

How rapid changes in body mass affect the locomotion of terrestrial vertebrates: ecology, evolution and biomechanics of a natural perturbation

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Animals rarely move through their natural habitat without experiencing an environmental perturbation, such as an obstacle or drop in height. However, rapid perturbations due to mass changes are little studied, and these can have significant impacts on the ecology and evolution of animal locomotion due to associated changes in relative muscle mass, altered body shape, shifts in the position of the centre of mass and changes in the overall load on the animal. These ecologically important situations arise during gravidity, parturition/oviposition, feeding, load bearing and autotomy. How these ubiquitous changes shape the function of animals in their natural habitat will have profound impacts on survival, and are thus crucial for understanding the functional ecology of locomotion. We first discuss locomotor perturbations, with an emphasis on the duration associated with them. We then address how commonly studied modes of rapid mass changes (e.g. parturition, autotomy, feeding) perturb locomotion by examining the effects of natural and artificial changes in mass on locomotor performance, kinematics, kinetics and muscle function in terrestrial animals, with an emphasis on non-human vertebrates. After a detailed discussion of the functional ecology of rapid mass changes, we generate a framework for future studies, including predictions for why some animals are more robust to changes in mass.

ADDITIONAL KEYWORDS: autotomy – biomechanics – ecomechanics – loading – locomotion – mass – parturition.

INTRODUCTION

An animal's ability to move effectively is critical for survival, as locomotion plays a pivotal role in catching prey, escaping predators, foraging, mating and migrating. In their natural environment, animals encounter demands that can have diverse effects on the locomotor system, affecting their ability to perform these ecologically relevant tasks (Irschick & Garland, 2001). Here, we define any sudden change, internal or external, that alters the demand on an animal's locomotor system as a perturbation. Locomotor perturbations stem from several sources (Fig. 1), many of which result in a sudden shift in an animal's centre of mass and/or destabilizing locomotion that alters the mechanical demands and constraints on the locomotor system. Traditionally, perturbations have been explored

in the context of terrestrial animals negotiating complex terrain in their natural environments. For example, behavioural and neuromechanical responses to environmental perturbations have been demonstrated using obstacles (Birn-Jeffery & Daley, 2012; Olberding, McBrayer & Higham, 2012), a drop in substrate height (Daley & Biewener, 2006; Daley *et al.*, 2006), a decrease in surface roughness (i.e. a slip) (Clark & Higham, 2011), a change in surface compliance (Ferris, Liang & Farley, 1999) and unexpected lateral forces (Jindrich & Full, 2002) (Fig. 1). Recovery from these perturbations generally occurs within a single stride (Jindrich & Full, 2002; Daley & Biewener, 2006), suggesting that feedforward and intrinsic mechanics contribute to maintaining dynamic stability. Like these environmental perturbations, physical factors such as changes in body mass can exert unavoidable physical demands that also perturb locomotion (Taylor, Heglund & Maloiy, 1982; Garland, 1984; Higham & Irschick, 2013; Fig. 1). How rapid changes in mass

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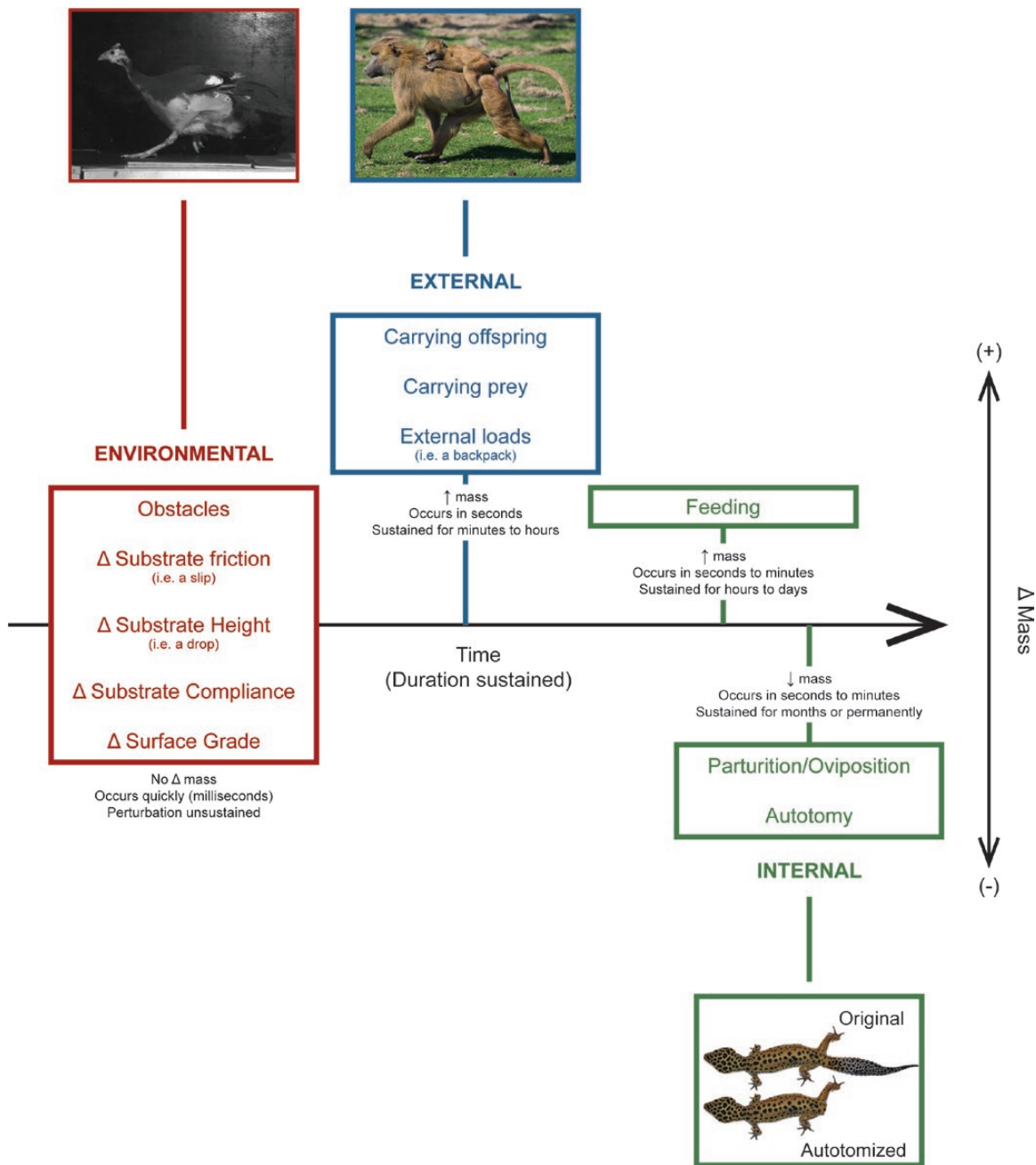


