. Similarly, we will not consider allometric scaling of energy use and COT because this is quite a separate field with an extensive literature that is tangential to our purpose here. We will begin by summarising the measurement of COT, and exploring the physiological mechanisms underlying differences in COT. We then summarise differences in COT between individuals and species, and the environmental drivers that influence COT. We finish with suggestions for further research.

Measurement

Experimentally, COT is determined by measuring the oxygen consumption (e.g. $\mu\text{mol O}_2 \text{ g}^{-1} \text{ min}^{-1}$) of animals across different speeds, which, when divided by speed, gives COT ($\mu\text{mol O}_2 \text{ g}^{-1} \text{ m}^{-1}$) (Lighton et al., 1993). Gross or total COT (COT_{tot} ; see Glossary) represents the total amount of energy required for movement plus resting metabolic rates (Fig. 2). Net COT (COT_{net} ; see Glossary) includes only the cost of movement, excluding resting metabolic rates (Claireaux et al., 2006). Below, we

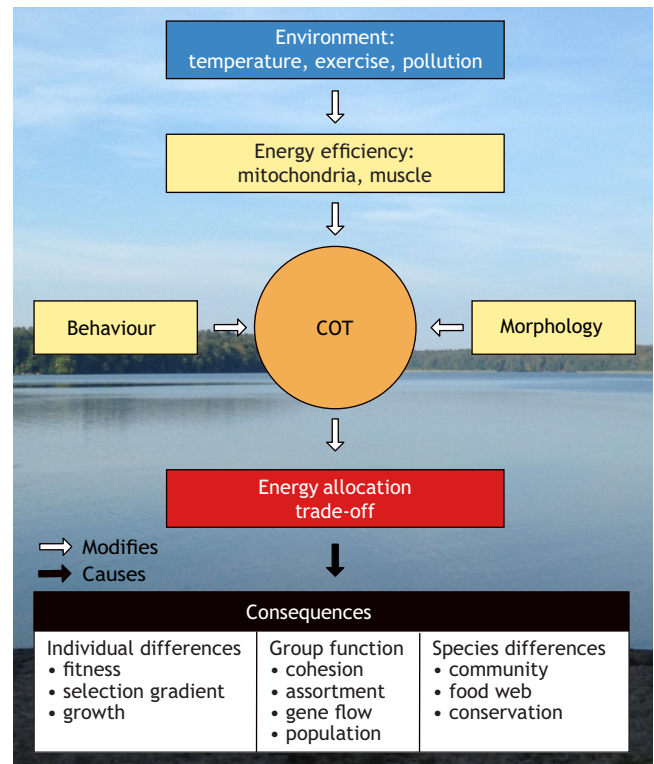


Fig. 1. Schematic outline of the Review. Environmental conditions, including temperature, exercise-promoting environments and pollution, modify cost of transport (COT) possibly by influencing the energy efficiency of mitochondrial ATP production and muscle contractile function. Behaviour and morphology can also influence COT and, together, COT and the factors that modify it alter energy allocation trade-offs between locomotion and other fitness-related functions such as reproduction and immunity. The resulting effects on individuals, groups and species can have important ecological and evolutionary consequences.

use COT to refer to COT_{tot} and explicitly state when we refer to other variants such as COT_{net} .

The function of COT when plotted against speed may take on a variety of different shapes (e.g. U-shaped, J-shaped or more L-shaped) (Fig. 3A,B). L-shaped functions of COT demonstrate that as speed increases, COT decreases across the speeds attainable by a given individual (Adams and Parsons, 1998; Jahn and Seebacher, 2019; Seebacher et al., 2016a). In U-shaped or J-shaped functions, there is initially a reduction in COT as speed increases until it reaches a minimum (COT_{min} ; see Glossary), following which there is an increase in oxygen consumption as speed increases (Behrens et al., 2006; Claireaux et al., 2006). U-shaped functions for COT have been predicted by models derived from hydrodynamic theory in fish (Wakeman and Wohlschlag, 1981). The non-linearity of the COT versus speed curve stems from the decreasing importance of maintenance (resting) and postural costs of the non-moving animal relative to the increasing cost of locomotion (Claireaux et al., 2006; Dlugosz et al., 2009; Halsey, 2016). The difference in curve shape may simply reflect the range of speeds attainable by different species so that L-shaped curves reflect a more limited range.

COT_{min} is the minimum amount of energy an animal has to invest to move itself a given distance (Halsey, 2016; White et al., 2016) and occurs at the 'optimal' speed (U_{opt} ; Fig. 3A) (Claireaux et al., 2006; Williams, 1999). Some animals have a preferred speed that coincides with U_{opt} (Tudorache et al., 2011). However, U_{opt} , COT and COT_{min} can vary with the environment, such as with changes in

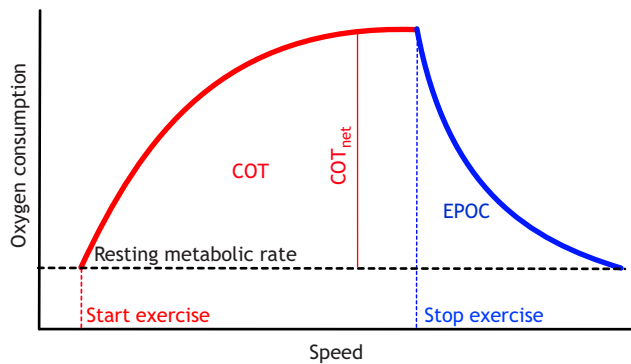


Fig. 2. Schematic representation of oxygen consumption during and following exercise. Increases in metabolic rate following the start of exercise (indicated by vertical red dashed line) are added to resting metabolic rate (horizontal black dashed line) while animals are inactive. Resting plus exercise-induced oxygen consumption together comprise total COT, while exercise-induced metabolic rate alone represents net COT (COT_{net} , red vertical line). Oxygen consumption remains elevated after cessation of exercise (excess post-exercise oxygen consumption, EPOC, vertical blue dashed line) as a result of energy used to restore pre-exercise cellular equilibrium.

terrain (Lees et al., 2013; Warncke et al., 1988; Wickler et al., 2000) or with carrying load in horses (Wickler et al., 2001). However, animals do not always assume speeds that minimise COT (Chappell et al., 2004; Han et al., 2017; Seebacher et al., 2016a), and COT across a range of speeds can be estimated by the integral of COT across speeds ('integrated COT'; $W\ kg^{-1}$; see Glossary) (Jahn and Seebacher, 2019; Seebacher et al., 2016a). This metric is useful in offering a single value to compare individuals while incorporating the changes in costs across speeds.

