UQAR
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FLEXIBILITÉ DE LA PERFORMANCE MÉTABOLIQUE SUITE À DES CHANGEMENTS SOUDAINS DE TEMPÉRATURE AMBIANTE CHEZ TROIS ESPÈCES DE PASSEREAUX NORD AMÉRICAINS

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Composition du jury :

Joël Bêty, président du jury, Université du Québec à Rimouski

François Vézina, directeur de recherche, Université du Québec à Rimouski

David Swanson, examinateur externe, University of South Dakota

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RÉSUMÉ

Le présent mémoire a pour but principal d'apporter une meilleure compréhension de la capacité des organismes à répondre rapidement à des changements soudains de paramètres abiotiques de leur environnement. Comme les prévisions actuelles sur les changements climatiques laissent présager une augmentation de l'amplitude et de la fréquence des fluctuations de température, il est impératif de se questionner sur la vitesse à laquelle les organismes peuvent s'ajuster à de telles variations. L'acclimatation thermique chez les oiseaux, étudiée depuis une cinquantaine d'années, implique notamment des ajustements au niveau de la performance métabolique. Cependant, les études effectuées à ce jour portent principalement sur les patrons saisonniers observés en conditions naturelles, ainsi que sur l'amplitude de réponse en environnement contrôlé (généralement sur plusieurs semaines). Ainsi, nous manquons d'information sur ce qui se déroule à très court terme. Trois espèces de passereaux contrastées par leur environnement thermique naturel (mésange à tête noire (*Poecile atricapillus*), bruant à gorge blanche (*Zonotrichia albicollis*), plectrophane des neiges (*Plectrophenax nivalis*)) ont été acclimatées à 10°C pendant au moins un mois avant d'être soumises à un traitement de température froid (-5°C) ou thermoneutre (28°C) (changement effectué à l'intérieur d'une heure). Aux quatrième et huitième jours d'acclimatation, les paramètres de la performance métabolique et les composantes corporelles qui y sont associées ont été mesurés et ont été comparés aux niveaux enregistrés en pré-acclimatation (un jour avant les changements de température, à 10°C). Les oiseaux ont tous répondu significativement à l'intérieur de huit jours. Cependant, les espèces n'ont pas présenté pas les mêmes patrons de flexibilité phénotypique. La vitesse d'ajustement variait entre les paramètres métaboliques et les traitements de température. Ainsi, il semble que la rapidité des modifications phénotypiques dans les premiers jours d'ajustement à des fluctuations importantes des conditions climatiques puisse dépendre des mécanismes physiologiques sous-jacents, de la direction du changement thermique, ainsi que de l'espèce étudiée.

Mots clés : flexibilité phénotypique, acclimatation thermique, taux métabolique de base, capacité thermogénique maximale, taux métabolique maximal, composition corporelle, passereaux

ABSTRACT

The main purpose of this thesis is to bring new knowledge on how organisms respond to sudden changes in environmental parameters. Since current projections on climate change suggest an increase in the amplitude and frequency of temperature fluctuations, it is imperative to investigate the rate at which organisms can adjust to such changes. Thermal acclimation and acclimatization in birds, which have been studied for the last 50 years, typically involve adjustments in metabolic performance. However, studies conducted to date tend to focus on seasonal patterns observed in natural conditions, as well as the amplitude of response in experimental settings (usually over several weeks). Therefore, there is a lack of knowledge on potential adjustments appearing over short time spans. Three passerines species contrasted by their natural thermal environments (black-capped chickadee (*Poecile atricapillus*), white-throated sparrow (*Zonotrichia albicollis*), snow bunting (*Plectrophenax nivalis*)) were acclimated to 10°C for at least one month before being transferred to one of two temperature treatments, either cold (-5°C) or thermoneutrality (28°C) (transfer carried out within an hour). After four and eight days of acclimation, metabolic parameters and the body components they reflect were measured and compared with recorded pre-acclimation levels (one day before temperature changes). All birds responded significantly to temperature fluctuations within eight days. However, flexibility patterns differed among species while the rates of adjustment varied between metabolic parameters and thermal treatments. Thus, it seems that the rate at which phenotypic adjustments occur in the first days following a change in temperature may differ depending on the underlying mechanisms involved, the direction of temperature change as well as the examined species.

Keywords: phenotypic flexibility, thermal acclimation, basal metabolic rate, maximal thermogenic capacity, maximal metabolic rate, body composition, passerines

TABLE DES MATIÈRES

LISTE DES ABRÉVIATIONS, DES SIGLES ET DES ACRONYMES

BMR	Taux métabolique de base.
M_{sum}	Capacité thermogénique maximale.
MMR	Taux métabolique maximal.

INTRODUCTION GÉNÉRALE

VARIABILITÉ ENVIRONNEMENTALE ET STRATÉGIES DE RÉSISTANCE

Les populations animales qui vivent à des latitudes élevées doivent faire face à un environnement variable dont les paramètres abiotiques et biotiques fluctuent parfois de façon importante. Pour ces animaux, l'hiver est une période particulièrement contraignante accompagnée d'une dégradation des conditions climatiques et d'une productivité souvent limitée.

Un des paramètres climatiques le plus étudié dans le contexte des contraintes associées à l'hiver est la température ambiante. Par exemple, de par son influence sur le budget énergétique (McNab, 1963), la température aurait un impact sur la distribution des homéothermes (Root, 1988). Les écarts de température saisonniers les plus importants étant retrouvés près des pôles, les différences saisonnières de température s'accroissent avec une augmentation de la latitude. Chez les espèces des latitudes élevées, plusieurs stratégies sont donc utilisées afin d'échapper aux inconvénients liés aux températures froides. Par exemple, plusieurs reptiles, amphibiens et petits mammifères hibernent durant la saison froide (Carey et al., 2003 ; Storey et Storey, 1992). Chez les espèces aviaires, une stratégie largement répandue est la migration. Cependant, certaines espèces sont résidentes et demeurent sur leurs lieux de reproduction toute l'année. Celles-ci recourent alors à d'autres moyens afin de contourner les conditions difficiles liées à l'environnement hivernal. Par exemple, l'hypothermie contrôlée permet d'abaisser momentanément la température corporelle et ainsi de diminuer les coûts énergétiques de thermorégulation (Olson et Grubb, 2007). Similairement, l'utilisation de cavités naturelles aide à minimiser la différence de température entre l'air ambiant et le corps pendant les périodes d'inactivité (Cooper, 1999 ;

Walsberg, 1986). Certaines espèces améliorent aussi leur isolation durant la période hivernale en augmentant la densité de leur plumage (Cooper, 2002 ; Lill, 2006).