Figure 1. Proposed classification for locomotor perturbations. (A) Environmental perturbations rapidly alter an animal's centre of mass without changing mass. These occur very rapidly, thus requiring a quick recovery, but are not sustained changes. Image: Guinea fowl (*Numida meleagris*) experiencing a rapid change in surface friction. (B) External perturbations involve a load rapidly added onto an animal, which can be sustained for several hours. Image: Guinea baboon (*Papio papio*) carrying its young on its back. (C) Internal perturbations can involve a rapid gain or loss of mass. These changes also occur rapidly, but are sustained for an extensive amount of time. Image: Leopard gecko (*Eublepharis macularius*) before and after autotomy of the tail.

impact locomotor function and performance is poorly understood, however.

Body size and mass play a significant role in shaping the evolution of terrestrial animals, as the scaling of

structural elements with mass has been shown to have profound implications for how animals of different sizes move (Heglund, Taylor & McMahon, 1974; McMahon, 1975; Biewener, 1990, 2005). At the individual level,

organisms must also manage the demands imposed by changes in mass that occur throughout their lifetimes. Intra-individual body mass changes are ubiquitous and occur in response to a range of behavioural and physiological factors. These changes can also occur over a range of temporal scales (Fig. 1). Mass change is typically a gradual process occurring over a period of months (e.g. pregnancy) or years (e.g. ontogeny). However, mass can also be gained rapidly, such as when an infant attaches to a parent, or lost quickly, such as during parturition or autotomy (voluntary loss of an appendage). In these examples, the time an individual has to compensate for the change in mass is significantly reduced compared to gradual shifts, and mass loss can be quite significant. For example, short-horned lizards can lose up to 70% of their body mass during parturition (Powell & Russell, 1991). In comparison, ostriches will lay up to ten eggs at a time, which reflects approximately 10% of their body mass (1.5 kg per egg; Ar, Rahn & Paganelli, 1979). Rapid mass changes thus require rapid compensation in order to correct for shifts in the individual's centre of mass, relative muscle mass and loading on the musculoskeletal system. It is likely, given the importance and ubiquity of these events, that animals have undergone evolutionary changes that favour the ability to adjust to these rapid alterations.

The purpose of this review is to reveal how rapid mass changes affect animals (with a focus on non-human animals) and how these animals overcome the functional challenges associated with locomotion that occur with the change. We utilize what is already known on how animals respond to locomotor perturbations that occur from environmental changes to predict how animals might be responding to the physical perturbation that occurs with a rapid change in mass. In addition, we integrate information regarding the relationships between mass changes and locomotion across diverse taxa, and use this to generate perspectives for future studies on the skeletal, mechanical, neural and muscular responses to rapid mass change. By understanding the functional consequences and adaptations to rapid changes in mass, an evolutionary framework can be used to determine how selective pressures have shaped these responses.

RAPID MASS CHANGE AS A LOCOMOTOR PERTURBATION

Aside from terrain disturbances, rapid perturbations also occur from external and internal alterations of mass (Fig. 1). External mass changes involve an added load to an animal, such as carrying offspring,

prey or various objects in the environment (Lighton, Bartholomew & Feener, 1987). Although our focus is on vertebrates, it is worth noting that some beetles may be capable of carrying up to 850 times their body mass (Kram, 1996). Losing mass usually requires an internal physiological mechanism, such as when a lizard autotomizes its tail (Arnold, 1984) or gives birth to young (Powell & Russell, 1991). A commonality between environmental perturbations and rapid changes in mass is the sudden onset of the event. Slipping on a surface following a habitat transition and suddenly carrying or losing a load all occur within seconds or milliseconds. However, a key difference between an environmental perturbation and a rapid mass change perturbation is the duration over which the perturbation is sustained. Although occurring suddenly, mass changes can persist and must be accompanied by longer term shifts in neural control and mechanics (Jagnandan, Russell & Higham, 2014). This is in contrast to sudden environmental perturbations, which although potentially catastrophic, typically go away as quickly as they appear. For these cases, the ability to reflexively recover is paramount, but long-term control shifts are probably not necessary.

Perturbation experiments are useful for determining the control strategies that animals use in response to a sudden change. Generally, these experiments aim to rapidly displace an animal's centre of mass to observe the its response as it attempts to return to a normal locomotor cycle (Jindrich & Full, 2002). This may require some sensory input from the perturbation (e.g. mechanoreceptors sensing a change in substrate height) leading to a shift in neural signalling and a reactive motor response that alters limb kinematics or neuromuscular activity (Fig. 2). Mechanisms for intrinsic mechanical stability may also play a role, allowing for perturbation recovery that occurs more quickly than explained by short-latency reflexes. Mass changes that are concentrated in one region of the body can significantly alter the distribution of mass within an individual in a similar manner (Jagnandan *et al.*, 2014), and can thus prove useful for understanding how animals recover from different perturbations that occur naturally. Alternatively, sensory input before encountering the perturbation (e.g. visual cues) may lead to a proactive motor response to prevent a destabilizing motion (Fig. 2). In mass change perturbations, it is unclear if control is primarily proactive or reactive. Can animals sense an upcoming change in mass and make the necessary adjustments in preparation? Rapidly changing mass presents a notable perturbation that warrants neuromechanical compensation (or preparation) by the locomotor system.