Field COT can be estimated by tracking movement in the field in conjunction with published oxygen consumption data, and modelling of environmental constraints such as drag from water in aquatic environments (Sato et al., 2010; Trassinelli, 2016; Watanabe et al., 2015). This approach may be the best estimate for large marine animals such as sharks (Andrzejczek et al., 2020; Gleiss et al., 2011; Payne et al., 2016; Watanabe et al., 2019), whales (Christiansen et al., 2014; Rodríguez de la Gala-Hernández et al., 2008), polar bears (Griffen, 2018), penguins (Culik and Wilson, 1991) and seals (Maresh et al., 2014) that cannot be used in the laboratory.

In fish, field COT can be estimated from tail beat frequencies, which are a predictor of swimming speed and oxygen consumption during forced swimming (Steinhausen et al., 2005). Given that tail beat frequency is far easier to measure in the field, it may serve as a predictor for the energetic cost of locomotion for species that are difficult to maintain in laboratory conditions (Li et al., 2021). In horses, COT was estimated from field heart rate data, which tend to change linearly with oxygen consumption and speed (Coelho et al., 2021; Piccione et al., 2013; Williams et al., 2009).

Mechanism underlying differences in COT Mitochondria

Locomotion is constrained by the amount of ATP that can be supplied to working muscles (Hargreaves and Spriet, 2020), and animals with higher COT require increased ATP production for movement (Guderley and Pörtner, 2010). It is possible therefore that differences in COT between individuals may be related to differences in the efficiency of mitochondrial ATP production (Salin et al., 2015). Mitochondrial efficiency is measured either as the amount of oxygen used to synthesise a molecule of ATP (P/O ratio), or as the ratio of maximal substrate oxidation (S3) rates to uncoupled (S4) rates in mitochondria (respiratory control ratio, RCR) (Brand and Nicholls, 2011; Salin et al., 2018). The efficiency of mitochondrial ATP production can be compromised by the re-entry of protons into the mitochondrial matrix through the inner mitochondrial membrane without contributing to the production of ATP (Brand, 2005), either resulting from proton leak or via dedicated uncoupling proteins (Jastroch et al., 2010). Mitochondrial efficiency can fluctuate substantially between individuals (Salin et al., 2015). However, there is no experimental support for the hypothesis that mitochondrial efficiency determines COT, and COT did not correlate with mitochondrial efficiency (P/O ratios or RCR) in zebrafish (Jahn and Seebacher, 2019; Teulier et al., 2018). The increased content of uncoupling protein 3 observed in the marsupial *Monodelphis domestica* following cold exposure (Schaeffer et al., 2005) may have decreased mitochondrial efficiency and thereby led to the observed increase in COT (Salin et al., 2015; Schlagowski et al., 2014), although this link would need to be shown experimentally. The role of mitochondrial efficiency in influencing COT has been explored under a very limited range of environmental, developmental and phylogenetic contexts, and more research is needed. For example, mitochondrial efficiency can change during

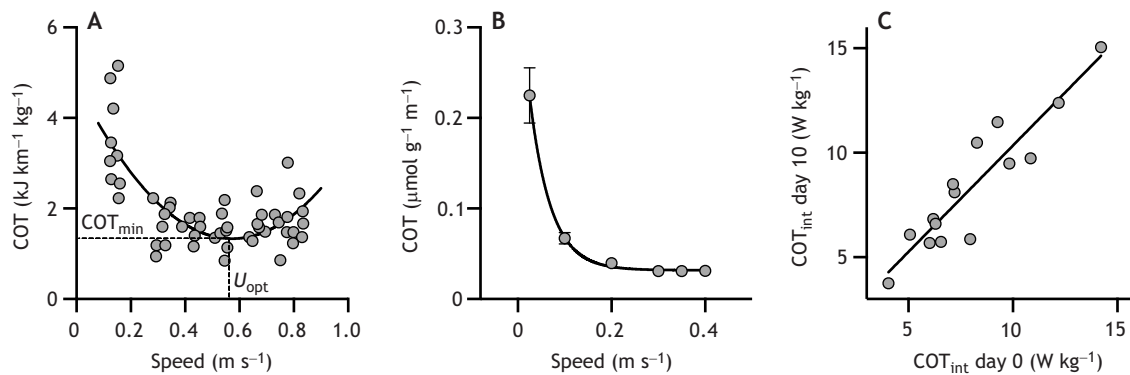
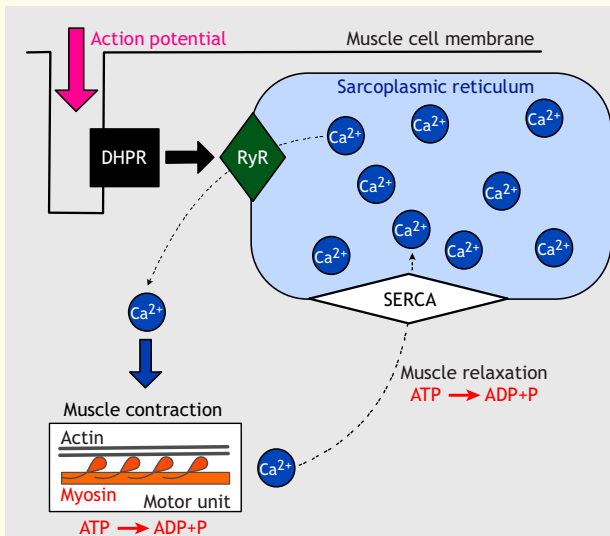


Fig. 3. Examples of COT measurements. (A) A representative J-shaped COT curve with minimum COT (COT_{min}) and the speed at which COT_{min} occurs (optimal speed, U_{opt}) indicated. (B) An L-shaped COT curve in zebrafish; decreasing COT with increasing speed reflects the diminishing proportion of resting metabolic rate in total oxygen consumption as fish swim at higher speeds. (C) Integrated cost of transport (COT_{int} =integral of COT across speeds) is a repeatable trait over 10 days between measurements in zebrafish. COT_{int} summarises energetic COT across a range of speeds, and the data shown here indicate that COT is a stable trait within individuals. Data in A are replotted from Claireaux et al. (2006), and data in B and C are replotted from Jahn and Seebacher (2019).