En plus des variations saisonnières de température, les organismes doivent aussi faire face aux fluctuations rapides de température, pouvant survenir en quelques heures ou en quelques jours. En hiver, celles-ci s'illustrent par exemple par de subits redoux accompagnés de pluie en alternance avec des périodes de gel (Desjarlais et Blondlot, 2010). Les prédictions actuelles laissent présager une hausse en fréquence et en amplitude de ces variations de température ambiante pour les prochaines années (Easterling et al., 2000 ; IPCC, 2013 ; Katz et al., 2005). Les populations animales devront donc affronter plus régulièrement les contraintes associées à cette variation environnementale. Plusieurs études suggèrent d'ailleurs que la variabilité climatique est tout aussi importante à considérer en terme d'impact sur la fitness que les moyennes globales de température (Bozinovic et al., 2011 ; Marshall et Sinclair, 2010 ; Rojas et al., 2014).

FLEXIBILITÉ PHÉNOTYPIQUE ET PERFORMANCE MÉTABOLIQUE

La flexibilité phénotypique est la capacité des organismes de modifier de façon réversible certains aspects de leur comportement, morphologie et/ou physiologie (Piersma et Drent, 2003). Celle-ci permet donc de tamponner jusqu'à un certain point les variations de l'environnement. Chez les oiseaux, la flexibilité du phénotype est particulièrement visible dans la capacité à moduler la performance métabolique en réponse aux contraintes associées à l'environnement thermique (Marsh et Dawson, 1989 ; Swanson, 2010). La performance métabolique peut se mesurer de plusieurs façons, mais deux paramètres, le taux métabolique de base (BMR) et la capacité thermogénique maximale (M_{sum}) sont associés à l'endurance au froid (Swanson, 2010).

Le BMR représente l'énergie minimale dépensée par un organisme pour les fonctions vitales telles que la maintenance des tissus et des organes (McKechnie, 2008). Il est mesuré chez des individus adultes au repos, à jeun et à une température ambiante se situant à l'intérieur de la zone de thermoneutralité (Klaassen et al., 2004). Le BMR est de loin le paramètre le plus utilisé comme outil de comparaison des besoins énergétiques des espèces. À ce jour, cette variable a été mesurée sur plusieurs centaines d'espèces (McKechnie et Swanson, 2010). Dans le contexte de l'acclimatation thermique, les variations de BMR sont généralement interprétées comme étant le reflet des variations de la taille et de l'activité des organes responsables de l'acquisition de l'énergie, tels le foie, l'intestin, les reins et le gésier (Maldonado et al., 2009 ; Sabat et al., 2009 ; Williams et Tieleman, 2000 ; Zheng et al., 2008). Par exemple, Maldonado et al., (2009) ont observé chez le bruant chingolo (*Zonotrichia capensis*) acclimaté au froid en captivité des augmentations parallèles du BMR et de la masse du foie et des reins. De la même manière, en conditions naturelles, les moineaux friquets (*Passer montanus*) ont un BMR plus élevé et des intestins et un foie plus lourds en hiver qu'en été (Zheng et al., 2008).

Le M_{sum} est une mesure de la dépense énergétique maximale résultant du frissonnement pendant l'exposition au froid. Cet état n'est pas soutenable sur de longues périodes mais est positivement corrélé à la tolérance à des températures froides plus modérés. Le M_{sum} informe donc sur la capacité à supporter des pertes de chaleur sur de longues périodes (Swanson et al., 1996). Comme le M_{sum} résulte du frisonnement, les variations dans la taille des muscles, principalement ceux employés pour le vol, ont une forte influence sur les variations de M_{sum} (Petit et Vézina, 2014 ; Swanson et al., 2013 ; Vézina et al., 2006). En effet, Petit et al. (2014) ont démontré expérimentalement qu'augmenter la taille des muscles pectoraux résulte en un M_{sum} plus élevé chez la mésange à tête noire (*Poecile atricapillus*).

Un troisième paramètre, le taux métabolique maximal (MMR), semble également varier avec les ajustements physiologiques associés à la thermorégulation, possiblement parce qu'il implique les mêmes organes effecteurs que ceux utilisés dans la production active de chaleur. Le MMR représente l'énergie maximale dépensée durant un exercice physique intense et, chez les oiseaux, l'essentiel de la dépense énergétique lors de la locomotion est due aux muscles squelettiques, en particulier les muscles pectoraux qui sont responsables du vol (Wiersma et al., 2007a). Ainsi, tout comme pour le M_{sum}, un changement dans la taille et/ou l'activité métabolique des muscles pectoraux résultant d'une acclimatation thermique risque d'influencer le MMR. Une étude récente a d'ailleurs démontré qu'une exposition au froid de quelques heures par jour pendant 3 semaines provoque une augmentation significative du MMR, en plus de celle du M_{sum} chez le moineau domestique (*Passer domesticus*) (Zhang et Swanson, 2014). L'inverse a également été observé, où durant la migration, période de demande physique élevée, une hausse de M_{sum} a été enregistrée (Swanson et Dean, 1999 ; Vézina et al., 2007). Ceci dit, les corrélations entre le M_{sum} et le MMR (ou entre leurs résidus contrôlant pour la masse) ne sont pas significatives pour plusieurs espèces de passereaux (Swanson et al., 2012 ; Wiersma et al, 2007a), suggérant que les capacités musculaires pour l'exercice et le frissonnement ne varient pas nécessairement de manière synchrone. En effet, le MMR est généralement plus élevé que le M_{sum} puisque les contractions musculaires responsables du frissonnement sont plus faibles que celles liées à la locomotion (Marsh et Dawson, 1989). Ainsi, bien qu'une meilleure capacité physique dans un environnement froid puisse se révéler bénéfique dans le cadre d'activités journalières telles que la quête alimentaire, il est possible que les changements de taille ou d'activité métabolique se déroulant dans les muscles durant l'acclimatation thermique, surtout à court terme, produisent un effet marqué sur le M_{sum}, mais de moindre ampleur sur le MMR. Pour l'instant, très peu d'études portent sur les variations parallèles de BMR, de M_{sum} et de MMR (McKechnie et Swanson, 2010).