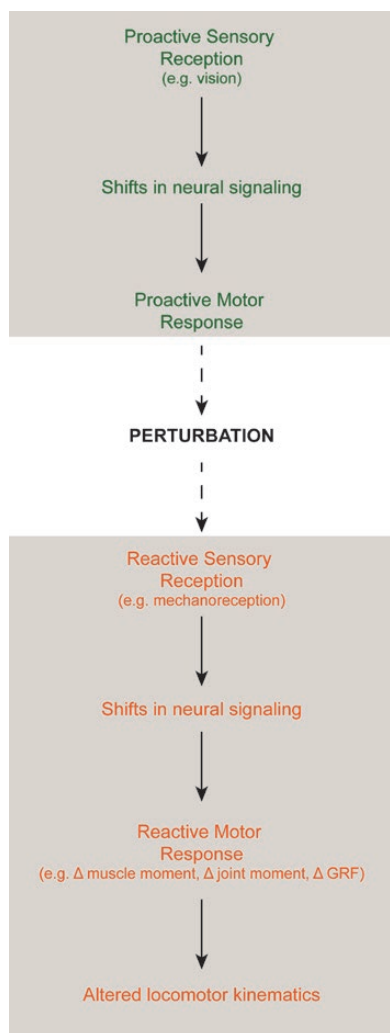


Figure 2. Proactive and reactive control of perturbations. Proactive control requires an initial sensory input before encountering the perturbation, such as a visual cue, which leads to a proactive motor response in preparation for the event. Reactive control occurs after experiencing the perturbation and instead involves a recovery phase consisting of sensing the perturbation and adjusting the locomotor system accordingly. Control strategies to maintain dynamic stability during a perturbation can be proactive, reactive or both.

MECHANICAL DEMANDS AND CONSEQUENCES OF RAPID CHANGES IN MASS

The shape and size of an animal largely determine its movement due to the intricate relationship between locomotor mechanics and posture (Biewener, 1989b, 1990, 2005; Dick & Clemente, 2017). During terrestrial locomotion, an animal exerts a force onto the ground with its limbs, generating a ground-reaction force

(GRF). This force generates moments (or torques) at the limb joints, which must be balanced by a force generated by the muscles at those joints to support the body and sustain locomotion (Fig. 3; Biewener, 2003). These relationships are demonstrated in the following equations (eqns 1, 2):

$$\text{GRF} \times R = F_m \times r \quad (1)$$

$$M_j = M_m \quad (2)$$

The joint moment (M_j) is equal to the product of the GRF and R (the moment arm of the GRF, or the length between the joint and line of force acting on that joint). The muscle moment (M_m) that balances the joint moment is equal to the product of F_m (the muscle force) and r (the muscle moment arm). Because the ground-reaction force is proportional to body mass, it is not surprising that peak ground-reaction forces increase in direct proportion to body mass (Farley, Glasheen & McMahon, 1993). Increasing the ground-reaction force results in a greater joint moment, thus requiring more force from the limb muscles to support a greater mass (assuming a fixed muscle moment arm) (Biewener, 1989b, 2005).

However, increasing the magnitude of muscle force generates greater stresses on the bones and tendons (Biewener, 1990), which can increase the risks of injury. An alternative for supporting increased mass is to shorten the moment arm of the ground-reaction force by adopting a more erect posture (Fig. 3). This lowers the muscle force requirement for supporting the joint and avoids potentially damaging stresses (Biewener, 1989b, 1990, 2005). This shift in posture increases the animal's effective mechanical advantage (EMA), defined as the ratio of the muscle moment arm to the ground-reaction force moment arm (Biewener, 1989b; eqn. 3):

$$\text{EMA} = r / R = \int \text{GRF} / \int F_m \quad (3)$$

Effective mechanical advantage generally increases with body size, as larger animals are observed to have more upright postures, reducing the magnitude of muscle force required to support the animal's mass (Biewener, 2005). However, this posture is hypothesized to limit manoeuvrability and acceleration compared to animals that support smaller masses while assuming more sprawled or crouched stances (low effective mechanical advantage) (Biewener, 1983, 1989a, b; Dick and Clemente, 2017).

The relationships between mass, effective mechanical advantage, muscle force and locomotor ability are generally considered in the evolution of terrestrial locomotion. However, these principles are