Box 1. Muscle contractile function

Most oxygen consumed during movement is a consequence of ATP use during muscle contraction and relaxation. Muscle contraction is instigated by an action potential from a motor neuron to the muscle fibre, which causes dihydropyridine receptors (DHPR) to interact with ryanodine receptors (RyR) on the sarcoplasmic reticulum (SR) membrane to release Ca^{2+} from the SR (Barclay, 2017; Gundersen, 2011). Ca^{2+} binding to troponin on the motor unit leads to cross-bridge formation between myosin and actin, and muscle contraction. Muscle contraction uses ATP, which is hydrolysed by myosin ATPase activity (Gundersen, 2011). Muscle relaxation is initiated by active, ATP-consuming transport of Ca^{2+} back into the SR by the sarco(endo)plasmic reticulum Ca^{2+} -ATPase (SERCA) (Gundersen, 2011). During the muscle contraction–relaxation cycle, ~65% of ATP is used by myosin ATPase and ~30% by SERCA (Barclay, 2017). Hence, inefficiencies in energy conversion that could lead to increases in COT would most likely be associated with myosin ATPase or SERCA activities.



ontogeny, and mitochondria tend to be more coupled early in development when maximal rates of growth occur (Salin et al., 2019). Variation in mitochondrial efficiency during development could have pronounced impacts on growth and at the same time have compounding effects on COT. Energy allocation to growth is particularly important during early development so that the consequences of energy allocation trade-offs during development would be pronounced. Mitochondrial efficiency also increased with reduced food supply, particularly at high temperatures (LeRoy et al., 2021; Salin et al., 2015), and the role of mitochondrial efficiency in modifying COT should be investigated at different life-history stages and under different environmental conditions.

Efficiency of muscle contractile function

The activity of myosin ATPase modifies the speed at which muscles contract and can differ between muscle fibre types (Gundersen, 2011) (Box 1). Type I (slow twitch) muscles have lower myosin ATPase activity and use ATP more efficiently than type II (fast twitch) fibres (Baylor and Hollingworth, 2012). Muscle fibre types vary between individuals, and within individuals over a lifetime, and change in response to environmental factors such as exercise (Egan and Zierath, 2013; Simmonds and Seebacher, 2017). Changes in muscle fibre types may therefore alter the efficiency with which ATP is used during locomotion and influence COT. Field data from migrating

wildebeests showed that muscle contractile efficiencies were higher in wildebeests than in the same muscle group in a ruminant sedentary cow (Curtin et al., 2018). It could be possible that the observed low cost of myosin and actin interaction (cross-bridge cycling) and muscle contraction (Box 1) in the wildebeest reduced COT, allowing wildebeest to make long migrations in arid and hot conditions (Curtin et al., 2018).

Similarly, the efficiency of SERCA can change with environmental context and between individuals and species. SERCA operates most efficiently with a coupling ratio of 2:1, where two Ca^{2+} are transported for every ATP hydrolysed (Gamau et al., 2020). However, the efficiency of SERCA can be compromised by the magnitude of the Ca^{2+} gradient, the regulatory peptide sarcolipin, membrane phospholipid composition (Verkerke et al., 2019) and through oxidative damage (Xu and Van Remmen, 2021). Additionally, different isoforms of SERCA have different efficiencies of Ca^{2+} transport. There is a negative correlation between SERCA coupling ratio and resting metabolic rate, and a positive correlation between higher ratio of SERCA 1 to SERCA 2 and resting metabolic rate (Gamau et al., 2020). Diminished Ca^{2+} cycling can reduce the rate of force production, which can result in reduced locomotor performance (Seebacher et al., 2012). Both myosin ATPase and SERCA could cause individual differences in COT as muscles regularly operate away from optimal conditions (Curtin et al., 2019; Syme et al., 2008). However, these ideas need to be tested experimentally.

Inefficiencies introduced by muscle fibre types or SERCA activity are likely to reduce locomotor performance while increasing COT. Hence, an energy allocation trade-off would be compounded by lower performance, which would exacerbate the negative fitness consequences. There is considerable variation between individuals in these aspects of muscle function (James et al., 2011), so that muscle contractile efficiencies may be particularly important in introducing variation in COT between individuals. Investigating these dynamics would be an important area for future research.

Differences between species and individuals

Differences between individuals

COT can differ substantially between individuals of the same species (Jahn and Seebacher, 2019; Kraskura et al., 2021; Seebacher et al., 2016a). However, COT was highly repeatable within individual zebrafish (*Danio rerio*) over a 10-day period, indicating that COT is a stable trait within individuals (Jahn and Seebacher, 2019) (Fig. 3C). Similarly, in laboratory mice, COT was significantly repeatable between days after accounting for line type, body mass and age in females (Rezende et al., 2006).

Individuals may alter their biomechanical gaits to maintain COT_{\min} at different speeds (Griffin et al., 2004). For example, horses may spontaneously switch between a walk and a trot to minimise COT (Griffin et al., 2004). Aquatic animals can alter their behaviour to minimise COT, and in bottlenose dolphins (*Tursiops truncatus*) and hammerhead sharks (*Sphyrna mokarran*), tagging of wild individuals did not appear to affect COT significantly. Dolphins reduced their speeds to compensate for the increase in drag from the tags (van der Hoop et al., 2014) and hammerhead sharks spent 90% of the time swimming at roll angles, which hydrodynamic modelling showed reduces drag and therefore COT by ~10% compared with level swimming (Payne et al., 2016). Animals can also exploit different spatial or temporal habitats that reduce COT. For example, fish can reduce movement costs by up to 40% by selecting tidally generated currents known as ‘selective tidal stream transport’: fish enter the water column when the current is

flowing in a favourable direction and can use the flow to aid in movement and reduce COT (Kelly et al., 2020; Weihs, 1978).