Chez les espèces non migratrices vivant dans l'hémisphère nord, les valeurs de BMR et de M_{sum} sont normalement élevées pendant la saison froide et plus faibles durant la période estivale. En effet, en conditions naturelles, le BMR peut augmenter de 0,4 % à 63,1 % en hiver relativement à l'été (McKechnie et al., 2015). La hausse hivernale de M_{sum}, quant à elle, varie entre 4,3 % et 44,9 % (McKechnie et al., 2015). De la même manière, en conditions expérimentales, les taux métaboliques sont plus élevés aux températures d'acclimatation froides qu'aux températures chaudes (jusqu'à 96 % pour le BMR (Salvante et al., 2010) et jusqu'à 13 % pour le M_{sum} (Vézina et al., 2006)). Cependant, dans ce contexte, les études expérimentales sur la flexibilité de la performance métabolique en réponse à l'environnement thermique portent essentiellement sur l'amplitude finale des changements de phénotype. Les oiseaux sont typiquement divisés en 2 traitements de température, un froid et un chaud. Après plusieurs semaines ou mois d'acclimatation (Klaassen et al., 2004 ; Maldonado et al., 2009 ; McKechnie et al., 2007), les paramètres métaboliques sont mesurés et la différence entre les valeurs obtenues correspond alors à l'amplitude de réponse. C'est cette amplitude qui est ainsi considérée comme un indice de la flexibilité du phénotype. Cependant, si certaines études ont rapporté l'amplitude de la flexibilité phénotypique en réponse à l'environnement thermique (Klaassen et al., 2004 ; Maldonado et al., 2009 ; McKechnie et al., 2007), il n'existe à ce jour que très peu d'information sur la vitesse à laquelle les oiseaux arrivent à ajuster leur phénotype. Cette lacune est critique dans le contexte où il est attendu que les variations journalières de température deviendront plus importantes, particulièrement pendant la saison froide (Easterling et al., 2000 ; IPCC, 2013 ; Katz et al., 2005).

En ne considérant que le phénotype final après ajustement, des espèces ou des populations d'oiseaux pourraient être considérées à tort comme étant similairement flexibles alors qu'en réalité certaines pourraient être en mesure de modifier leur phénotype plus rapidement que d'autres. Adapter un phénotype à un nouvel environnement contraignant est certes bénéfique, mais l'ajuster trop tardivement ou trop lentement pourrait cependant entraîner un décalage entre le phénotype de l'animal et son environnement. À ce jour, une seule étude s'est intéressée à la vitesse d'ajustement du phénotype en réponse à l'environnement thermique. Swanson et Olmstead (1999) ont découvert qu'en milieu naturel, les variations de température à court (moins de 5 jours) ou moyen terme (14-30 jours) prédisent mieux les changements de BMR et de M_{sum} chez la mésange à tête noire, le junco ardoisé (*Junco hyemalis*) et le bruant hudsonien (*Spizella arborea*) que les températures historiques à long terme (100 ans). Cependant, cette étude corrélative n'informe pas sur le patron de variation de la performance métabolique dans les jours qui suivent un changement de température et ne permet donc pas de détecter la présence ou l'absence de décalage phénotypique.

Une autre lacune dans les connaissances sur la flexibilité phénotypique en réponse à l'acclimatation thermique est mise en évidence dans une étude expérimentale récente. Barcelo et al. (2009) ont étudié l'acclimatation thermique chez le bruant chingolo (*Zonotrichia capensis*) et ont mesuré une hausse du BMR de 28,5 % en 4 semaines chez des individus passant de 22°C à 15°C contre une baisse de 13,2 % pendant la même période chez des individus passant de 22°C à 30°C. Bien que cette étude ne se soit intéressée qu'à une seule composante de la performance métabolique, elle laisse cependant présager que la vitesse de réponse est plus rapide quand les oiseaux font face à un refroidissement des températures que lorsqu'ils sont exposés à un réchauffement. Cette observation est logique considérant que les ajustements reliés à l'acclimatation au froid permettent d'éviter les conséquences négatives d'une capacité thermogénique trop faible par rapport aux pertes de chaleur, alors qu'à une température près de la zone de thermoneutralité, les oiseaux ne font pas face à ces contraintes et peuvent ainsi maintenir une performance élevée en cas de rechute de la température ambiante. Cependant, le BMR est un indice de maintenance physiologique qui informe peu sur la capacité des individus à endurer un environnement froid. Par contre, une hausse du M_{sum} est considérée comme étant une amélioration de l'endurance au froid (Swanson et Garland, 2009) positivement reliée à la survie (Petit et al., en prép). Il est donc attendu qu'un patron similaire soit visible dans les variations de Msum et, potentiellement dans les variations de MMR. Cependant, les données actuelles ne permettent pas de déterminer si les extrêmes minimaux (i.e. BMR) et maximaux (i.e. Msum/MMR) de la performance métabolique s'ajustent en suivant des patrons comparables aux variations de température. Une approche expérimentale est donc requise pour tester cette hypothèse.

MODÈLES D'ÉTUDE

Certaines études récentes suggèrent que la performance métabolique varie en fonction des groupes phylogénétiques. Par exemple, Swanson et Bozinovic (2011) ont observé que la capacité thermogénique diffère entre deux sous-ordres de passereaux, les oscines ayant un M_{sum} 74% plus élevé que les suboscines. Pareillement, les passereaux présenteraient un BMR significativement plus élevé que les autres groupes d'oiseaux (Rezende et al., 2002). Dans le cas plus précis de l'acclimatation thermique, McKechnie et al. (2007) ont observé que chez des alouettes, sirlis, fauvettes et tourterelles soumis à des traitements de température semblables (un froid et un chaud), les ajustements du BMR entre groupes expérimentaux diffèrent, quoique faiblement, entre les espèces. Cependant, les analyses interspécifiques se font souvent sous une panoplie de conditions expérimentales, ce qui limite la valeur des comparaisons entre taxons et donc notre capacité à interpréter les observations dans un contexte général (McKechnie, 2008). Pour déterminer si et comment des espèces provenant d'environnements contrastés diffèrent dans leur réponse à l'environnement thermique, il importe donc d'obtenir des données en conditions standardisées et comparables. Nous avons ainsi choisi comme modèles d'étude trois espèces de passereaux qui, bien que relativement proches phylogénétiquement (sous-ordre des oscines), diffèrent de par leur répartition géographique et donc de par leur environnement thermique naturel.

La mésange à tête noire est un passereau de petite taille (10-12 g) retrouvé principalement en milieu forestier et dont l'aire de répartition s'étend sur une grande partie de l'Amérique du Nord, allant du centre des États-Unis à l'Alaska. Dans la région d'où proviennent les individus étudiés, le Bas-Saint-Laurent, les mésanges font face à un environnement où les variations saisonnières de température forcent les oiseaux à ajuster leur phénotype (températures moyennes de -8,9 °C en hiver à 16,8°C en été (données d'environnement Canada, station de Pointe-au-Père). Elles présentent en effet un cycle saisonnier de performance métabolique typique, avec des valeurs de BMR et de M_{sum} plus élevées en hiver qu'en été, incluant un pic de performance au plus froid de l'hiver (Petit et al., 2013).

