

On the use of body mass measures in severity assessment in laboratory passerine birds

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Abstract

Criteria for assessing the severity of scientific procedures in laboratory rodents include the loss of body mass. However, guidance is limited for passerine birds and application of criteria developed for mammals risks poor welfare decisions. Here, I ask whether, and how, body mass criteria could be incorporated into laboratory welfare assessment of passerines. Passerine birds strategically adjust their body mass to minimise combined mortality risk from starvation and predation. A systematic literature review found that strategic mass changes can be sizeable (sometimes > 10%) even over short timescales. Many aspects of a bird's current or past environment, including husbandry and experimental procedures, may alter perceived starvation or predation risks and thus drive strategic mass change via evolved mechanisms. Therefore, body mass criteria used for rodents may be too stringent for passerines, potentially leading to over-estimated severity. Strategic mass changes might obscure those stemming from experimental interventions yet could also offer insights into whether birds perceive an intervention or altered husbandry as a threat. Mass criteria for severity assessment should be species- and context-specific in order to balance needs for refinement and reduction. To guide the development of appropriate criteria, a future research priority is for greater data collection and sharing based on standardised routine monitoring of mass variation under a representative range of husbandry conditions and procedures.

Keywords: animal welfare, avian model, body mass, mass regulation, passerine, severity

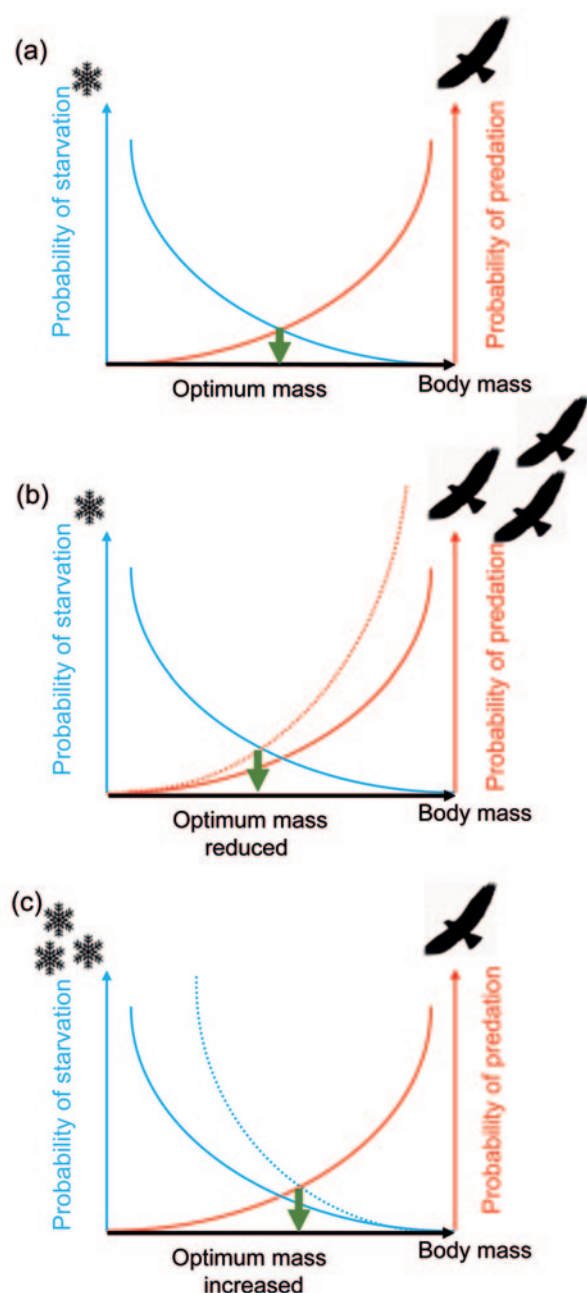
Introduction

A key component of laboratory animal welfare and a legislative requirement in many countries is the assessment and minimisation of 'severity' during planning and undertaking scientific procedures (eg UK Animals [Scientific Procedures] Act 1986; EU Directive 2010/63/EU). A severity limit sets an absolute maximal limit to any pain, suffering or lasting harm experienced (Home Office 2014). General severity assessment guidelines have been developed for laboratory rodents, based on physiological parameters and clinical signs (Jones *et al* 1996). However, there is a paucity of guidance for passerine birds despite them being important animal models (Bateson & Feenders 2010; Schmidt 2010a,b; Scott *et al* 2010; Mello 2014; Clayton & Emery 2015; Mori & Wada 2015; Flores-Santin & Burggren 2021). Applying existing criteria developed for rodents to passerines could result in poor welfare decisions and poor science (Schmidt 2010a,b). Here, I ask whether, and how, body mass measures could offer a useful component for severity assessment in passerines.