Morphological differences between individuals of the same species can occur when individuals experience differences in habitat use and food preference (Rouleau et al., 2010). For example, in brook trout (*Salvelinus fontinalis*), a littoral ecotype with longer pectoral fins is found in shallow water and feeding on zoobenthos, whereas the pelagic ecotype with shorter pectoral fins is found in deeper water and feeding on zooplankton (Rouleau et al., 2010). COT increased more rapidly with increasing speed in littoral than in pelagic ecotypes (Rouleau et al., 2010). However, littoral individuals did not incur a higher COT_{min} than pelagic fish, which was likely due to lower resting metabolic rate and U_{opt} in the littoral ecotype (Rouleau et al., 2010). Similarly, pale chub (*Zacco platypus*) collected from locations with reduced predator stress and fast water flow had lower COT compared with individuals collected from slow-flowing streams with increased predation (Fu et al., 2013). Lower COT was associated with more streamlined body shape and increased water velocity (Fu et al., 2013). Populations of Chinese hook snout carp (*Opsariichthys bidens*) from different habitats differed in their morphology and COT, but these differences could not be explained by genetic differences (Fu et al., 2012). However, COT was measured under different environmental conditions, which may have confounded comparisons (Fu et al., 2012).

In leghorn chickens (*Gallus gallus domesticus*), bantam chickens selectively bred for small size had lower than predicted COT_{min} for their body mass compared with chickens bred for large size. The relatively low COT_{min} in bantams was associated with a more erect posture and lower energetic costs per stride (Rose et al., 2015). The more vertical limb in the miniature chicken decreased the muscle force needed to support body weight and improved the mechanical advantage of the muscles compared with chickens bred for larger body size (Rose et al., 2015). Mice bred for increased running capacity (Dlugosz et al., 2009; Rezende et al., 2006) were morphologically different to wild-type mice, and increased running capacity was associated with increased COT (Dlugosz et al., 2009). The increased COT could be attributed to increased resting metabolic rate and less favourable posture (Dlugosz et al., 2009).

When climbing lizards were modelled with robots, there was a distinct trade-off between speed and stability, where high speeds decreased stability and low speeds increased COT (Schultz et al., 2021). Hence, the trade-off between speed and agility (Wynn et al., 2015) can also have an energetic dimension that modifies a potential energy allocation trade-off. For example, complex habitats would require greater agility and lower speed, which would therefore increase COT. However, increased agility in complex habitats can increase survival of individuals (Rew-Duffy et al., 2020; Wilson et al., 2020), so that increased COT must be interpreted in a broader fitness context. These dynamics need to be understood at a greater resolution to clarify the ecological dimension of COT-induced energy allocation trade-offs.

Increased COT and its attendant trade-offs can be offset by behavioural changes. For example, individual zebrafish with relatively high COT showed reduced movement in a novel environment (Jahn and Seebacher, 2019). Female guppies (*Poecilia reticulata*) that were exposed to higher levels of male harassment showed a decrease in COT, which may have been the result of less pectoral fin-assisted swimming (Killen et al., 2016). Predation pressure can also lead to increased COT that may be associated with concomitant changes in behaviour such as selection

of different flow environments in fish (Fu et al., 2015). Predation-induced change to COT may be driven by morphological changes of prey (Pettersson and Brönmark, 1999). Predator cues induced deeper body shape in crucian carp (*Carassius carassius*), which increased drag and therefore increased COT at speeds other than U_{opt} (Pettersson and Brönmark, 1999; Pettersson and Hedenström, 2000).

At least within similar environments, differences in COT between individuals are particularly important because they may lead to selection gradients within populations. Individuals with increased COT could experience reduced fitness, particularly under environmental circumstances that promote increased COT such as climate warming (see below). These fitness differentials could lead to a reduction in genetic diversity within populations if differences in COT are mediated genetically (Seebacher and Krause, 2019).

Implications for social groups

The impacts of differences in COT between individuals can scale up to impact social groups. An increase in magnitude of differences between individuals would make social groups less homogeneous, which can affect group behaviour (Conradt and Roper, 2000; Seebacher and Krause, 2017). Group cohesion is important for information transfer about predator presence, food detection and reproduction, for example (Kурvers et al., 2014). Individuals with increased COT may compromise their own energy efficiency to stay within a group, and group cohesion may require different energetic investments to be made by different group members (Killen et al., 2021; Seebacher and Krause, 2017). Consequently, the magnitude of allocation trade-offs between locomotion and reproduction, for example, would also vary between individuals within groups, and particularly for animals with relatively high COT, there would be a balance between the benefits of group living (Kурvers et al., 2014) and potential fitness decrements. However, if these energetic costs become too large, group cohesion may break down and individuals with similar physiological make-ups may group together (Killen et al., 2017). Hence, differences in COT may drive fission and re-assembly of conspecifics that are more physiologically similar to each other (Seebacher and Krause, 2017). These fission–fusion dynamics can affect gene flow within populations (Sexton et al., 2011).

Just as individuals can exploit their environment (Kelly et al., 2020) or moderate their behaviour to reduce COT (Griffin et al., 2004; van der Hoop et al., 2014; Tudorache et al., 2011), social groups can be beneficial in reducing COT (Weihs, 1973b). For example, fish schooling is associated with increased endurance (Weihs, 1973b) and reduced costs of swimming mediated via altered hydrodynamic conditions (Marras et al., 2015). Fish following in the wake of other individuals experience the greatest energy savings (Domenici et al., 2017). In male European eels, COT at the optimal swimming speed was significantly lower when swimming in a group compared with in solitary individuals (Burgerhout et al., 2013). Similarly, group coordination in flying birds, such as the typical V-formation of many birds, alters aerodynamics so that individuals within the group experience lower energetic costs (Portugal et al., 2014; Voelkl et al., 2015). Hatchling green turtles (*Chelonia mydas*) digging out of a nest use less energy when digging in larger groups, partly because the digging duration is shortened and partly because individual digging effort is reduced (Rusli et al., 2016). These interesting dynamics would warrant further research to clarify the relationships between energy reduction as a result of group living, and differences in COT between group members that may lead to group fission.

Differences between species

Identifying the factors that lead to interspecific differences in COT can be important to understand energetics of movement and responses of different species within communities to changing environments. COT tends to be lower in larger animals (Rose et al., 2015), although measured COT and COT_{min} values often do not align with predicted values from allometric scaling (Langman et al., 2012; Maloiy et al., 2009; Rose et al., 2015). This discrepancy may be explained at least partly by the dependence of COT and COT_{min} on mode of locomotion. At any given body size, COT is typically lowest for swimming, followed by flying, and it is highest when walking and running (Butler, 2016; Schmidt-Nielsen, 1972; Tucker, 1970). Mode of locomotion per se therefore can make different species more or less vulnerable to allocation trade-offs.