Le bruant à gorge blanche (*Zonotrichia albicollis*) est un passereau migrateur associé aux régions boisées peu denses. Il se reproduit au Canada et passe les mois les plus froids de l'hiver dans le sud des États-Unis. Bien que cette espèce soit apte à s'acclimater à des températures ambiantes froides (Kontogiannis, 1968 ; McWilliams et Karasov, 2014 ; Metcalfe et al., 2013 ; Seibert, 1949), elle demeure associée à un climat relativement clément et stable (0-20°C en hiver (Odum, 1949) à 5-21°C en été (données d'Environnement Canada)).

Le plectrophane des neiges (*Plectrophenax nivalis*) est un oiseau spécialiste des régions nordiques. Il se reproduit sur les aires ouvertes de la toundra. Il effectue ensuite une migration vers le Sud durant la période hivernale, mais ne dépasse pas le nord des États-Unis. Ainsi, à l'exception d'une courte période estivale (température moyenne en juin de 3,1°C sur un site de reproduction de l'île Southampton (Love et al., 2010)), cette espèce fait face à un climat froid et enneigé durant la majorité de l'année. La capacité d'acclimatation thermique de cette espèce est encore très peu connue (Scholander et al, 1950).

OBJECTIFS ET HYPOTHÈSES

Cette étude examine la réponse phénotypique d'oiseaux pré-acclimatés à une température ambiante de départ commune (10°C) puis soumis à un changement soudain de température (froid, -5°C, ou thermoneutre, 28°C).

OBJECTIF 1

Le premier objectif de l'étude est de déterminer le patron de réponse des espèces aviaires dans les huit jours suivant un changement soudain de température. Comme l'acclimatation au froid provoque typiquement une augmentation de la performance métabolique et l'acclimatation aux températures élevées entraîne un patron inverse (Cooper et Swanson, 1994 ; Klaassen et al., 2004 ; Liknes et al., 2002 ; Maldonado et al., 2009 ; Petit et al., 2013 ; van de Ven et al., 2013), il est attendu que **les paramètres métaboliques**

devraient refléter une hausse de performance au froid et une baisse de performance à thermoneutralité.

OBJECTIF 2

Les évidences récentes suggèrent que la vitesse d'ajustement de la performance métabolique survenant durant l'acclimatation au froid est plus élevée que celle associée à l'acclimatation aux températures élevées (Barcelo et al, 2009 ; McKechnie et al., 2007). Le deuxième objectif de l'étude vise donc à tester cette hypothèse. Ainsi, il est attendu que **la vitesse d'ajustement de la performance métabolique soit plus élevée chez les groupes d'oiseaux soumis à une température froide comparativement à ceux soumis à une température à l'intérieur de leur zone de thermoneutralité.**

OBJECTIF 3

Le dernier objectif de l'étude est de déterminer si les trois paramètres de la performance métaboliques (BMR, M_{sum} et MMR) sont modifiés en suivant des patrons comparables durant l'acclimatation thermique. Compte tenu des variations parallèles de BMR et de M_{sum} généralement observées pendant l'acclimatation saisonnière ou expérimentale, **il est attendu que le BMR, le M_{sum} et le MMR répondent à l'environnement thermique de façon comparable.**

CHAPITRE 1
FLÉXIBILITE PHÉNOTYPIQUE DANS L'ACCLIMATATION THERMIQUE DE TROIS ESPÈCES DE PASSEREAUX NORD-AMÉRICAINS

RÉSUMÉ EN FRANÇAIS DU PREMIER ARTICLE

Chez les espèces aviaires de petite taille, l'acclimatation thermique est généralement associée à des ajustements du taux métabolique de base (BMR), de la capacité thermogénique maximale (M_{sum}) et du taux métabolique maximal (MMR). Les études expérimentales se sont concentrées sur la différence entre les valeurs finales de ces traits, obtenues après plusieurs semaines d'acclimatation à divers traitements thermiques (i.e. l'amplitude de réponse). Cependant, cette approche ne nous renseigne pas sur la vitesse à laquelle les espèces peuvent ajuster leur phénotype en réponse à des variations thermiques soudaines. Les objectifs de l'article sont de déterminer (1) le patron d'ajustement de la performance métabolique suite à un changement rapide de température, (2) si la performance varie à des taux similaires durant l'exposition à des températures froides ou chaudes et (3) si le BMR et le M_{sum}/MMR sont modifiés à des vitesses comparables lors de l'acclimatation thermique. Nous avons mesuré ces paramètres chez les bruants à gorge blanche (*Zonotrichia albicollis*), les mésanges à tête noire (*Poecile atricapillus*) et les plectrophanes des neiges (*Plectrophenax nivalis*) après une acclimatation à 10°C d'une durée minimale de six semaines (jour 0). Les oiseaux ont ensuite été exposés à des températures constantes de -5°C ou 28°C et mesurés de nouveau aux 4^{e} et 8^{e} jours d'acclimatation. Les résultats montrent que tous les oiseaux ont modifié leur phénotype métabolique dans les 8 premiers jours, selon différents patrons interspécifiques. Les bruants

ont démontré, tel qu'attendu, des augmentations métaboliques au froid et des diminutions à thermoneutralité. Par contre, la performance des mésanges et des plectrophanes n'a pas été influencée par la température, mais a varié dans le temps; les mésanges ont présenté des hausses des paramètres métaboliques, alors que les plectrophanes ont suivi le patron inverse. En considérant les changements obtenus entre les jours 0 et 8, nos résultats montrent également que le BMR a varié à des vitesses comparables aux deux traitements thermiques (+/- 7-8% par rapport aux valeurs de pré-acclimatation, après 8 jours), mais a augmenté plus rapidement que les taux métaboliques maximaux au froid (1-4%), probablement en raison de limitations intrinsèques du taux de croissance des organes reliés au BMR et au M_{sum}/MMR. Le MMR et le M_{sum} ont décliné plus rapidement à thermoneutralité (8-15%) qu'ils n'ont augmenté au froid (1-4%). Dans un contexte où les prédictions laissent présager une hausse de la stochasticité environnementale aux latitudes nordiques, une perte de capacité thermogénique lors des jours plus chauds d'hiver pourrait être nuisible si les oiseaux peinent à réajuster leur phénotype avec le retour du froid.

Ce premier article, intitulé «Rate of change in metabolic in response to thermal variations in three North American passerine species», a été rédigé par moi-même ainsi que mon superviseur François Vézina et ma collègue Fanny Hallot. Il sera soumis sous peu au Journal of Experimental Biology. En tant que première auteure, j'ai été engagée dans la conception du projet, le travail bibliographique, la mise en place de la méthode, l'acquisition de données, l'analyse des résultats et la rédaction de l'article. François Vézina a également participé à toutes ces étapes hormis l'acquisition de données. Fanny Hallot a été impliquée dans l'acquisition de données et la révision de l'article.