Mass is commonly used in severity assessment in rodents (Wallace *et al* 1990; Jones *et al* 1996; Ullman-Culleré & Foltz 1999; LASA/APC 2008; European Commission 2012; Home Office 2014). An advantage is that measures are objective and straightforward to monitor. Guidelines for rodents suggest mass loss of up to 10% over a seven-day period to rate as 'mild' severity, while 10–25% is 'moderate' (Jones *et al* 1996). Mass loss of 20% compared to baseline has been adopted as a convention for a humane end-point (European Commission 2013). As in rodents, mass loss in birds can be a symptom of ill-health (eg Bonneaud *et al* 2003; Garamszegi *et al* 2004). Guidance for refinement in the use of birds also lists mass-loss as a component of health monitoring (Hawkins *et al* 2001). Mass changes have been used as a welfare indicator in zebra finches (*Taeniopygia guttata*) (Krause & Ruploh 2016; Yamahachi *et al* 2017).

However, the biology of mass-regulation in birds may differ markedly to mammals due to fundamental differences in energetic physiology and the requirements of flight (Ricklefs *et al* 2018). My objective is to consider the biology and ecology of mass-regulation in passerine

Figure 1



This illustrates the theory of strategic mass-regulation whereby (a) the starvation-predation trade-off implies animals should adopt a body mass (green arrow) which minimises the joint probability of starvation (blue solid line) and predation (red solid line), (b) carrying greater body mass increases the risk of predation, hence when predation risk in the environment increases (dotted red line), the optimum body mass declines and (c) carrying greater body mass reduces the risk of starvation, hence when starvation risk in the environment increases (dotted blue line), the optimum body mass increases.

birds, and whether mass loss criteria are appropriate for severity assessment. I discuss the theory of strategic mass-regulation and systematically review the magnitude of strategic mass changes observed in passerines in response to manipulations of starvation or predation risks

(for review methods, see Appendix 1). I consider possible proximate mechanisms and discuss how strategic mass-regulation may be relevant in laboratory environments. Based on this evidence, I evaluate the appropriateness of applying mass criteria similar to those currently used in rodents to passerine severity assessment. Since passerines are a diverse group, ranging widely in ecology, physiology and behaviour, it would not be feasible to define specific, single severity criteria appropriate for all species. Instead, my goal is to stimulate further consideration, and appropriate data collection and sharing, in order to refine future guidance concerning severity assessment to the benefit of laboratory bird welfare.

Theory of optimal body mass and strategic mass-regulation

Wild animals face a trade-off between finding food and avoiding predators (Clinchy *et al* 2004). Storage of body fat is an adaptation enabling survival and reproduction in the face of temporary food shortages — carrying too little fat risks starvation (Nettle *et al* 2017). Fat can also serve in thermoregulation (Knight 2018). However, an increase in fatness also has disadvantages. As mass increases, so too do metabolic requirements (Johnstone *et al* 2005). Moreover, in birds, increased body mass hampers flight performance (Witter *et al* 1994; Metcalfe & Ure 1995; Kullberg *et al* 1996; Van Den Hout *et al* 2010; O'Hagan *et al* 2015), reducing the ability to escape predators (Witter & Cuthill 1993; Gosler *et al* 1995; Kullberg *et al* 1996). Heavier birds also pay higher energetic costs of flight (Pennycuik 1990; Brodin 2001; Ward *et al* 2004), necessitating more foraging and hence greater exposure to possible predation (McNamara & Houston 1990).

Behavioural ecologists recognise that there is an optimal amount of fat for an individual to carry at which the benefits balance the disadvantages (Figure 1[a]). Optimum fatness varies depending on environmental conditions (Lima 1986; McNamara & Houston 1990; Houston & McNamara 1993; Houston *et al* 1993, 1997; Bednekoff & Houston 1994a; Adriaensen *et al* 1998; Gosler 2002; Macleod *et al* 2005a; Brodin 2007; Higginson *et al* 2012). If predation risk increases (eg predator numbers rise), then optimal mass will be lower in order to reduce the risk of being captured (Figure 1[b]). Conversely, if predators decline, optimal mass increases to guard against starvation. If starvation risk goes up (eg cold weather or unreliable food availability), optimal mass will shift upwards (Figure 1[c]). In other words, if food supplies are uncertain then fat has to be carried as an insurance against starvation, to be paid for in terms of the drawbacks for predation. Vertebrates possess decision-making mechanisms that strategically regulate energy intake and expenditure, and thus mass, according to the environments individuals find themselves in (Nettle *et al* 2017).