Aquatic animals must navigate through a denser medium than terrestrial animals, but have the advantage of being near-neutrally buoyant and therefore do not need to consume energy to maintain posture against gravity (Schmidt-Nielsen, 1972). A considerable proportion of the movement cost of terrestrial animals stems from the need to maintain body posture (Kram and Taylor, 1990). Interestingly, smaller primates (<0.5 kg) experience the same COT when walking or climbing for a given distance (Hanna et al., 2008). Additionally, COT for climbing was not significantly different across an eightfold range in body mass, but it did differ among five nonhuman walking primates (Hanna et al., 2008). These patterns allow primates to enter novel arboreal environments without increasing metabolic costs (Hanna et al., 2008). Between-species differences in terrestrial animals could also be explained by effective limb length (Pontzer, 2007). Effective limb length, which is the length of the leg as a strut (not the total length of skeletal bones), explained 98% of the observed variance in locomotor cost across birds and terrestrial mammals (Pontzer, 2007). However, these results are controversial because the log-transformed data used in Pontzer (2007) conceal the absolute size of the residuals, and many comparisons among pairs of species did not support the hypothesis that longer effective limb length is negatively associated with COT (Halsey and White, 2019). Simulation modelling suggests that improved foot posture and heel contact with the ground can reduce the COT of bipedal locomotion in the Japanese macaque (Oku et al., 2021).

Generalist species that use a broader range of locomotor modes to traverse wider ranges of habitats tend to experience increased COT compared with animals specialised to particular modes (Williams, 1999). For example, surface swimming in air-breathing fish is more costly than submerged swimming (John et al., 2021; Lefevre et al., 2013), and in the catfish *Pangasianodon hypophthalmus*, surface swimming incurred a significantly higher energetic cost (25%) (Lefevre et al., 2013). Similarly, increased COT for aquatic locomotion in semi-aquatic animals can largely be attributed to incomplete streamlining of the body, increased drag owing to surface swimming, and the paddle-based swimming mode imposed by structures that evolved for terrestrial locomotion (Fish and Baudinette, 1999; Fish et al., 2001; Videler and Nolet, 1990). Conversely, a semi-aquatic lifestyle can reduce the efficiency of terrestrial locomotion, and in the platypus (*Ornithorhynchus anatinus*), COT for terrestrial locomotion was greater than for swimming (Bethge et al., 2001; Fish et al., 2001). Similarly, COT during running in the North American river otter (*Lontra canadensis*) was greater than in fully terrestrial mammals of comparable size and limb length (Williams et al., 2002). Additionally, diving in aquatic birds can be more costly than surface swimming, in part owing to the increased cost of

overcoming buoyancy, which contrasts with fish and other fully aquatic animals (Ancel et al., 2000; Butler, 2000). Burrowing in terrestrial animals also incurs high energetic costs (Withers et al., 2000). In the semi-fossorial (surface burrowing animals) spinifex hopping mouse (*Notomys alexis*), COT_{net} for burrowing was greater than for specialised fossorial animals (White et al., 2006).

Even when locomotor modes are similar, gait differences between species change locomotor efficiency. COT_{net} was ~20% higher in Indonesian blue-tongued skink (*Tiliqua gigas*), which engage in belly-dragging locomotion, compared with the savannah monitor (*Varanus exanthematicus*), which has a raised quadrupedal gait (Dickinson et al., 2022). However, gait transition between walking and trotting or pacing in terrestrial animals does not always change COT_{min} (Maloiy et al., 2009). Fish change gaits to negotiate different habitats or perform different activities (Cannas et al., 2006). Median paired-fin swimming, where fins are the primary means of locomotion, is associated with more complex habitats that require manoeuvrability (Kendall et al., 2007). Undulatory or body-caudal fin swimming is common in fish that live in open habitats and during migrations (Kendall et al., 2007). In labriform fish, median paired-fin swimming transitions to body-caudal fin swimming at high speeds, resulting in increased COT (Kendall et al., 2007; Korsmeyer et al., 2002). Unsteady burst swimming in the striped surfperch (*Embiotoca lateralis*) increased EPOC, and anaerobic metabolism constituted 25% of total swimming costs (Svendsen et al., 2010). The hydrodynamic environment can influence COT and potentially cause differences between species and even individuals. For example, increased frequency of undulations changed the hydrodynamic environment from laminar to turbulent (low to high Reynolds numbers) and increased COT (Shelton et al., 2014). However, these relationships are complex and modified by body stiffness and dimensions, and mode of locomotion (Chung, 2009; Liu and Jiang, 2021; Shelton et al., 2014).

In fish, fineness ratio (body slenderness; ratio between standard body length and maximum body depth) correlated negatively with COT and COT_{net} (Ohlberger et al., 2006; Rubio-Gracia et al., 2020b). More streamlined fish (higher fineness ratio) experienced reduced drag, tailbeat frequency and oxygen consumption compared with less streamlined morphotypes of the same length (Blake et al., 2009). Relatively high COT in goldfish (*Carassius auratus*) can be explained by their relatively low fineness ratio associated with greater drag and lower stability when swimming, together with a reduced percentage of oxidative (red) muscle and low muscle efficiency (Blake et al., 2009). In the toothcarp (*Aphanius iberus*) and mosquitofish (*Gambusia holbrooki*), U_{opt} increased with increasing fineness ratio while COT decreased (Rubio-Gracia et al., 2020b), and there was a negative correlation between caudal peduncle depth and COT in *A. iberus* and *G. holbrooki* as well as in *Oncorhynchus mykiss* (Gamperl et al., 2002; Rubio-Gracia et al., 2020b). Energetically efficient fish with high fineness ratio can travel at a much wider range of speeds without pronounced changes in energy expenditure (Ohlberger et al., 2006; Rubio-Gracia et al., 2020b). In contrast, higher-drag fish (lower fineness ratio) experience a more dramatic change in COT when they deviate from U_{opt} (Pettersson, 2007; Pettersson and Hedenström, 2000). Anguilliform swimming in fish (e.g. eels) is particularly efficient energetically (van Ginneken et al., 2005; Tudorache et al., 2015), and it is restricted to species with elongate and highly flexible bodies, where the body undulates along its length in a wave-like motion pushing the animal forward (Tack et al., 2021).

Species comparisons in the literature are somewhat eclectic. However, there appear to be some generalities: mode of locomotion and gait are important in determining COT. Similarly, differences in body shape between (and even within) species modify COT. Mode of locomotion would introduce differences in trade-offs across broader taxonomic groups (e.g. fish versus birds versus mammals), whereas differences in shape also affect species within communities of taxonomically similar animals (e.g. fish). Species comparisons are complicated by phylogenetic differences, and locomotor traits and their associated COT should be placed within a phylogenetically corrected framework in future work.