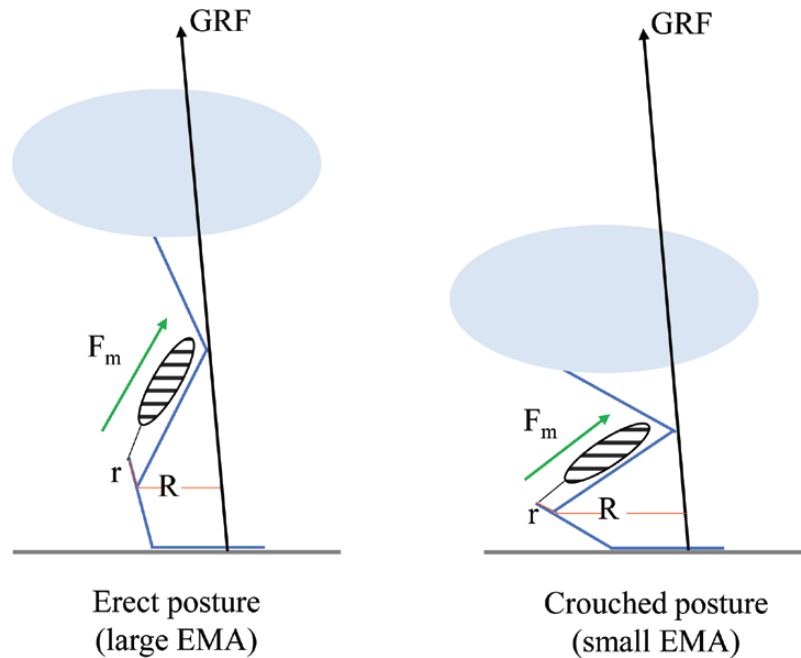


Figure 3. Limb effective mechanical advantage in erect and crouched postures. Effective mechanical advantage is defined as the ratio of the muscle moment arm (r) to the ground-reaction force moment arm (R). Assuming a fixed muscle moment arm, increasing the length R by assuming a crouched posture decreases the effective mechanical advantage. To support this posture, the ground-reaction force (GRF) must decrease (by reducing the animal's mass) or the muscle force (F_m) must increase. (Figure adapted from [Biewener, 2005](#).)

also applicable to mass changes that occur at the individual level. When mass is added to an individual, the ground-reaction force must increase, consequently increasing the ground-reaction force moment and muscle moment at the joints if no postural shifts occur ([Fig. 4](#)). Thus, an individual gaining mass can be problematic in terms of potential injury due to damaging stresses when muscle force increases. In natural systems, mass can increase substantially when animals carry loads in the form of prey, young or materials. Whether these animals change their posture to reduce muscle force and consequent injury risk is a topic to be explored.

Can what is known about gaining mass be used to understand how animals respond to losing mass? When the ground-reaction force and joint moment decreases with the reduced mass, does effective mechanical advantage decrease as well ([Fig. 4](#))? This would generate a more crouched posture, which is suggested to increase the mechanical advantage for horizontal ground-reaction force production, allowing for greater manoeuvrability ([Walter, 2003](#)). Alternatively, if no postural shift occurs, muscle force would be reduced, making locomotion more efficient.

Autotomy, a predator-escape strategy defined by a voluntary self-amputation of an appendage in response to a stimulus, can involve a significant loss

of mass in seconds. Autotomy typically takes place in the form of tail loss in vertebrates ([Bateman & Fleming, 2009](#); [Higham, Russell & Zani, 2013](#)), and the tail can usually be regenerated ([Arnold, 1984](#); [Bellairs & Bryant, 1985](#)). In leopard geckos (*Eublepharis macularius*), autotomy of the tail resulted in geckos employing a more sprawled posture to account for a 22% reduction in mass ([Jagnandan *et al.*, 2014](#)). This posture gradually recovered to the pre-autotomy state as the tail regenerated and mass was regained. These postural shifts may reflect the relationships between mass and effective mechanical advantage in response to altered muscle force requirements, as effective mechanical advantage may be reduced to augment manoeuvrability or stability. Direct measures of manoeuvrability (the ability to rapidly change velocity direction) and stability (the ability to recover from a perturbation) before and after autotomy are required to test this hypothesis. Parturition and oviposition also involve a rapid reduction in mass as eggs or young are released, although postural effects are undocumented. However, the physiological costs associated with recovering from gravidity is probably a factor in an animal's locomotor response ([Olsson, Shine & Bak-Olsson, 2000](#)).

External loads added to turtles ([Marvin & Lutterschmidt, 1997](#); [Wren, Claussen & Kurz, 1998](#)),

geckos (Irschick *et al.*, 2003), horses (Hoyt, Wickler & Cogger, 2000; Wickler *et al.*, 2001) and other mammals (Baudinette & Biewener, 1998; Young, Patel & Stevens, 2007) demonstrate similar locomotor impacts across these taxa. Generally, terrestrial quadrupeds exhibit reductions in stride length, stride frequency and/or duty factor when mass is added. These kinematic changes could be related to altered demands for muscle force, mechanical work and other costs associated with body weight support. One would also predict that rapidly altering mass may have a dramatic impact on balance and stability. Perhaps most significant is any rapid change in mass that alters an animal's centre of mass (Fig. 4). Many animals carry their young or prey in their mouth, adding substantial mass to the cranial end of the body and shifting the centre of mass in that direction. A loss of caudal mass, such as occurs in tail autotomy, should have a similar effect. These centre of

mass shifts alter the distribution of mass and change the contributions of each set of limbs to support and propulsion (Arnold, 1984; Lee *et al.*, 2004; Lee, 2011; Walter and Carrier, 2011; Kilbourne & Carrier, 2016). A large centre of mass shift could also generate a toppling moment that would alter locomotor forces and kinematics (Jagnandan *et al.*, 2014).

Locomotor performance is a critical ecological factor that often relates to fitness, and the effects of mass changes on locomotor performance are well documented (Table 1). Sprint speed and endurance usually increase when mass is lost (Bauwens & Thoen, 1981; Cooper *et al.*, 1990; Qualls & Shine, 1998; Wapstra & O'Reilly, 2001; Finkler, Sugalski & Claussen, 2003), due to reduced force requirements for support and propulsion (Scales & Butler, 2007). In contrast, performance decreases in recently fed animals (Huey *et al.*, 1984; Martin, 1996) and in animals carrying