Biology and ecology of strategic mass-regulation in passerines

Strategic mass regulation may be more pronounced in passerine birds compared to non-flying mammals due to physical and energetic requirements of flight (Butler & Bishop 2000). Passerines have higher metabolic rates and body temperatures for their size compared to non-passerines or mammals, giving higher energy requirements (Lasiewski & Dawson 1967; Schmidt-Nielsen 1997). Combined with heat loss and fewer total reserves due to small size, this makes starvation a real threat — particularly overnight. Small passerines rely on stored fat since they cannot sustain themselves overnight on food carried in the gut (Brodin 2007). Excess mass may carry greater penalty for locomotion by birds than by flightless mammals. Consequently, birds have evolved different mechanisms of fat storage and usage compared to rodents, as well as differences in digestive and energetic physiology and regulation mechanisms (Braun & Sweazea 2008; Guglielmo 2018; Ricklefs *et al* 2018). Bird physiology is highly plastic, with muscles, digestive system and other organs undergoing considerable atrophy or hypertrophy when flight or dietary demands change (Piersma & Lindström 1997; Bauchinger *et al* 2005; McWilliams & Karasov 2005). In this section, I review evidence that passerines' body mass is altered by manipulations of actual or perceived starvation and predation risk, and that mass varies with environmental factors that likely affect birds' perceptions of these risks.

Experimental manipulations of starvation or predation risk

Experiments varying the predictability of food supplies generally confirm the prediction that birds are heavier under heightened starvation risk: a systematic literature review (see Table S1) demonstrates that such mass changes are commonly of the order of < 10%, although sometimes larger. Fat storage also increases when starvation risk is raised by shortening the time food is available, or if energetic requirements increase due to lowering temperatures (Bednekoff & Krebs 1995; Rogers 1995; Lilliendahl *et al* 2011). Responsiveness may depend on whether birds are in the photosensitive or photorefractory period (Witter *et al* 1995). The prediction that individuals adopt lower mass when they perceive predation risk to be elevated is well supported (although not universally so, see Table S2 and below). A systematic literature review (Table S2) demonstrates that generally mass decreases < 10% under heightened predation. Effects of this size are nevertheless biologically relevant relative to daily energy budgets or diurnal mass changes (Gentle & Gosler 2001; Macleod *et al* 2008). However, some studies report the opposite effect to that predicted, with birds becoming heavier in response to increased predation (Table S2). A suggested explanation is that predators interrupt foraging and thus increase perceived starvation risk, incentivising mass gain — termed the 'interrupted foraging (IF)' response (MacLeod *et al* 2007). How a bird responds to increased predation risk depends on the foraging

environment: if food is plentiful and predictable, birds have the option to avoid foraging at times or places of highest risk. But, by interrupting foraging in this way, they increase their starvation risk and thus should carry *more* fat. However, in poor foraging environments, birds may face no option but to continue to forage despite risking predation — they should then reduce their mass to improve their escape prospects — the 'Mass Dependent Predation Risk (MDPR)' response (MacLeod *et al* 2007). Several studies corroborate these predictions (Krams 2000; Rands & Cuthill 2001; Macleod & Gosler 2006; MacLeod *et al* 2007; Morosinotto *et al* 2017; Walters *et al* 2017). If predation risk is chronically elevated, foraging behaviour may be altered in such a way as to impose food-limitation even in environments with abundant food, with consequent reduction in mass (Brown & Kotler 2004; Travers *et al* 2013; Gallagher *et al* 2017). Which strategy birds adopt in response to predation risk may also depend on their size (Cucco *et al* 2002; Zimmer *et al* 2010, 2011), the time of day when predators are encountered (Macleod & Gosler 2006), or on seasonal processes (Fransson & Weber 1997).

Seasonal variation in starvation or predation risks

Many wild birds increase mass in response to, or in anticipation of, times of year when starvation risks rise due to reduced food availability or higher energy demands for thermoregulation (Witter & Cuthill 1993; Rogers *et al* 1994; Cresswell 1998; Gosler 2002; Rintamäki *et al* 2003; Rogers & Reed 2003; Macleod *et al* 2005a, 2008; Krams *et al* 2010; Rogers 2015). Fattening thus occurs in winter for temperate birds or in the dry season for tropical species (Cox *et al* 2011; Nwaogu *et al* 2017), with temperature playing a causal role (Ekman & Hake 1990; Gosler 2002; Goymann *et al* 2006; Lilliendahl *et al* 2011). Fattening also increases with latitude, shortening days (Witter & Cuthill 1993; Rintamäki *et al* 2003; Rogers & Reed 2003; Polo *et al* 2007), or cues of impending bad weather (Middleton 1982; Kelly *et al* 2002; Krams *et al* 2010; Breuner *et al* 2013; Metcalfe *et al* 2013). Seasonal mass variations can be substantial. For example, starlings (*Sturnus vulgaris*) may be up to ~11% heavier in winter and blackbirds (*Turdus merula*) up to 25% (Meijer *et al* 1994; Cresswell 1998; Cuthill *et al* 2000; Macleod *et al* 2005a, 2008), with similar or even greater variation among tropical passerines (Cox *et al* 2011).