RATE OF CHANGE IN METABOLIC PERFORMANCE IN RESPONSE TO THERMAL VARIATIONS IN THREE NORTH AMERICAN PASSERINE SPECIES

Karine Dubois*, Fanny Hallot, François Vézina

Département de biologie, chimie et géographie, Université du Québec à Rimouski, 300 Allée des Ursulines, Rimouski (QC), G5L 3A1, Canada. Groupe de recherche sur les environnements nordiques BOREAS, Centre d'Etudes Nordiques, Centre de la Science de la Biodiversité du Québec.

* Corresponding author. E-mail: francois_vezina@uqar.ca

Abstract

In small avian species, acclimation and acclimatization to temperature are associated with changes in basal (BMR), summit (M_{sum}) and maximal (MMR) metabolic rates. In this context, experimental studies have focused on the difference between stable trait values obtained after several weeks of acclimation to different thermal treatments (i.e. amplitude of phenotypic flexibility). However, this approach does not inform on the rate at which species can adjust their phenotype in response to short-term temperature variations. With this study our aims were (1) to determine the pattern of adjustment in metabolic performance following a rapid temperature change, (2) to determine whether performance varies at similar rates during exposure to warm or cold environments, and (3) to determine if BMR and M_{sum}/MMR change at comparable rates during thermal acclimation. We measured these parameters in white-throated sparrows (*Zonotrichia albicollis*), black-capped chickadees (*Poecile atricapillus*), and snow buntings (*Plectrophenax nivalis*) after acclimation to 10°C for a minimum of six weeks (day 0). Birds were then exposed to constant temperatures of either -5°C or 28°C and measured again on the 4th and 8th day of acclimation. Results showed that all birds changed their metabolic phenotype within 8 days with patterns differing among species. Sparrows expressed the expected metabolic increases in the cold and decreases at thermoneutrality. However, performance in chickadees and buntings was not influenced by temperature but changed over time; chickadees presented increases in metabolic parameters while buntings followed the inverse pattern. Considering changes between day 0 and day 8 in sparrows, our results also showed that BMR varied at comparable rates in both thermal treatments (7-8%) but increased faster than maximal metabolic rates in the cold (1-4%), likely due to intrinsic limitations in growth rate of organs related to BMR and M_{sum}/MMR. However, MMR and M_{sum} declined faster at thermoneutrality (8-15%) than it increased in the cold (1-4%). In the context of an expected increase in environmental stochasticity at northern latitudes, a loss of thermogenic capacity during warm winter days could therefore be detrimental if birds are slow to readjust their phenotype with the return of cold days.

Keywords: thermal acclimation, phenotypic flexibility, bird, basal metabolic rate, summit metabolic rate, maximal metabolic rate, body composition.

1. Introduction

In small avian species, thermal acclimation and acclimatization are typically associated with flexible adjustments of two components of metabolic performance (Swanson, 2010). Basal metabolic rate (BMR) represents the minimal amount of energy used to maintain vital functions in a resting animal (McKechnie, 2008) while summit metabolic rate (M_{sum}) is a measure of maximal shivering heat production during cold exposure. As M_{sum} is positively correlated with cold tolerance (Swanson et al., 1996), it is commonly interpreted as an indicator of a birds' ability to endure cold environments. Both BMR and M_{sum} are known to increase in response to experimental and natural cold exposure (Cooper and Swanson, 1994; Klaassen et al., 2004; Liknes et al., 2002; Maldonado et al., 2009; Petit et al., 2013; van de Ven et al., 2013), and evidences suggest that this variation partly results from underlying changes in size and/or metabolic intensity of internal organs (Vézina et al., 2006; Williams and Tieleman, 2000; Zheng et al., 2008). For instance, cold-induced increases in BMR have been associated with the enlargement of organs responsible for energy acquisition, such as the intestines, gizzard, liver or kidneys (Liu and Li, 2006; Sabat et al., 2009; Williams and Tieleman, 2000; Zheng et al., 2008 but see Petit et al., 2014) while larger muscles, particularly those used for flight, have been shown to result in higher thermogenic capacity (Petit and Vezina, 2014; Swanson et al., 2013; Swanson and Vézina, 2015; but see Swanson et al., 2014b).

Birds preparing for migration also show increases in M_{sum} (Swanson and Dean, 1999; Vézina et al., 2007). This results from the development of pectoral muscles typically seen during the period preceding departure (Swanson and Dean, 1999; Vézina et al., 2007). Since both shivering and locomotion use the same muscles, larger flight muscles for migration brings the added benefit of increasing cold endurance (Swanson and Dean, 1999; Vézina et al., 2007). Perhaps not surprisingly, cold acclimatization also appears to induce the reverse pattern, where larger skeletal muscles and heart (Cooper, 2002; O'Connor, 1995; Saarela and Hohtola, 2003; Vézina et al., 2006), as well as the associated increase in oxygen carrying capacity (Petit and Vezina, 2014), seems to improve maximal locomotor performance (Zhang et al., 2015). The maximal amount of energy spent during intense exercise is called maximal metabolic rate (MMR). Like M_{sum}, MMR is thought to reflect physical endurance (McKechnie and Swanson, 2010; Piersma, 2011) and varies with pectoral muscle size (Wiersma et al., 2007).

Studies on flexible adjustment of metabolic performance during thermal acclimation typically report final amplitudes of response. Birds are generally separated into two temperature treatments and parameters are measured after an acclimation period varying between a few weeks (Bush et al., 2008; Maldonado et al., 2009; McKechnie et al., 2007; Williams and Tieleman, 2000) to several months (Klaassen et al., 2004). The amplitude of response is then determined as the difference between final phenotypes in cold and warm treatments. However, although the amplitude of metabolic flexibility informs on the response of a species, it does not allow for predicting the rate at which that species can change its phenotype. For instance, two species could have similar amplitudes of response, which would make them considered equally flexible, while they may not be able to reach their new phenotype at the same rate.

As far as we know, only one study investigated the rate of change in metabolic performance in response to temperature variations in free-living birds. Swanson and Olmstead (1999) found that free-living dark-eyed juncos (*Junco hyemalis*) and black-capped chickadees (*Peocile atricapillus*), which are generally associated with forest habitats (Mobley, 2008), tended to adjust their BMR and M_{sum} within 14-30 days following changes in average ambient temperature while American tree sparrows (*Spizella arborea*), a species associated with open areas (Poole, 2005), responded much more rapidly, within 5 days after a temperature change. Experimental evidences also suggest that the rate of change can differ depending on whether the environment is warming up or cooling down. Indeed, Barcelo et al. (2009) found that BMR of rufous-collared sparrows (*Zonotrichia capensis*) changed more rapidly when temperature went from 22°C to 15°C (cold treatment), increasing by 28.5% over 4 weeks compared to birds showing only a 13.2% decline in BMR when temperature changed from 22°C to 30°C (warm treatment) over the same period (see also McKechnie et al., 2007 for a similar study). Whether a similar pattern also exists for M_{sum}/MMR remains, however, to be determined.