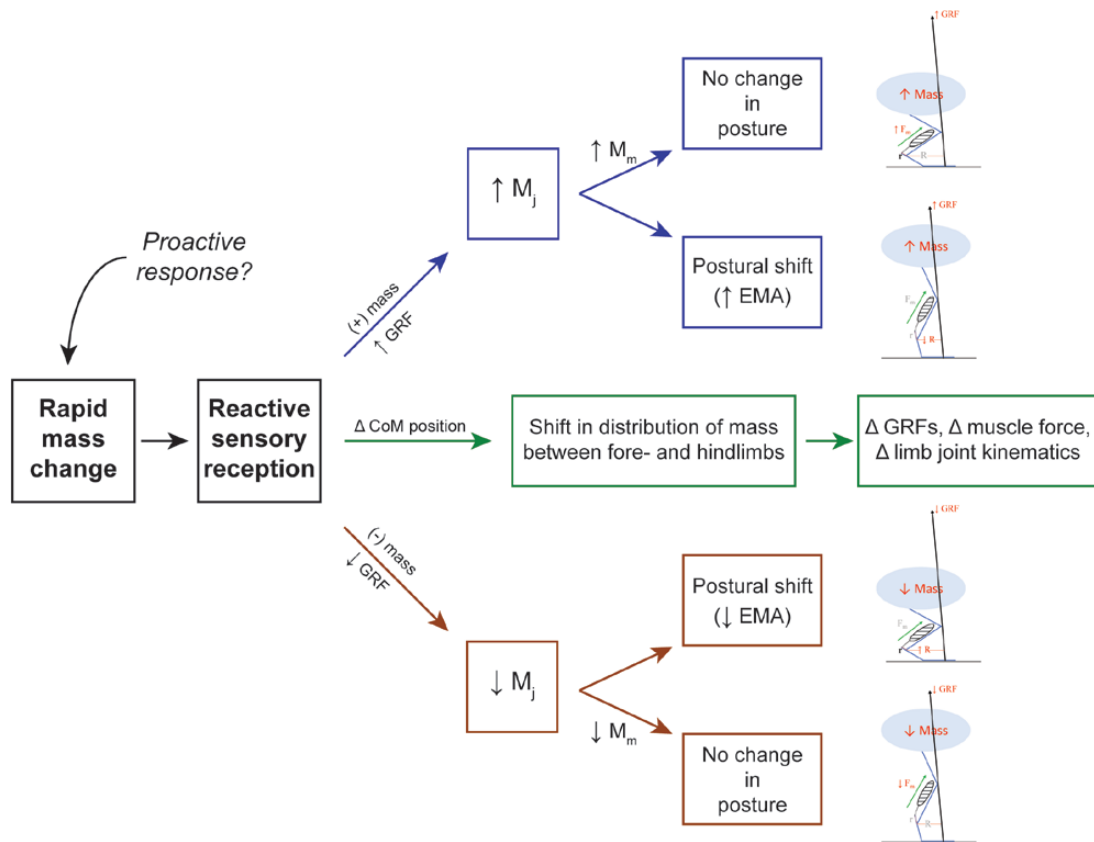


Figure 4. Motor responses to rapid mass changes. Increases in mass (blue) increase ground-reaction forces (GRFs), which increase the joint moments (M_j). To compensate for change, the limb muscles can generate more force, thereby increasing the muscle moment (M_m), or the animal can increase its limb effective mechanical advantage (EMA) and switch to a more erect posture. When mass is lost (orange), GRFs decrease, reducing M_j . The muscles can generate less force to lower M_m and make locomotion more efficient, or the animal can decrease its limb EMA and switch to a more sprawled posture and increase its base of support. Mass changes that shift the centre of mass (CoM) (green) alter the distribution of the mass between the limbs, which can lead to changes in GRFs, muscle force and kinematics in either or both sets of limbs, thus impacting posture and locomotor mechanics.

Table 1. Effects of mass change on locomotor speed

Type of mass change	Mass gain or loss	Change in speed	Taxon	References
Autotomy	Loss	Decrease	Lizards	Anderson <i>et al.</i> (2012) , Ballinger <i>et al.</i> (1979) , Chapple & Swain (2002) , Chapple <i>et al.</i> (2004) , Cooper & Smith (2009) , Cooper <i>et al.</i> (2004, 2009) , Cromie & Chapple (2012) , Downes & Shine (2001) , Formanowicz <i>et al.</i> (1990) , Goodman (2006b) , Kelehear & Webb (2006) , Lin & Ji (2005) , Lin <i>et al.</i> (2006) , Martin & Avery (1998) , McConnachie & Whiting (2003) , Punzo (1982)
		Increase	Snakes Lizards	Jayne & Bennett (1989) Brown <i>et al.</i> (1995) , Daniels (1983) , Daniels (1985) , Medger <i>et al.</i> (2008)
Energy storage	Gain	Decrease	Mammals	Young <i>et al.</i> (2007)
External loading	Gain	Decrease	Lizards	Shine (2003)
			Mammals	Lee <i>et al.</i> (2004) , Wickler <i>et al.</i> (2001) , Young <i>et al.</i> (2007)
Feeding	Gain		Turtles	Marvin & Lutterschmidt (1997) , Wren <i>et al.</i> (1998) , Zani & Claussen (1995)
		Decrease	Lizards	Huey <i>et al.</i> (1984) , Martin (1996) , Shine (2003)
Parturition/oviposition	Loss		Snakes	Ford & Shuttlesworth (1986) , Garland & Arnold (1983) , Mehta (2006)
		Decrease	Lizards Salamanders	Qualls & Shine (1997) Finkler <i>et al.</i> (2003) , Wapstra & O'Reilly (2001)
Pregnancy/gravidity	Gain		Lizards	Bauwens & Thoen (1981) , Cooper <i>et al.</i> (1990) , Le Galliard <i>et al.</i> (2003) , Qualls & Shine (1998) , Scales & Butler (2007) , Sinervo <i>et al.</i> (1991)
		Decrease	Snakes Lizards	Plummer (1997) , Seigel <i>et al.</i> (1987) Garland (1985) , Goodman (2006a) , Husak (2006) , Le Galliard <i>et al.</i> (2003) , Olsson <i>et al.</i> (2000) , Shine (2003)

loads ([Hoyt *et al.*, 2000](#); [Wickler *et al.*, 2001](#); [Kuo, Gillis & Irschick, 2011](#)). Greater variation is observed when mass is lost via tail autotomy, however, probably due to the functional role of the tail in different species (references listed in [Table 1](#)).