Larger mass increases occur in preparation for increased energy demands made by seasonal biological processes, such as migration or breeding (Blem 1976; Scott *et al* 1994; Kullberg *et al* 1996, 2000; Burns & Ydenberg 2002), with birds sometimes reaching obese levels by human standards (Clark 1979; Scott *et al* 1994; Gómez *et al* 2017; Guglielmo 2018). Conversely, birds can undergo voluntary anorexia and mass reduction (even though food is readily available) during breeding, incubating, moult, territorial or harem defence, or migration itself (for a review, see Dunn *et al* 2015), in some cases to compensate for increased predation risk (Norberg 1981; Senar 2002; Carrascal & Polo 2006). Some species increase mass in anticipation of these interruptions to feeding (Nwaogu *et al* 2017).

Diurnal variation in starvation or predation risks

Many passerines gain mass in anticipation of night-time, when predation risks are lower (due to inactivity, and absence of diurnal predators) and starvation risks rise (due to cessation of foraging and lower temperature). Observed diurnal changes are often moderate compared to seasonal changes, typically < 10% (Table S3). Diurnal variations are greatest ahead of predicted colder nights or in harsher environments (Bednekoff *et al* 1994; Thomas & Cuthill 2002; Krams *et al* 2012), for smaller species (Cresswell 1998), species that do not hoard food (Brodin 2000; Lilliendahl 2002; but see Pravosudov & Grubb 1998) or that occupy niches with less predictable food availability (Rogers 1987; Rogers & Smith 1993; Barluenga *et al* 2001).

Predicted patterns of diurnal mass change depend on the balance between starvation and predation risks (Houston *et al* 1993; Bednekoff & Houston 1994b; McNamara *et al* 1994; Polo & Bautista 2006a): If starvation risk is greatest or foraging interruption likely, it is optimal to gain mass early in the day because starvation risk is highest following overnight mass-loss. However, if predation risk is greatest, it is optimal to delay mass-gain to avoid paying a predation cost throughout the day (Macleod *et al* 2005b). When both starvation and predation are important, a bimodal pattern is expected with mass gained around dawn and dusk. All three diurnal patterns are observed (Houston *et al* 1993; Witter & Cuthill 1993; Polo & Bautista 2006b; Brandt & Cresswell 2009; Moiron *et al* 2018). As expected, the diurnal pattern is affected by changes in predation or starvation risk (van der Veen & Sivars 2000; Polo & Bautista 2006b), and can vary seasonally (Rintamäki *et al* 2003; Polo *et al* 2007).

Social competition affects starvation and predation risks

Subordinates are, by definition, often displaced from food resources during competition, making their access to food less reliable than dominants and environmental starvation risks disproportionately affect subordinates (Clark & Ekman 1995). As expected therefore, subordinates of many passerines are fatter than dominants (Ekman & Lilliendahl 1993; Witter & Swaddle 1995; Gosler 1996; Hake 1996; Witter & Goldsmith 1997; Pravosudov *et al* 1999; Haftorn 2000; Pravosudov & Lucas 2000; Krams *et al* 2012). Subordinates lost mass in experiments where dominants were removed from the group (Ekman & Lilliendahl 1993; Witter & Swaddle 1995). Subordinate starlings gained more mass than dominants when food was unpredictable (Witter & Swaddle 1995), while dominant great tits (*Parus major*) reduced their reserves more than subordinates when predation increased (Krams 2000; Gentle & Gosler 2001). Subordinates can also differ in diurnal mass variations compared to dominants (Cuthill *et al* 1997; Krams *et al* 2012). While group living intensifies competition for food, it also reduces the predation risk of group members (Krause & Ruxton 2002), perhaps particularly dominants. Dominants may also win preferential access to feeding sites with lower predation risk (Ekman 2004), or suffer lower

predation overall (Verhulst & Hogstad 1996). This is one explanation proposed to explain why dominants are *sometimes heavier* than subordinates (Koivula *et al* 1995; Verhulst & Hogstad 1996; Krams 2000; Krams *et al* 2012). Reduced predation in groups perhaps also contributes to seasonal fattening in passerines that flock only during autumn/winter.

Disease risk or early-life experience may alter mass

A recent hypothesis is that the risk of disease alters mass strategically because immune responses incur metabolic costs, and sickness reduces foraging efficiency or increases susceptibility to predation (Speakman 2018). Conditions experienced early in life may also influence adult mass because they carry information about the starvation or predation risks likely to be faced later, allowing individuals to strategically adapt their physiology and behaviour in anticipation (Nettle & Bateson 2015). Starlings competitively disadvantaged as nestlings went on to become heavier in adulthood (Andrews *et al* 2015), while starlings made to beg harder for food as nestlings were lighter as adults (Dunn *et al* 2018).