Altogether, these findings suggest that the rate of change in metabolic performance in response to temperature variation may differ, not only among species, but also depending on whether animals are facing an increase or a reduction in temperature. This is important in the context of ongoing climate change, since acute weather events as well as rapid daily temperature fluctuations are expected to increase in frequency and amplitude (Easterling et al., 2000; IPCC, 2013; Katz et al., 2005). Adapting a phenotype to a new constraining environment is admittedly beneficial but adjusting it too late or too slowly could potentially have negative fitness consequences. As of today, we are not aware of experimental studies that have precisely described patterns of avian metabolic flexibility in response to thermal changes within a time period shorter than 3 weeks.

For this experiment, we worked with three passerine species contrasted by their natural thermal environments, black-capped chickadees ($n = 25$), white-throated sparrows (*Zonotrichia albicollis*, $n = 24$), and snow buntings (*Plectrophenax nivalis*, $n = 24$). Our objectives were (1) to characterize the pattern of adjustment in metabolic performance following a rapid change in temperature, (2) to determine whether metabolic parameters vary at similar rates during exposure to warm or cold environments, and (3) to determine whether BMR and M_{sum}/MMR change at comparable rates during thermal acclimation. We therefore measured these metabolic parameters, as well as components of body composition and food intake, in captive birds kept for a minimum of six weeks at 10°C (day 0) and then on the 4th and 8th days of thermal acclimation to constant temperature of either -5°C or 28°C.

2. Materials and methods

(a) Experimental birds and acclimation protocol

For this study, we worked with three North American species that live in contrasted thermal environment. Black-capped chickadees (10-14g) are non-migratory birds mostly found in forested habitats of the United States and Canada. Since they are non-migratory, chickadees must face highly seasonal environments throughout the year. For example our source population, in eastern Québec, Canada, experience a range of monthly mean temperatures varying between 16.8°C (±2.1°C) in July and –8.9 (±4.1°C) in February (Environment Canada climate database, Pointe-au-Père weather station, 48°30'50" N, 68°28'06" W, 24 km from the field site). White-throated sparrows are associated with woodlands (Mobley, 2008) and migrate between their breeding grounds in southern Canada and their wintering habitat in southern USA. Therefore, although they can acclimate to cold ambient temperatures (Kontogiannis, 1968; McWilliams and Karasov, 2014; Metcalfe et al., 2013; Seibert, 1949), these birds remain in relatively warm environments throughout the year (0-20°C in winter, (Odum, 1949) to 5-21°C in summer at our location (Environment Canada climate database)). In contrast, the snow bunting is a circumpolar species that breed in the Arctic tundra. In North America, these birds spend the cold season in open fields of southern Canada and northern USA. Therefore, except for a few weeks during the breeding season where temperatures are above freezing (e.g. mean June temperature is 3.1 ±1.5°C at a breeding site on Southampton island, Nunavut Canada, Love et al., 2010), this species remains in a cold and snowy environment year round (Poole, 2005).

Snow buntings (n = 24) were captured using baited walk-in traps in open fields around Rimouski, Québec, Canada between February 24th and March 2nd 2013. White-throated sparrows (n = 24) were captured at the Forêt d'enseignement et de recherche Macpès, near Rimouski, by mist net as well as in a private garden using a walk-in trap at Le Bic, Québec, Canada between April 27th and May 7th 2013. Black-capped chickadees were captured at the Forêt d'enseignement et de recherche Macpès using Potter traps (Mandin and Vézina, 2012). A first group of 24 chickadees that was planned for this experiment was captured between December 2012 and May 2013. However, part of our captive population died before the experiment due to a bacterial infection and only 9 healthy birds could be measured. Another 16 chickadees were then captured in October and November 2013 for a second round of measures. The potential difference between groups was considered in statistical analyses but no significant differences were found. Therefore data from all individuals were combined and are presented here (n = 25).

All birds used in this experiment were housed at the avian facility of the Université du Québec à Rimouski, where the experiment took place. After capture, birds were kept at room temperature and constant photoperiod (12L: 12D) in individual cages (31 cm D x 40 cm H x 40 cm W) where they had access to water and food ad libidum. The experiment began by first maintaining the birds at 10°C (± 2°C) for a minimum of six weeks, which gives time for stabilizing the metabolic phenotype (Barcelo et al., 2009). Then each species experienced the same procedure. All birds were randomly assigned to either of two groups of 12 individuals, one to be acclimated to a "thermoneutral treatment" and the other to be acclimated to a "cold treatment" (final n for chickadees: 12 in the thermoneutral treatment and 13 in the cold treatment).

A day prior to the change in temperature (day 0), a first series of measurement (body mass, food intake, muscle thickness and fat reserves, BMR, Msum and MMR) were obtained (see below). The next morning (at around 8:00), birds were transferred from the 10°C room to a second identical room where temperature was set to either 28°C (± 4°C) for the thermoneutral group (within the thermoneutral zone for all species, Cooper and Swanson, 1994; Kontogiannis, 1968; Scholander et al., 1950) or -5°C (± 2°C) for the cold group. The transfer took place in less than 20 minutes and birds were kept in this new thermal environment until the end of the experiment. We then proceeded to repeat all measurements on the 4th and 8th day after the change in temperature for all birds. Our respirometry procedure limited the number of individuals that could be measured simultaneously to 3 birds a day. To insure that all birds were measured at the same time after the change in temperature, we used an experimental sequence where 3 individuals of a single species were transferred to the experimental room every day until 12 birds had been moved (species were randomly picked each day). This allowed for monitoring each group of 3 birds at their 4th and 8th day of acclimation.

(b) Food intake

We measured individual food intake on the day preceding metabolic measurements to evaluate raw energy input but also because an increase in daily food consumption could indirectly influence BMR through adjustments in gut size (Williams and Tieleman, 2000).

Snow buntings and white-throated sparrows (granivores) were fed with oil sunflower seeds and a commercial wild bird seed mix (Coopérative fédérée de Québec, Trois-Rivières, Canada) while black-capped chickadees (mainly insectivores) were fed with oil sunflower seeds and a commercial preparation of insect mash (Insect Patee, Orlux, Deinze, Belgium). A pre-weighted amount of food was offered in the morning (at around 8:00h) in a 1.7L glass recipient placed on the cage floor to limit food spillage. The next morning, the remaining food was removed at the same hour before ad libidum access was resumed. This food was kept dry and weighed within the next day. As birds could have preferred sunflower seeds over other foodstuff (Devost et al., 2014), sunflower seeds were manually separated from the other seed types and weighed again. Although analyses were performed by food type (see Results), food intake is presented in figures for sunflower seeds and for other food types (insect mash for chickadees and mixed seeds for buntings and sparrows).