UTILIZING MASS CHANGE TO UNDERSTAND THE NEUROMECHANICS OF LOCOMOTION

Considering the importance of muscles in driving locomotion and supporting body weight ([Marsh, 1999](#)), surprisingly little data are available on how the limb muscles adapt to changes in loading. This is despite the fact that the mechanical actions of muscles depend on the loads resisting motion. Are locomotor muscles

capable of rapidly changing their function in the face of mechanical disturbances, such as rapid mass change? Are species that commonly undergo large and rapid changes in mass better at altering their neural control in the face of changing mass? If not, how long does it take to alter neural control after a perturbation, and what mechanisms might underlie differences in this time period?

We predict that unique patterns of muscle function will emerge when animals experience a rapid change in mass, including changes in operating lengths, force generation and the relative timing of activation among different limb muscles. To make predictions about shifts in muscle function with changes in mass, we draw from the literature on rapid perturbations. Recent work has focused on neuromuscular strategies

for running over uneven terrain. One possibility is that the nervous system is not involved in the rapid response to a perturbation, but rather the dynamically stable mass-spring behaviour of the locomotor system may result in passive leg adjustments (Daley, 2008). In other words, the pattern of locomotion in terrestrial vertebrates might be robust enough to adjust without higher control.

However, many animals probably use a reactive strategy, in which muscle activation is altered following the reception of sensory information from the perturbation (Fig. 4). In humans, a slip perturbation leads to a rapid shift in neuromuscular control in order to recover balance. For example, Marigold & Patla (2002) found that, in humans, mean muscle onset latencies ranged from 146 to 199 ms, indicating that polysynaptic reflexes were utilized to recover balance during a slip. In running birds, navigating an obstacle requires an 80% increase in electromyography (EMG) intensity by the lateral gastrocnemius (LG) in comparison to level locomotion (Daley & Biewener, 2011). This is in contrast to the perturbations involving a sudden drop, in which no significant change in LG EMG activity was observed (Daley, Voloshina & Biewener, 2009). Given that the transmission delay for the stretch reflex of the gastrocnemius is about 6 ms, this suggests that a monosynaptic stretch reflex is involved. This alteration in control highlights the ability of the sensorimotor system to adapt to changing conditions.

The same is expected for a sudden change in body mass. Unlike environmental perturbations, in which vision might play a role in providing sensory input prior to the perturbation, changes in mass will convey internal proprioceptive information. It is likely that articular mechanoreceptors are important for determining the magnitude of mass change. For example, a sudden drop in body mass after losing the tail will alter the amount of knee and ankle extension (probably more than elbow and wrist extension, due to the position of the tail), assuming that muscle activation remains the same. This altered joint position will be reported to the central nervous system via joint mechanoreceptors (Riemann & Lephart, 2002). The animal can then reduce the level of neuromuscular activation, returning the joint angular excursion to normal. Whether this occurs in animals that exhibit caudal autotomy is not known, but forms a prediction for future studies.

Much of what is known about neuromuscular changes in relation to changes in mass stems from artificial load studies. As load is added to animals, a common strategy is to increase duty factor and decrease stride length and frequency, suggesting a shift in motor unit recruitment from propulsive to supportive muscles,

perhaps to enhance stability. Ellerby & Marsh (2006) measured muscle energy use in Guinea fowl (*Numida meleagris*) carrying external loads, which increased under all experimental loading conditions, but differed between individual muscles. In trunk-loaded birds, most increases in energy use were restricted to stance-phase muscles, while distally loaded birds exhibited increases in both stance- and swing-phase muscles. Trunk loads also altered the contractile patterns of hind limb extensor muscles (indicated by enhanced stretch activation early in stance), as well as the intensity of muscle activation, demonstrated by an increase in the intensity of EMG signals from the muscles (McGowan *et al.*, 2006). These findings provide further evidence for the increased demand on the muscles responsible for support and stability when mass is added, and may explain the kinematic changes observed in other species.

Aside from these data, studies that quantify *in vivo* muscle function in response to added or decreased loads are rare. Additionally, no data exist on how the locomotor muscles respond to natural changes in mass, such as those that occur with gravidity and autotomy. Some of the most significant demands ever placed on the neuromuscular system of non-human animals might be during a rapid gain or loss of mass, thus reflecting a critical gap in our understanding of how muscles can respond to change. This essentially addresses how plastic muscle function can be over short periods of time, in contrast to the large body of research examining atrophy and hypertrophy of muscles over longer durations (Edgerton *et al.*, 2002).

THE FUNCTIONAL ECOLOGY OF RAPID CHANGES IN MASS

Much of what is known about perturbations involves artificial situations. For example, Clark & Higham (2011) examined how Guinea fowl respond to a sudden decrease in the friction of the substrate. Although informative, this reflects an unnatural situation. We propose that examining natural perturbations, such as parturition and tail autotomy, will not only provide sensorimotor and mechanical insight into locomotor stability, but will also provide information regarding the evolution and ecology of perturbation recovery. Many of the main causes of rapid mass changes are events critical to survival, whether it is giving birth to young or surviving a predator–prey interaction. These are obviously under strong selection, which means the responses to these changes in mass are also probably under strong selection.