Environmental impacts

Temperature

Temperature is the most studied environmental influence on COT, particularly in fish. There is a consensus in the literature that COT consistently increases with increasing test temperature in ectothermic animals (Clark and Seymour, 2006; Duthie, 1982; Jahn and Seebacher, 2019; Lim and Ellerby, 2009; Meskendahl et al., 2019; Seebacher et al., 2016a; Tu et al., 2012; Whitney et al., 2016; Yin et al., 2021). Similarly, the overall magnitude of EPOC was greater at warmer temperatures (Kraskura et al., 2021; Lee et al., 2003). Modelling suggests that COT_{min} increases exponentially with an increase in environmental temperature (Hein and Keirsted, 2012). Interestingly, temperature also increased individual variability in COT (Jahn and Seebacher, 2019; Kraskura et al., 2021). However, the effects of increasing temperature on COT were not influenced by the oxygen saturation of water in brown trout (*Salmo trutta*) (Nudds et al., 2020), indicating that exercise was not oxygen limited. Thermal effects on COT are not always linear, and in vendace (*Coregonus albula*), COT_{net} was lowest at 8°C, but increased at 4°C and 15°C (Ohlberger et al., 2007). COT was independent of temperature in adult pink salmon (*Oncorhynchus gorbuscha*) and sockeye salmon (*Oncorhynchus nerka*) (Macnutt et al., 2006). Changes in temperature can affect mitochondrial efficiency, although the effects are not consistent across taxa (Salin et al., 2015), and a direct link between temperature, mitochondrial efficiency and COT has not been made experimentally. However, as we pointed out above, the role of mitochondrial efficiency would need to be investigated across a broader range of contexts. Similarly, temperature affects muscle contractile function (James, 2013), which may provide a mechanistic link between environmental change and COT, although (and as for mitochondria) experimental evidence is not available. Increases in temperature decreased COT in larval fish as a result of reduced viscosity of water (Herbing, 2002), indicating that temperature effects on COT can interact with other environmental variables and with life-history stages in fish. Overall, these acute effects of temperature show that energy efficiency of locomotion decreases in warmer habitats, in warmer seasons and under climate warming.

Laboratory acclimation to warmer temperatures increased COT (Claireaux et al., 2006; Dickson et al., 2002; Kirby et al., 2020; Pang et al., 2013; Rouleau et al., 2010; Wolfe et al., 2020; Xia et al., 2017), which means that acute temperature effects are not compensated for by acclimation. Similarly, COT increased in response to seasonal acclimatisation to warmer summer temperatures in field-sampled buffalo fish (*Ictiobus bubalus*) (Adams and Parsons, 1998). There was a sex-dependent effect of season, and during winter, COT_{net} was significantly higher (24%) in males than in females (Adams and Parsons, 1998). Acclimation can alter sensitivity to acute temperature changes, and the impact of acute temperatures may vary between populations with different

thermal histories (Sylvestre et al., 2007). COT in cod (*Gadus morhua*) acclimated to 7°C increased when fish were exposed to 11°C, but remained stable when fish were cooled to 3°C (Sylvestre et al., 2007). These responses may increase the proportion of the energy budget spent on locomotion in fish populations at higher latitudes with cool thermal histories when exposed to increasing temperature owing to climate change. In two trout (*Oncorhynchus mykiss* ssp.) populations that were genetically similar but occupied different thermal habitats, COT and COT_{min} were both lower for the population of trout that originated from the warmer habitat (Gamperl et al., 2002). Nonetheless, COT_{min} was lower at cooler temperatures in both populations (Gamperl et al., 2002). Interestingly, both populations had the same relatively low temperature preferences (~13°C), which minimised COT_{min} (Gamperl et al., 2002), demonstrating that environmental impacts can be modified by behavioural adjustments. COT may increase with increasing temperature as a result of increased resting metabolic rates or increased energetic cost of locomotion, or both. However, COT_{net} increased with increasing temperature in zebrafish and European sea bass, indicating that increased resting metabolic rates were not the driving mechanism (Claireaux et al., 2006; Jahn and Seebacher, 2019).

The trend of increasing COT with temperature in fish is largely reflected in terrestrial ectotherms. For example, COT was greater at higher temperatures (35–40°C) than at 25°C in several lizards [*Heloderma suspectum* (John-Alder et al., 1983); *Tupinambis nigropunctatus* (Bennett and John-Alder, 1984); *Dipsosaurus dorsalis* (John-Alder and Bennett, 1981)]. In red-spotted newts (*Notophthalmus viridescens*) locomotion at 1°C or 5°C was less costly than travelling at 25°C (Jiang and Claussen, 1992, 1993). Interestingly, costs were lower when newts travelled on land compared with in water at 5°C, but this difference disappeared at 25°C (Jiang and Claussen, 1994). In contrast, COT_{net} in the lungless salamander (*Desmognathus ochrophaeus*) was reduced in warm-acclimated (21°C) compared with cool-acclimated (5°C or 13°C) salamanders when tested at a common temperature (13°C) (Feder, 1986), although these data may be misleading because animals were not tested at each acclimation temperature.

Only a limited number of studies exist detailing the effect of temperature on COT of endotherms. Prolonged cold exposure in the marsupial *Monodelphis domestica* increased COT by 15% compared with thermoneutral controls, and was unaffected by exercise training (Schaeffer et al., 2005). This increase in COT was accompanied by upregulation of an uncoupling protein 3 homologue that may reduce ATP production efficiency while increasing thermogenesis and COT (Schaeffer et al., 2005). Endothermy in some sharks and tunas allows fish to maintain some muscles above water temperature and thereby improve swimming performance (Sepulveda and Dickson, 2000). However, the elevated muscle temperature doubled COT in endothermic relative to comparable ectothermic fish (Watanabe et al., 2015). Nonetheless, the benefits of increased travel distances outweighed the disadvantage of increased COT in endothermic fish (Watanabe et al., 2015).

The consensus in the literature is that increasing temperature is a major driver for increased COT and can potentially exacerbate energy allocation trade-offs. Allocation trade-offs can lead to decreased growth and thereby decreased energy conversion efficiencies across trophic levels at warmer temperatures, and these dynamics could pose serious threats to ecosystems and ecosystem services (Barneche et al., 2021). Nonetheless, thermal effects on allocation trade-offs are not well characterised, and this is an important area for future research.