(c) Body mass, fat scores, muscle scores and ultrasonography

On days 0, 4 and 8, we measured body mass (0.01g) as well as the size of fat reserves and pectoral muscles of all birds. We estimated the size of fat reserves visually using standard fat scores (on a scale of 1 to 5), according to Gosler (1996). The size of pectoral muscles was then first estimated by visual examination using scores ranging from 0 to 4 according to Busse (2000). Pectoral muscle thickness and cross-sectional area of thigh muscles were then determined non-invasively using ultrasonography (Dietz et al., 1999; Royer-Boutin et al., 2015; Swanson and Merkord, 2013). This was done using a LOGIQe ultrasound scanner fitted with a linear probe set at 12 MHz (GE Healthcare, Wauwatosa, WI, USA). We obtained three independent measurements of the left pectoral muscles and the right thigh muscles for each bird on each measurement day. To avoid wetting the birds' feathers with ultrasound transmission gel, the gel (Parker Aquasonic 100) was contained in a latex condom attached around the probe, which was dipped in lukewarm water before measurements. This arrangement created a cushion of gel on the probe tip, which covered the left pectoral muscles or the whole thigh during measurements. To expose the skin, we wetted the birds' feathers with water and pushed feathers aside. Pectoral muscle thickness was measured by placing the probe transversally on the breast at an angle of 90° to the keel, 1–2 mm from the upper keel tip. This formed a cross-sectional image on which the length between the base of the keel and the muscle surface could be measured with a 45° angle relative to the keel. The size of thigh muscles was obtained by fitting an ellipse measuring tool on images and by measuring the length of horizontal and vertical axes to calculate thigh cross-sectional area. Using an average of the two closest measures (data not shown) rather than the mean of the three replicates did not change our results and therefore means of the three measures are presented here. Ultrasound examinations lasted 8-12 min per bird.

(d) Respirometry

For each respirometry trials, we followed the same sequence. MMR was measured first in the morning starting at around 10:30 (one hour after ultrasound measurement), followed by a minimum of 2 hours of rest before Msum measurement. BMR was started at the end of the day (between 18:00 and 19:00) after a rest period ranging from 1 to 5.5 hours (depending on duration of Msum, see below).

MMR

We measured MMR using a handmade PVC hop-flutter wheel (Chappell et al., 1999) with an effective volume of 2.97 L. Before a trial, the wheel was first flushed for at least 5 minutes with dry, CO2-free air (analyzer set to 21.95% oxygen). Birds were then weighed (± 0.01 g) and introduced into the wheel, which was covered with a sheet, where they were allowed to calm down for 10 minutes. The sheet was then removed and wheel rotation was initiated and accelerated every 5 minutes. During MMR trials, all individuals were active, engaging in short jumps and fluttering. When birds showed signs of fatigue (reluctance to move, resting on the wheel floor) and/or O2 levels were stable for several minutes even if the bird kept exercising, the wheel was stopped. Trials lasted around 10-15 minutes. Birds were then given a few minutes of rest in the chamber and were weighed a second time. Reported body mass was calculated as the average between values measured before and after MMR measurement. During trials with snow buntings, four ping-pong balls were added into the chamber to stimulate the birds to move. This technique was not needed for the other two species.

M_{sum}

M_{sum} was measured using a sliding cold exposure protocol (Swanson et al., 1996), measuring three birds simultaneously. Birds were first weighed (± 0.01 g) and placed in airtight stainless steel metabolic chambers (1.5 L for black-capped chickadees and 2.1 L for white-throated sparrows and snow buntings) fitted with perches and copper-constantan thermocouples connected to a Sable Systems TC-2000 thermocouple reader (Sable Systems, Las Vegas, NV, USA) for chamber temperature measurements. The chambers were placed inside a homemade temperature cabinet controlled with the software EXPEDATA (Sable Systems, Las Vegas, NV, USA). Birds were then exposed to air for a 10-min habituation period. Average flow rates and temperatures during this period were 450 mL/min and 3°C for black-capped chickadees, 550 mL/min and -6°C for white-throated sparrows, and 650 mL/min and -15°C for snow buntings. We then switched gas influx to helox (79% helium and 21% oxygen) and used respective flow rates of 900 mL/min, for chickadees and sparrows and 1200 mL/min for snow buntings. Flow rates were controlled by mass flow valves (Sierra Instruments, Side-Trak®, Monterey, CA, USA) previously calibrated for air and helox with a bubble-O-meter (Dublin, OH, USA). Using a Servomex gas purity analyzer (model 4100, Boston, MA, USA), we measured a helox baseline value for approximately 3-5 min. before recording the birds' oxygen consumption every 5 seconds until the end of trial. During this time, temperature was lowered by 3°C every 20 min until the birds entered hypothermia, (i.e. oxygen consumption steadily declining for several minutes), or until birds reached the end of their species-specific program (145 min for chickadees, 125 min for sparrows, and 155 min for buntings). Birds were then immediately removed from chambers and, to confirm hypothermia, their body temperature was measured with a thermocouple reader (Omega model HH-25KC, NIST-traceable, Omega, Montréal, QC, Canada) using a copper-constantan thermocouple inserted into the cloacae approximately 10 mm deep. Following this procedure, we found that two chickadees, 6 sparrows and 13 buntings measurements did not result in birds being hypothermic at the end of the trial. However, hypothermia is not a necessary prerequisite to validate M_{sum}, as the maximal oxygen consumption occurs earlier than the decline indicating hypothermia during cold exposure (Dutenhoffer and Swanson, 1996). Removing non-hypothermic measures from analyses had no influence on final findings. These data were therefore kept in our datasets. As for MMR, birds were weighed again at the end of trials and average body mass was used for M_{sum} analyses.

BMR

Birds were placed into metabolic chambers for BMR measurements between 18:00 and 19:00, and taken out the next morning between 08:00 and 08:30. Metabolic chambers were put in a PELT-5 (Sable Systems, Las Vegas, NV, USA) temperature cabinet in which temperature was set at 25°C (within the thermoneutral zone for all species: Cooper and Swanson, 1994; Kontogiannis, 1968; Scholander et al., 1950) . Birds received constant dry, CO2-free air (450 mL/min, 550 mL/min and 650 mL/min for chickadees, sparrows and buntings, respectively) throughout the night. During recordings, the air sent to the analyzer alternated between reference air (10 min) and chambers' air (40 min) using a multiplexer (Sables Systems MUX, Sable Systems, Las Vegas, NV, USA). Body mass was measured before and after BMR trials and average values were used in analyses.