Strategic mass-regulation in a laboratory environment

Laboratory environments are free from predators, harsh winters and many pathogens, yet animals' evolved decision-making mechanisms controlling strategic mass-regulation could nevertheless respond to cues present in captivity which affect *perceptions* of predation or starvation risk. Reliable food supplies may, counterintuitively, lead animals to perceive low starvation risk and hence strategically adopt *low mass*. Short-term food deprivations during experiments could induce strategic mass gains.

Birds in outdoor housing may be exposed to real predator cues. Many anxiogenic husbandry or scientific procedures could increase perceived predation risk, including human disturbances (eg Zimmer *et al* 2011), capture and handling (Lilliendahl 1997; van der Veen & Sivars 2000; Gosler 2001; Macleod & Gosler 2006), or unfamiliar objects (Van Den Hout *et al* 2006). Some instances of stress-induced voluntary anorexia in response to restraint might be evolved responses to perceived predation. For example, a brief escape-and-recapture of zebra finches by humans resulted in mass loss averaging 11% (Yamahachi *et al* 2017). Handling and room transfer of yellowhammers (*Emberiza citrinella*) caused mass loss similar to that following exposure to a model predator (van der Veen & Sivars 2000). Capture or change of environment can have long-lasting effects on mass. Wild great tits altered their mass for at least seven days after capture (Macleod & Gosler 2006; Lilliendahl *et al* 2011), while greenfinches (*Chloris chloris*) and house sparrows (*Passer domesticus*) took several weeks to stabilise in mass after capture and transfer to an aviary (Ekman & Hake 1990; Love *et al* 2017; Fischer *et al* 2018). Reliable food as well as capture and handling may contribute to mass-loss when wild birds are brought into captivity (Dickens *et al* 2009; Fischer *et al* 2018).

Subtleties of husbandry could also alter birds' perceived predation risk. Water-bath enrichments influence starlings' perceived predation risk (Brilot & Bateson 2012), although bathing provision did not affect zebra finches' mass (Krause & Ruploh 2016). Birds could perceive husbandry counterintuitively; an individual captured then released (direct 'predation' event) may perceive the threat to have ceased, while exposure to alarm-calling might be perceived as longer-term elevated predation risk (Rands & Cuthill 2001). Birds with plentiful food might adopt an IF response (see *Experimental manipulations of starvation or predation risk*) to perceived predation risk and so gain mass. Responses to human handling versus real or model predators might differ in this regard (Macleod & Gosler 2006). Which response a bird adopts could be influenced by enrichments providing refuges from (perceived) predators. Indeed, captive starlings carried least fat when there was no protective cover (Witter *et al* 1994). Toxins could also affect how birds respond to altered predation risk — zebra finches exposed to methylmercury lost more mass than controls when perceived predation risk increased (Kobiela *et al* 2015). Similar influences in pharmacological studies warrant investigation.

Seasonal variations in mass can occur even in laboratories. Birds taken from the field and kept under constant laboratory conditions may continue to exhibit seasonal mass fluctuations for over a year (Clark 1979). Differences between species are likely, with some species (or age or sex classes) thought to follow a fixed seasonal pattern of mass-change coinciding with the predicted environmental conditions in which they evolved, while others directly monitor their environment and adjust mass according to current experiences (for a review, see Dall & Witter 1998). Alterations to the light cycle, temperature or humidity could serve as cues triggering evolved seasonal mass changes.

Husbandry, as well as experimental procedures, frequently require altering social groups or moving birds between group- and individual-housing, thus altering competitive interactions and so driving strategic mass changes. An individual's social status likely affects the direction of mass changes: a subordinate taken from a group (where access to food is competitive) to an individual cage (where food is freely available) might strategically reduce mass owing to lowered perceived starvation risk. If it perceives solitary housing as increasing its predation risk (because predation risk is no longer 'diluted' nor vigilance shared), this could be further impetus for mass loss. Starlings, zebra finches and Carolina chickadees (*Poecile carolinensis*) are indeed heavier when housed socially than when caged individually (Witter & Goldsmith 1997; Pravosudov & Lucas 2000; Yamahachi *et al* 2017; Dunn *et al* 2018). Many factors affect competition: the enclosure size and position, number or design of feeders influences the ability of dominants to monopolise food. Species' ecology may play a role — for instance subordinate parids carry food to handle it away from interference by dominants, while zebra finches do not (Pravosudov & Lucas 2000). Changes in mass will be difficult to interpret for welfare assessment if social group structure or husbandry that affects competition has been recently altered.