Exercise

Exercise in the sense of regular or consistent movement that elevates metabolic rates to well above resting has pronounced physiological impacts, including on muscle contractile function and mitochondria (Egan and Zierath, 2013; Memme et al., 2021). Exercise can lower COT while increasing aerobic capacity. In juvenile bream (*Megalobrama pellegrini*), exercise training in fast-flowing water (4 BL s^{-1}) or exhaustive chasing training daily for 5 weeks increased swimming performance (U_{crit} , see Glossary) and reduced COT to a greater extent than in controls or slow exercise training programs (1 and 2 BL s^{-1}), indicating that fish swam with greater aerobic efficiency (Li et al., 2017). Similarly, exercise training reduced COT in juvenile whiting (*Merlangius merlangus*) (Hammer and Schwarz, 1996). However, COT did not change following exercise training in zebrafish (*Danio rerio*) (Jahn and Seebacher, 2019). Rearing rainbow trout (*Oncorhynchus mykiss*) in flowing water (0.9 BL s^{-1}) reduced U_{opt} compared with similar sized fish raised in still water (Skov et al., 2011). However, at swimming speeds greater than 1.4 BL s^{-1} COT increased significantly in fish reared in flowing water compared with still water (Skov et al., 2011), which may reflect greater aerobic capacity in flow-reared fish and therefore less reliance on anaerobic pathways at high speeds. In field populations of the Chinese hook snout carp (*Opsariichthys bidens*) and pale cub (*Zacco platypus*), river habitats with higher water velocities seemed to correlate negatively with COT (Fu et al., 2012, 2013). However, these habitats also differed in temperature and predation stress, which can affect COT (Fu et al., 2012, 2013, 2015).

Similar to COT, there is variation in EPOC between individuals and species (Kraskura et al., 2021; Lee et al., 2003), although intensity of exercise is the best indicator of EPOC magnitude (Borsheim and Bahr, 2003; Cordero et al., 2019). Unsteady burst swimming which occurs at high speeds in fish is positively correlated with the magnitude of EPOC following exercise, and may make a substantial contribution to total energetic cost of locomotion (Lee et al., 2003; Svendsen et al., 2010). Exercise training did not reduce overall EPOC in juvenile common carp (*Cyprinus carpio*) (He et al., 2013), but exercise-trained fish had higher oxygen consumption for 1–7 min following exhaustive exercise and recovery during this time was faster compared to non-trained fish (He et al., 2013). Exercise-trained fish took longer to reach exhaustion, but their greater aerobic capacity meant that EPOC was similar to non-trained fish that exercised for less time (He et al., 2013).

There can be a link between exercise training and growth, mediated by the relationship between aerobic scope and COT (Davison and Herbert, 2013). Aerobic scope is the difference between resting and maximum metabolic rates, and is correlated with the metabolic power available for activity, growth and other fitness-related functions (Clark et al., 2013). If energy investment into locomotion is minimised, the excess energy may be allocated to growth (Palstra et al., 2015). For example, long-term (7 weeks) exercise in juvenile yellowtail kingfish (*Seriola lalandi*) resulted in reduced COT and COT_{min} compared with non-exercised fish (Brown et al., 2011). In parallel, exercised fish showed a 10% increase in growth (at 21.1°C) (Brown et al., 2011). However, the relationship between exercise and growth is not consistent across species. In juvenile hapuku (*Polyprius oxygeneios*), exercise training did not affect COT and there was a limited effect of exercise training on growth (Khan et al., 2014).

There is limited work on terrestrial animals (excluding humans) regarding the impact of exercise on COT. In the marsupial *Monodelphis domestica* and goats (*Capra hircus*), exercise training did not affect COT (Schaeffer et al., 2001, 2005).

Exercise-trained lizards (*Anolis carolinensis*) had lower resting metabolic rates, indicative of lower maintenance costs following training. However, sprint-trained lizards had higher rates of oxygen consumption and longer recovery times (EPOC) than untrained lizards, indicating that sprint training increased COT (Lailvaux et al., 2018).

The literature indicates that exercise frequently, but not always, reduces COT so that habitat characteristics that promote exercise (e.g. wind and water currents, or dispersed resource distribution; Gudmundsson et al., 2021; Lihoreau et al., 2017) would also lead to increased growth rates. Increased individual growth is a principal input into population dynamics (Savage et al., 2004) so that habitat-modified COT and the resultant shifted trade-off with growth can have impacts on populations. Temperature can modify these relationships via its effects on COT, metabolic rates, mitochondrial efficiency, and hence growth and population dynamics (Loughland et al., 2022; Savage et al., 2004). It will be challenging but essential to disentangle the relative impacts of these factors on COT and the extent of allocation trade-offs in different species to predict the impacts of environmental change on populations.

Pollution

Most environments on Earth now contain a cocktail of chemicals derived from human activity (Borrelle et al., 2020; Godfray et al., 2019; Wilkinson, 2022) that can affect almost all biological processes. Impacts of pollutants are unpredictable because they can modify the way organisms respond to natural environmental variables such as temperature (Wu et al., 2022). Given the enormous diversity of environmental pollutants, very little is known about their effects on animal physiology and ecology. Most of the research testing the impact of pollutants on COT was conducted in fish, and very few environmental pollutants have been studied to date. Perfluorinated compounds (PFCs), specifically perfluorooctane sulfonic acid (PFOS), which are used in the production of adhesives, cosmetics, paints, cleaners and pesticides, among other uses (Zhang and Lerner, 2012), are relatively common in aquatic systems (Houde et al., 2011). Juvenile goldfish (*Carassius auratus*) exposed to PFOS (32 mg l^{-1}) for 48 h showed marked increases in COT (Xia et al., 2013). PFOS-induced changes in COT were accompanied by decreases in spontaneous activity and distances moved, while U_{crit} remained unchanged (Xia et al., 2013). Chronic exposure of juvenile qingbo (*Spinibarbus sinensis*) to PFOS for 30 days across a range of ecologically relevant concentrations increased COT_{net} regardless of temperature; however, the effect of PFOS on COT increased at the combination of high concentrations at high temperature (28°C) (Xia et al., 2015). Temperature and PFOS also reduced social interactions and spontaneous movement at high but not low temperatures (Xia et al., 2015). There may be a link between increased COT_{net} and decreased activity, which could be tested experimentally.