Evolution has shaped the ability of animals to deal with natural perturbations. We have yet to tap

into this information to understand the ecology and evolution of neuromuscular and mechanical responses to destabilizing events. By examining terrestrial vertebrates that exhibit an array of responses to natural perturbations, we can tease apart the strategies that may enhance fitness. By doing so, we can identify phylogenetic constraints and perhaps multiple solutions to a similar problem (i.e. many-to-one mapping). Lizards may be ideal in this regard, as tail autotomy is widespread and varies considerably among different lineages. The shape and size of the tail also varies dramatically, providing a great opportunity to examine the role of mass reduction in stability. The probable variation in tail function across lizards will also translate into unequal impacts on the animal following tail loss. Thus, multiple strategies for dealing with this natural perturbation are very likely, but understudied. Below are some key questions that should guide future studies.

FUTURE DIRECTIONS

Rapid mass change is a ubiquitous phenomenon associated with key ecological factors, such as reproduction, autotomy, feeding and load bearing. Despite the commonality of this occurrence, many questions about how animals compensate for changes in mass remain unanswered. Here, we present some of these questions for future study, as well as predictions for each.

WHAT ARE THE ROLES OF RAPID MASS CHANGES IN POPULATION DYNAMICS?

Moving beyond the level of the individual, rapid changes in mass can impact community structure and processes. Changes in locomotion due to rapid changes in mass will have widespread impacts on behaviours that are important for survival, such as dispersal, foraging, mate selection and competition. Dispersal behaviour is defined as any movement of an animal that might result in gene flow across space (Ronce, 2007), and can involve both natal and breeding dispersal. Both of these incorporate a departure stage, a vagrant stage and a settling stage (Ronce, 2007). Therefore, dispersal plays a key role in ecology and evolution by impacting population dynamics. Given the important role of locomotion, perturbations that alter the mass of an animal will probably impact dispersal, with decreases in locomotor performance possibly reducing the success of a dispersal event. Indeed, body mass plays a role in dispersal distance (Jenkins *et al.*, 2007), although it is not clear how rapid changes in mass might impact dispersal on a finer scale.

An often-overlooked context of locomotor performance is that associated with social status and, like dispersal, can involve long bouts of locomotion. Dominance probably depends on acquiring and defending large territories, but will also involve encountering more mates (Robson & Miles, 2000). Dominance and locomotor performance are often correlated (Garland, Hankins & Huey, 1990; Robson & Miles, 2000), and sprint speed can be strongly correlated with territory size and the number of potential mates (Peterson & Husak, 2006). Given the widespread impact of mass change on locomotor performance (McElroy & Bergmann, 2013), it is likely that rapid mass changes are a mechanism underlying larger scale shifts in population dynamics.

Predator–prey interactions, as discussed earlier, are clearly impacted by body size. When escaping from a predator, the initial critical factor is acceleration, and it is often more important than maximum speed in dictating the outcome of an interaction (Huey & Hertz, 1984). These interactions are on a very short time scale, but foraging can last much longer. Therefore, it is not surprising that endurance performance is correlated with foraging behaviour. For example, closely related lacertid lizards in the Kalahari Desert of Africa exhibit considerable diversity in their foraging behaviour (Huey & Pianka, 1981). Some are sit-and-wait predators that move 10–15% of the time, whereas others are wide-ranging foragers and move 50–70% of the time. In these lacertid lizards, endurance capacity (measured on a treadmill) is greater for the widely foraging species, whereas sprint performance is greatest for the sit-and-wait predators (Huey *et al.*, 1984). Thus, it appears that foraging behaviour and locomotor performance are tightly linked. As an extension, it is likely that rapid changes in mass will have a strong impact on foraging behaviour. We predict that this might simply emerge as enhanced or depressed locomotor performance that is directly caused by the change in mass, but might also drive a shift in foraging strategy to compensate for the change in mass.

HOW ARE PERFORMANCE, MANOEUVRABILITY AND STABILITY IMPACTED BY RAPID CHANGES IN MASS?

We must first consider what is meant by *how good* an animal is at coping with changes in mass. The most direct way to determine the effects of mass change on locomotion is to measure locomotor performance before and after the change occurs. This can include performance measures such as sprint speed, endurance or acceleration (Irschick & Higham, 2016). Elevated performance after the rapid change in mass would be most important for animals that need

to escape a predator following the change, such as when a lizard autotomizes its tail (Dial & Fitzpatrick, 1984). We predict several outcomes that depend on the ecology and locomotor mode of the animal. First, if one looks only at the sensitivity (relative change in performance), then we would predict that the highest performers before the mass change would suffer the most from this internal perturbation. In addition, those species that already deal with a variety of conditions in their natural habitat will probably be able to readily overcome the challenges associated with changes in mass. In other words, those species or individuals that are inherently flexible will probably be less sensitive. In addition to the measures listed above, which may be less relevant for an animal that is carrying a load, the total load that the animal can carry without failure/injury may be a better determinant of how well the animal deals with the mass change.

Stability and manoeuvrability are likely to be impacted by shifts in the mass distribution of an animal after a rapid gain or loss of mass. The relative amount of mass loss or gain will probably determine the degree to which stability is impacted. Dynamic stability incorporates several hierarchical levels, including individual neurons, neural networks, muscle systems and behaviours (Full *et al.*, 2002). Therefore, more information than just forces and motions are needed to capture the ability of an animal to remain stable. Given that stability is often measured as the ability to recover from an external perturbation, one must consider all of the changes that accompany gains and losses of mass. As with tail autotomy, a large shift in the centre of mass (and overall body mass) will potentially impact the ability of mechanical sensory receptors in the limbs to respond to external perturbations. It is likely that the level of stability preceding the shift in mass will also influence stability following the internal perturbation. Future studies that examine dynamic stability following rapid gains and losses of mass will help answer this question, but may also provide fundamental insight into how systems are controlled and what aspects of animal morphology influence stability.