In summary, changes to feeding, husbandry, enrichment, and experimental procedures potentially interact, leading to mass losses or gains. Lowered appetite or mass ought not necessarily be interpreted as a sign of poor welfare in passerines (as previously noted by Bateson & Feenders 2010). The effect of capture and handling should be an important experimental design consideration when studying mass changes or monitoring mass. The food, social and physical environmental context, as well as the time of day of measurement, will require consideration and standardisation if using mass to monitor welfare. Recent changes to husbandry could obscure mass changes from informing us about welfare. But, with careful interpretation informed by an ecological perspective, changes in mass could offer clues as to how laboratory birds perceive alterations to their husbandry in terms of predation or starvation threats. The hypothesis that fattening is an evolved strategy to survive periods of disease (Speakman 2018) predicts that animals perceiving an increased prevalence or vulnerability to disease will gain mass. Thus, could poor welfare disease states, or models of chronic disease, sometimes counterintuitively drive mass upwards? Experiments will be needed to test this possibility, but it could pose difficulties for using mass criteria in severity assessment.

What mechanisms regulate mass, and is this really 'strategic'?

Four non-exclusive mechanisms exist by which birds could adjust their mass: (i) altering food consumption (quantity or energy-density); (ii) altering energy expenditure by varying activity levels; (iii) altering energy expenditure by varying metabolic rate (including nocturnal hypothermia) or amount of metabolically active tissue; (iv) altering energy extraction from food via changes to digestive efficiency (Witter *et al* 1995; Bateson *et al* 2021). The role of each is not yet well understood. Starlings experiencing experimentally elevated starvation risk gained mass without increasing food intake, an effect partly explained by increased roosting and digestive efficiency (Bateson *et al* 2021). Zebra finches experiencing unpredictable food spent more time inactive (Dall & Witter 1998). Birds can also regulate overnight energy expenditure by adjusting nocturnal hypothermia according to the night-time starvation and predation risks (Bednekoff *et al* 1994).

Stress hormones could serve as a proximate mechanism for responding to perceived predation or starvation risks (van der Veen & Sivers 2000). Stressors activate the hypothalamic-pituitary-adrenal (HPA) axis, releasing glucocorticoid hormones that co-ordinate physiological and behaviour responses to situations that are energetically demanding or potentially life-threatening (Wingfield *et al* 1998). Corticosterone (CORT), the most important avian glucocorticoid, is involved in the 'fight or flight' response, regulating food intake and metabolism (Wingfield *et al* 1998; Hiebert *et al* 2000; Sapolsky *et al* 2000; Ramage-Healey & Romero 2001; Yau & Potenza 2013). CORT is elevated by predation risk and unpredictable food (Pravosudov *et al* 2001; Clinchy *et al* 2004, 2011; Bauer *et al* 2011; Fokidis *et al* 2012), simulated predation (eg capture-handling-restraint; Ramage-

Healey & Romero 2001), unpredictable environments and seasonal processes (Witter *et al* 1995; Schultner *et al* 2013). However, overall, there is mixed evidence for CORT elevation in birds under chronic unpredictable food stress or predator cues (Clinchy *et al* 2013; Harris & Carr 2016).

The suggested involvement of glucocorticoids has begged the question as to whether changes in mass underpinned by elevated CORT imply a pathological chronic stress response rather than adaptive regulation (Clinchy *et al* 2013). This dichotomy is false because it confuses proximate mechanisms with ultimate evolutionary explanations: chronic CORT elevation could be a mechanism underlying adaptive mass-regulation, and chronic stress could occur when an individual is adaptively ‘making the best of a bad job’, adopting the optimal mass for a challenging environment (Clinchy *et al* 2004). Nevertheless, evidence in at least one case indicates pathological changes in mass alongside chronic stress: curved-billed thrashers (*Toxostoma curvirostre*) exposed to variable food supplies increased in activity and in baseline CORT while *losing* mass — the opposite effect to the expected adaptive response (Fokidis *et al* 2012).

Could mass-loss in response to predation risk be a non-adaptive direct consequence of energy expended in predator avoidance? Predation attempts and vigilance interrupt foraging, while energy is expended during escape, vigilance and movement to avoid areas of high predation. Ecologists have widely documented the impact of an ‘ecology of fear’ induced by predator presence (or anthropogenic disturbances perceived as predation) on the movement and foraging of many wild animals, in some cases elevating glucocorticoids and reducing body mass (Clinchy *et al* 2004, 2013; Harris & Carr 2016; Gallagher *et al* 2017). For the reasons stated above, however, elevated glucocorticoids could be a mechanism by which energy-balance is compensated and adaptive mass-regulation achieved under predation. In captivity, escape attempts from ‘predators’ (humans) may be thwarted, sometimes involving birds repeatedly flying around their enclosure. Energetic costs or elevations in CORT might be sustained compared to in the wild where escape is possible. Mass loss as a non-adaptive side-effect might arguably therefore be a greater possibility. When exposed to artificial chronic stress paradigms (repeated restraint/disturbance), starlings decreased in mass ~3–5% (Rich & Romero 2005; Cyr *et al* 2007), however blackbirds’ mass did not alter (Hau *et al* 2015). However, energy costs of escape may be lowered in the laboratory since captive birds (particularly captive-bred) show reduced fear responses to predators and humans compared to wild birds (Feenders & Bateson 2011; Feenders *et al* 2011; Carrete & Tella 2015). Moreover, when food is available *ad libitum* in captivity, it seems likely that birds could compensate for energetic costs of escape behaviours or foraging interruptions.