Selenium is an essential micronutrient and fish require low dietary concentrations to maintain growth and physiological functions; however, high concentrations of selenium can bioaccumulate to become toxic (Thomas and Janz, 2011; Thomas et al., 2013). Increased dietary selenomethionine (an organic form of selenium) for 60 days did not alter COT significantly in zebrafish (Thomas and Janz, 2011). However, increased dietary selenomethionine for 90 days significantly increased COT in zebrafish (Thomas et al., 2013) and fathead minnows (*Pimephales promelas*) (McPhee and Janz, 2014). In the 90 day treatment, standard metabolic rate also increased, which could explain the increased COT (Thomas et al., 2013). Exposure (14 days) of zebrafish to an acutely toxic form of

selenium, sodium selenite, significantly decreased active metabolic rates and aerobic scope but had no effect on COT (Massé et al., 2013).

Mining and smelting activities can lead to runoff of lead (Pb) into aquatic environments (Mager and Grosell, 2011). Acute (24 h) and chronic (33–57 days) exposure of fathead minnows (*Pimephales promelas*) to lead did not impact COT. However, aerobic scope and U_{crit} were reduced by lead compared with control fish (Mager and Grosell, 2011). Crude oil contains toxic polycyclic aromatic hydrocarbon (PAH) chains (Johansen and Esbaugh, 2017), but exposure (24 h) of red drum (*Sciaenops ocellatus*) to PAH did not alter COT or EPOC (Johansen and Esbaugh, 2017).

Increasing human use of synthetic glucocorticoids as anti-inflammatories and immunosuppressants has led to increases in their concentrations in waterways. Increased levels of the glucocorticoid medication prednisone in waterways (Creusot et al., 2014) can affect metabolism and endocrine function in fish (Thibault et al., 2021). After 21 days of prednisone exposure, sheephead minnow (*Cyprinodon variegatus*) had a significantly higher COT and EPOC compared with 7- and 14-day-exposed fish (Thibault et al., 2021). The neurotoxic protein botulinum serotype E is associated with visceral toxicosis, which can result in high mortalities of channel catfish (*Ictalurus punctatus*) (Beecham et al., 2014). Despite botulinum causing weakness and paralysis of skeletal muscles by preventing acetylcholine release at muscular junctions (Nigam and Nigam, 2010), there was no significant difference in COT between botulinum-injected fish and controls (Beecham et al., 2014). This indicates that COT was not impacted by changes in the neuromuscular physiology of the fish.

Given the sparsity of the literature, it is impossible to reach a consensus on the effects of pollutants on COT other than that pollutants with diverse chemical compositions can affect COT. The effects of pollution, and particularly of endocrine-disrupting compounds, is one of the greatest challenges currently in conservation (Sutherland et al., 2021), and understanding their impact on COT will greatly enhance predictions of their ecological consequences.

Conclusions and future directions

Life-history theory predicts that owing to a finite amount of resources available to organisms, the allocation of energy to one phenotypic trait prevents the same resources from being allocated to other, often fitness-related traits (Husak et al., 2016; King et al., 2011; Stearns, 1989). Hence, there may be a trade-off between traits such as movement, immunity, growth and reproduction (Husak et al., 2016; Stearns, 1989). High COT may limit the energy that can be allocated to growth and reproduction (Husak and Fox, 2008; Husak et al., 2016), so that COT can be closely related to individual fitness.

A major conclusion to be drawn from the literature is that allocation trade-offs are multidimensional and do not operate in isolation from other biotic or abiotic inputs. The requirements to respond to the broad range of environmental context experienced by animals in their daily life modifies the energy allocation trade-offs. The examples we gave above included the need to move at speeds other than U_{opt} to fulfil different ecologically relevant tasks, trade-offs between speed and agility, and interspecific and intraspecific interactions during courtship or predation. Environmental change, and particularly anthropogenic climate change and pollution, interacts with this biotic context. COT increases with temperature, and global temperature increases can place total energy budgets under greater pressure, which may aggravate allocation trade-offs. These changes may be exacerbated for aquatic animals by global changes in salinity (Durack et al., 2012), which can increase

COT (Palstra et al., 2008). Climate change causes flow rates in river systems to change more rapidly and at greater magnitude than would occur naturally (Gudmundsson et al., 2021; Morales-Marín et al., 2019). Substantial increases in water flow will place additional pressure on the energy budgets of aquatic animals by increasing the energy required for locomotion and to remain stationary in a flowing stream (Martin et al., 2015). Temperature, salinity and water flow changes may have pronounced consequences for migrating species such as salmon, which engage in long and energetically costly migrations that are closely linked to fitness (Farrell et al., 2008). When river temperatures or water flow rates rise above critical limits for metabolic scope, fish are unable to complete migrations (Farrell et al., 2008; Rand et al., 2006). Under these conditions, COT takes up a relatively larger proportion of metabolic scope and reduces remaining metabolic scope for tasks outside of locomotion (Butler, 2016; Martin et al., 2015).

COT and energy allocation trade-offs affect processes that are dependent on energy inputs; in a thermodynamically unfavourable world, this includes almost all biological processes. The consequences of biotic and abiotic impacts on COT and allocation trade-offs thereby extend to individual fitness, the function of social groups, population dynamics and potentially energy transfer in food webs. The overarching challenge now lies in resolving the relative impacts of these different drivers to enable predictions of how ecosystems respond to change. Based on the literature reviewed, we suggest a number of future research directions that could increase understanding of how COT affects these macroecological patterns: (1) the effects of multiple stressors: different environmental variables are likely to interact, and these interactions need to be tested experimentally to model responses to real-world environments; (2) pollution: COT is a function of metabolism and muscle performance, and is therefore likely to be affected by endocrine-disrupting pollution, and it is essential to test the effects of a wider range of pollutants; (3) underlying mechanisms: mitochondrial and excitation–contraction–relaxation efficiencies are likely to modify COT, but experimental work across a broader range of life-history, phylogenetic and environmental contexts is needed to clarify these relationships. Understanding the underlying mechanisms will enable more precise predictions about flow-on effects of changes in COT; (4) allocation trade-offs: there need to be more explicit experimental tests to quantify trade-offs so that reliable prediction can be made about changes in energy budgets and conversion efficiencies resulting from environmental change; and (5) consequences of differences in COT between individuals for social group function, with respect to group cohesion, assortment of phenotypes and gene flow.

Competing interests

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