The ability to execute turning manoeuvres will depend on an animal's ability to change heading. This depends on the impulse that is generated perpendicular to the direction of movement relative to the animal's forward momentum (Jindrich & Full, 1999; Full *et al.*, 2002). Both forward velocity and body mass will impact the change in heading, assuming a comparable perpendicular impulse. Increases in body mass and forward velocity will result in a decrease in the change in heading. Therefore, rapid decreases in body mass, as occur during tail autotomy in lizards, may actually elevate the ability to execute turning manoeuvres. In

addition, tail autotomy will also decrease the mass located far from the point of rotation during a turn, and this will lower the rotational inertia (Carrier, Walter & Lee, 2001). This is hypothesized to increase turning agility, adding to the prediction that turning ability might increase following a reduction in mass. Adding mass at the location of the centre of mass will not impact rotational inertia, but would decrease the ability to change heading (if all else is equal). Future work should test these predictions using natural (e.g. autotomy) or artificial (e.g. added mass) manipulation experiments.

WHY MIGHT SOME SPECIES ADOPT A SPECIFIC STRATEGY IN RESPONSE TO MASS GAIN OR LOSS?

When a terrestrial animal gains or loses mass, ground-reaction forces will also increase or decrease, respectively. To adjust for the resulting change in the joint moment, animals can either alter the magnitude of muscle force for support in the limbs or they can change their posture to alter the length of the ground-reaction force moment arm (Fig. 4). In the case of a loss of mass, decreasing muscle force would be the more efficient solution, but decreasing effective mechanical advantage may benefit balance, manoeuvrability and/or stability (although this remains to be tested). What determines which of these strategies is utilized? Ecological and morphological factors may play a role, as arboreal animals probably have a greater need for balance and stability than efficiency (Cartmill, 1985). The starting mass and/or posture of the animal are also likely to have an effect. An animal that normally assumes a hyper-sprawled posture may be less likely to lower its effective mechanical advantage even more after losing mass than an animal with a more erect posture originally.

HOW DO ANIMALS ALTER THEIR NEURAL CONTROL PRECEDING OR FOLLOWING RAPID MASS CHANGE?

Environmental perturbations often provide a visual cue that allows an animal to alter its neural control in preparation for the obstacle, drop, slip, etc. Rapid mass changes, however, are less likely to include a visual cue. In most cases, neural control is more likely to be altered following a rapid change in mass when joint mechanoreceptors sense the change and report this information to the central nervous system. The mechanisms by which animals receive and process information on how much they weigh are reviewed elsewhere (Duysens, Clarac & Cruse, 2000; Schilder, 2016). When mass is rapidly added to an animal, neuromuscular activation is predicted to immediately increase in order to retain posture and support the

added mass, and the opposite should occur if mass is rapidly lost. For the rapid loss of mass, a reduction in muscle activity (at least in the hind limbs) might be needed to avoid an unwanted increase in muscle force that could ultimately result in unstable movements (e.g. pitching the head down). When the centre of mass is shifted, the timing and amplitude of EMG activation in the limbs are also predicted to change as the distribution of mass between the fore- and hind limbs is altered, but more research is needed to identify the shifts in centre of mass position as mass is gained or lost.

Many forms of changes in mass involve a sudden increase or decrease that is sustained over a long period of time (e.g. tail autotomy and parturition). Unlike environmental perturbations that typically last only seconds or less, these changes in mass require a semi-permanent or permanent alteration in neural control. Motor unit recruitment, intensity of activation and timing of activation could all change permanently with the morphological change. For example, a rapid loss of mass is predicted to necessitate a reduced intensity of activation in load-bearing muscles for stability and energetic efficiency. Specifically, which muscles respond to these changes in demand should also be addressed. Tail autotomy is an ideal system for examining long-term changes given that the lost mass is eventually regained through regeneration (Jagnandan *et al.*, 2014). Another aspect of long-term adaptation to the loss of mass might be atrophy of limb muscles. Losing approximately 30% body mass almost instantaneously might begin a gradual reduction in propulsive muscle mass over time, analogous to a hind limb suspension model in rodents (Anderson, Almeida-Silveira & Pérot, 1999), although not as extreme. This might, in turn, alter the activation of the muscles over time.

HOW HAVE THE RELATIONSHIPS BETWEEN RAPID CHANGES IN MASS AND LOCOMOTION EVOLVED?

As outlined above, a key group for examining the evolution of responses to rapid changes in mass is lizards. When examining rapid changes in mass in an evolutionary context, a group that naturally changes mass is needed. Many lizards will autotomize their tail at some point during their life. In some groups, this number can approach 70–80% of individuals (Vitt & Zani, 1997). In such cases, we propose lizards will exhibit an innate ability to alter their neuromuscular responses to changes in mass, and that this ability will exceed lizards that do not exhibit autotomy. In other words, selection should favour the flexibility to deal with large-scale changes in mass. Leveraging the variation in propensity for autotomy across

lizards will enable one to determine what aspects of behaviour, morphology and physiology have evolved to compensate for rapid changes in mass, which would provide valuable insight into animal function. As noted by Full *et al.* (2002), function will be revealed when animals are subjected to perturbations. Therefore, evaluating natural internal perturbations will probably reveal evolutionary changes in function. The benefits of such knowledge will be far reaching, and could contribute to the formation of dynamically stable robots that change mass, such as when picking up or dropping off heavy objects.

CONCLUSIONS

Gaining and losing mass quickly has dramatic impacts on animal locomotion, muscle function and injury. However, very little is known about the role of rapid mass change in dynamic non-human locomotion, and how the ability to cope with these changes has evolved. We propose that tail autotomy in lizards will be an exceptional system for examining the role of rapid mass loss, given that it is a naturally occurring perturbation and is ultimately overcome through regeneration. The neuromuscular and mechanical alterations (both short- and long-term) following rapid changes in mass will illuminate a broader understanding of plasticity in physiological and biomechanical systems, and will provide a foundation for evolutionary studies.

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