How could mass monitoring contribute to severity assessment in passerines?

Many aspects of husbandry or experimental procedures could alter birds’ perceived predation or starvation risks and thus trigger mass changes as an evolved response. We must therefore decide whether any mass changes observed are likely strategic rather than due to chronic undernutrition or illness, and if so, whether strategic changes themselves indicate potential welfare concern. I turn now to these issues.

Establishing a baseline

Baseline mass should be sought at the individual level, due to between-individual variation in factors such as dominance (see *Social competition affects starvation and predation risks*). Baselines should be obtained when birds are believed to be healthy and in positive welfare states, under stable husbandry, housing and social grouping, and with *ad libitum* food. Multiple measurements should be taken over a period of weeks to obtain stable, representative baselines, because changes to the environment can have long-lasting effects (see *Strategic mass-regulation in a laboratory environment*). Time of measurement relative to the light cycle should be standardised and reported, due to diurnal mass variations (see *Diurnal variation in starvation or predation risks*). Ideally, mass should be obtained using automated weighing perches (for an example method, see Bateson & Nolan 2022) because capture and handling might itself drive strategic mass-regulation (see *Strategic mass-regulation in a laboratory environment*).

Is observed mass change strategic or not?

Understanding strategic mass-regulation allows us to anticipate laboratory situations in which birds may perceive altered starvation or predation risk and hence change mass: capture or handling, changes to the feeding regime, social grouping, light, temperature or humidity, environmental enrichments or presence of novel apparatus (see *Strategic mass-regulation in a laboratory environment*). A range of stressors may activate the HPA-axis, perhaps triggering mass-regulation. Strategic mass changes of ~10% appear common (see *Seasonal variation in starvation or predation risks*), with greater magnitude possible. Other normal biological processes could also cause greater mass changes, eg gravid females typically gain 10% in mass (Kullberg *et al* 2002) while migrants can gain over 40% (Blem 1976). Knowledge of the species along with longitudinal mass records also detailing husbandry conditions could be used to refine estimates of the likely magnitude of strategic mass variations. If mass alters following recent husbandry changes (including at least a month afterwards) it should be considered whether these are likely strategic responses, based on the magnitude and direction. As corollary, mass change in the absence of husbandry or seasonal changes are likely cause for welfare concern.

Is strategic mass change of welfare concern?

Even strategic responses could offer insight into whether birds perceive a procedure or husbandry alteration as threatening — hence a potential welfare concern. Mass loss could indicate an anxiety-like affective state due to perceived predation risk, although the psychological component remains under debate (Clinchy *et al* 2013). Mass gain could indicate perceived insecure food access — whether this is accompanied by negative affective states like anxiety or hunger awaits investigation. In addition to psychological welfare, strategic mass changes could indicate lower physical welfare — for example, mass loss driven by reduced predator escape ability due to poor health (Kobiela *et al* 2015) or mass gain due to increased perceived starvation risk following immune challenge (Nord *et al* 2014; Speakman 2018). Even strategic mass changes might have knock-on consequences for disease vulnerability. For instance, birds with relatively high mass have stronger cell-mediated immunity than lighter birds (for a review, see Alonso-Alvarez & Tella 2001), while blood parasite infection was found more prevalent in heavier birds (Scheuerlein & Ricklefs 2004). In some domestic and laboratory animals overweight or obesity has been identified as a welfare problem (D'Eath *et al* 2009; McMillan 2013), but this is not the case in passerines.

How should mass criteria for passerine severity assessment be determined?

Mass loss of the order of 10–25% is used in rodent severity assessments (Jones *et al* 1996). However, changes in mass of ~10% are common in passerines (see *Seasonal variation in starvation or predation risks* and *Experimental manipulations of starvation or predation*), with changes of greater magnitude possible, stemming from strategic mass-regulation rather than necessarily ill-health or undernourishment. Therefore, criteria used in rodents (especially close to 10% loss) would be excessively stringent for passerines, potentially resulting in over-classification of severity. Mass gain in passerines could be driven by conditions associated with poor welfare (such as insecure access to food) and thus ought potentially to be considered in severity criteria too. How then do we set thresholds to identify cases of mass-change caused by reduced welfare?

First, we should consider the cost of ‘false alarms.’ The species’ biology will determine how sensitive criteria are to detect reduced welfare; if the distribution of masses in birds with good welfare differs greatly from those with poor welfare then criteria will be more sensitive to detect compromised welfare. But we ourselves set the bias in our criteria for deciding when to raise the alarm — a trade-off between accepting frequent false alarms (concluding welfare is compromised when truly it is not) versus failing to alert on true welfare concern. Appropriate criteria balance the ethical consequences of false versus failed alarms. Failure to detect a true welfare compromise may carry serious consequences — missed veterinary

intervention or a failure to implement humane endpoints. False alarms carry economic and scientific costs, and unnecessary treatment could be detrimental to welfare or result in animals being euthanased unnecessarily, increasing the number of animals used. Therefore, appropriate mass criteria even for a given species, may differ to take account of circumstances affecting the costs to refinement and reduction of false versus failed alarms.

Ideal data to derive mass criteria would be obtained by experimentally inducing welfare states of different severity, as verified by independent welfare measures of affective state, while recording concomitant effects on mass. However, this would be a large-scale undertaking, carry ethical considerations, and obtaining affect measures could be challenging in animals experiencing a ‘severe’ state. Instead, could wild birds’ masses inform criteria? There are two key drawbacks. First, in the wild, it is often uncertain for how long an animal survived after being weighed. Hence, this approach risks judging as acceptable masses which were in fact seriously detrimental to welfare. To illustrate, the majority of juvenile starlings die of starvation over winter (Feare 1984), meaning criteria based on a sample of wild birds would not prevent laboratory birds entering severe states close to death. Second, natural environments are often harsher and more variable than captivity, likely resulting in greater strategic mass variation (Krams *et al* 2012). A valid contribution would be to use the minimum recorded wild masses to set absolute minimum thresholds at the extreme end of severity: a mass below which birds rarely survive. Even this should be attempted cautiously. For example, in harsh winter conditions, mass loss of great tits that died overnight was ~17% compared to ~13% for survivors, yet their absolute evening mass did not differ (Krams *et al* 2012). Hence, evening mass would not have warned of impending mortality.

In the first instance, guidelines should be informed by data on mass variation in laboratory birds in good health and believed to have good welfare at the time of measurement and long afterwards, under a representative range of stable husbandry conditions. For example, long-term monitoring of starlings showed individuals were lighter when individually caged than in aviary groups (Dunn *et al* 2018). Published data of this kind appear rare even for common laboratory species. More studies comparing variation in mass with that in measures of body condition (mass corrected for skeletal size) or fat stores are needed. In mice (*Mus musculus*), body condition may be preferable over mass for assessing health (Ullman-Culleré & Foltz 1999) and it is a commonly used measure in avian field studies. Which measure is the more sensitive measure for laboratory passerine welfare assessment will depend on how much the species in question varies in skeletal size. Fat scores are less well suited for routine monitoring, since handling is always required, and scores can change rapidly and suffer low between-observer repeatability (Brown 1996).

Animal welfare implications

Many aspects of laboratory passerine husbandry and experimental procedures may alter perceived starvation or predation risks, likely driving changes in mass that can be of sizeable magnitude (sometimes > 10%) over diurnal or longer timescales. Mass changes of the magnitude currently used in rodent severity assessments could, in passerines, result from strategic mass-regulation rather than ill-health or undernutrition. Hence, rodent criteria are likely overly stringent for passerines, causing excessive false alarms. Since passerines have evolved to tightly regulate mass to balance starvation and predation risks, it remains possible that other stressors unrelated to these risks might have limited effect on mass, perhaps causing 'false negatives' in welfare assessment. Further research is needed to resolve this question, although some evidence suggests a broad range of stressors affect mass, possibly via HPA-axis activation.

Mass monitoring strategies should control for time of day and season and be aware that husbandry or procedures could inadvertently induce strategic mass changes which may obscure early detection of those stemming directly from interventions such as disease induction. Even strategic mass changes potentially offer insight into whether animals perceive an intervention as a threat — hence a potential welfare concern. Mass criteria for severity assessment need to consider mass-gain as well as loss and be species- and context-specific to balance the needs for refinement and reduction. Greater data collection and sharing based on long-term, standardised routine monitoring of mass variations in laboratory passerines under a representative range of husbandry conditions and procedures is needed to enumerate and refine appropriate criteria. Consideration of strategic mass-regulation could also benefit welfare monitoring for exhibition or companion passerines in addition to laboratory birds.

Declaration of interest

None.

Acknowledgements

Melissa Bateson (Newcastle University) kindly contributed a version of Figure 1. I warmly thank Melissa Bateson, Daniel Nettle, Jonathon Dunn, Ryan Nolan, Tom Smulders, Lindsay Henderson, Chris Blau, Michelle Waddle and her team of technicians in the Comparative Biology Centre at Newcastle University for useful discussions on the topic. Melissa Bateson, Lindsay Henderson, two anonymous reviewers and the Editor provided helpful feedback on earlier versions of the manuscript. Clare Andrews was supported by European Research Council funding under the European Union's Horizon 2020 research and innovation programme (AdG 666669, COMSTAR, awarded to Daniel Nettle). The funders had no role in the preparation of the manuscript.

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