MMR, M_{sum}, and BMR calculations were respectively based on the highest averaged 1 min, highest averaged 10 min, and lowest averaged 10 min of oxygen consumption using equation 10.1 in Lighton (2008). M_{sum} and MMR were calculated using the instantaneous measurement technique (Bartholomew et al., 1981), whereas BMR was calculated with the steady state approach. Birds were fasted for an hour before BMR trials and the duration of trials insured a post-absorptive state at time of measurement (obtained after 4:45 ± 12 min on average). Shivering and exercise in birds are mainly supported by lipid oxidation (Vaillancourt et al., 2005). We therefore estimated energy consumption for all trials using a constant equivalent of 19.8 kJ/L02 and converted units to Watts (Gessaman and Nagy, 1988).

Factorial aerobic scopes for exercise (MMR/BMR) measured with a hop-flutter wheel typically varies around 10 X BMR in birds (McKechnie and Swanson, 2010) although lower values such as 6 to 7 X BMR have been observed for tropical birds (Wiersma et al., 2007) and juvenile house sparrows (Chappell et al., 1999). In our study, MMR exceeded BMR by 4.5 to 5.6-fold, which may be considered low relative to available observations (McKechnie and Swanson, 2010). However, although there are no comparable data for black-capped chickadees and snow buntings, it should be noted that Price and Guglielmo (2009) obtained MMR values ranging between 8.5 and 10.5 mL02/g*h in white-throated sparrows while our values in that species averaged 13.04 mL02/g*h. Given this comparable set of values, and the fact that all birds showed signs of fatigue justifying the end of measures after sustained efforts, we are confident in the values we obtained.

(e) Molt in snow buntings

In this experiment, all birds were exposed to constant photoperiod. This, however, did not prevent 16 snow buntings from entering into some level of feather molt during the course of the experiment. Since feather molt may influence metabolic parameters such as BMR (Lindström et al., 1993; Vézina et al., 2009) and influence heat loss in a cold environment, we measured the intensity of molt by scoring wing and tail feather growth as well as body plumage growth and included these variables in our analyses. The ten primary feathers of both wings together with the rectrix feathers were each scored on a scale of 0 (new, very small pin) to 5 (full grown feather) for a maximum score of 150 for a non-molting individual. Body plumage was scored on a scale of 0 to 2, with 0 = old plumage, 1 = few pins visible and 2 = more than half of the body surface covered with pins.

(f) Statistical analysis

We used linear mixed models (with REML approach) to investigate the effects of day (0, 4 or 8), thermal treatment (cold and thermoneutral), and their interaction on body mass, food intake, muscle size, fat reserves and metabolic performance (BMR, M_{sum}, and MMR). All models controlled for repeated measures by including "bird ID" as a random variable. When studying effects on metabolic performance, we also controlled for the influence of body size by including a composite measurement of structural size as a covariate in models. We used body size rather than body mass because metabolic variations in response to cold are likely to result in large part from body remodeling (Liknes and Swanson, 2011b; Petit et al., 2014; Swanson and Vézina, 2015; Zheng et al., 2008). Therefore, statistically removing the effect of body mass would likely remove part of variation that we were interested in. Structural size was computed using a principal component analysis combining variations in beak, head, tarsus, wing and tail length for each species. The first component was then extracted and used as the covariate in models including metabolic parameters. We estimated the rate of change of each metabolic parameter by calculating the percent change at day 4 and day 8 relative to day 0 (set at 100%) in each thermal treatment. In snow buntings, we considered the potential effect of feather molt on metabolic parameters by including molt scores (body plumage and wing plus tail feather) as covariates in models. One individual was molting heavily compared to the rest of the group (wing and tail score of 56 vs. mean score of 144) and was removed from analyses. Differences were then analyzed using post-hoc Tukey tests.

We used two approaches to investigate relationships between variations in food intake and BMR and between muscle size and M_{sum}/MMR. First, we included individual food intake variables as a covariate in each species' BMR models (one set of analyses per food intake variable). Similarly, we tested for effects of muscle size on MMR and M_{sum} by including ultrasound measures of either pectoral or thigh muscles as covariates in corresponding models. Second, we calculated the changes in food intake, muscle size, BMR, M_{sum} and MMR between day 0 and day 8. We then used least square linear regressions to test for relationships, across treatments, between the change in food intake and BMR as well as the change in muscle size and M_{sum}/MMR.

In all models, covariates and interactions were removed when non-significant and visual inspection confirmed normality of residuals. All statistical analyses were performed with JMP v.10.0 and data are presented as mean ± s.e.m.

3. Results

Body mass, muscle size and fat reserves

All species showed the same pattern of body mass variation. Body mass did not differ between thermal treatments (treatment: $p > 0.8$ in sparrows and chickadees), although snow buntings tended to be lighter in the cold ($p = 0.072$). However, body mass decreased significantly with time in all species (black-capped chickadees: $F_{2,48} = 4.64$, $p = 0.014$;

white-throated sparrows: $F_{2,46} = 9.69$, $p < 0.0005$; snow buntings $F_{2,38} = 36.04$, $p < 0.0001$) (Fig. 1). The loss of mass in chickadees appeared relatively gradual, being significant only when comparing day 0 and day 8 (-2.2%) (Fig. 1A). In the other two species, body mass declined within the first 4 days (white-throated sparrows: -3.7%, snow buntings: -14.7%) and remained stable afterwards, as it did not differ between day 4 and day 8 (Fig. 1B, C).

In black-capped chickadees, fat reserves changed over time in a way that differed between treatments (time*treatment: $F_{2,46} = 5.01$, $p = 0.011$). Birds exposed to the cold lost body fat within the first 4 days while those kept at thermoneutrality appeared to increase the size of their fat reserves. However the interacting effects of time and treatment were not strong enough to reach significance in post-hoc analyses (Fig. 1D). In sparrows, fat scores were higher in the thermoneutral group (mean score: 3.36 ± 0.16) than in the cold group (mean score: 2.36 ± 0.11, treatment: $F_{1,22} = 11.44$, $p < 0.005$). However, in both groups there was a loss of fat reserves in the first 4 days, which was partly recuperated by day 8 (time: $F_{2,46} = 6.14$, $p < 0.005$, Fig. 1E). In snow buntings, fat reserves were not affected by thermal treatments (treatment: $p = 0.2$) and declined over the 8 days of the experiment (time: $F_{2,40} = 3.38$, $p = 0.044$, Fig. 1F).

We found no significant time and treatment effects on muscle scores or on pectoral and thigh muscle size measured by ultrasound in black-capped chickadees ($p > 0.09$ in all cases). In white-throated sparrows, birds forming the thermoneutral group had 4.6% thicker pectoral muscles on average (5.94 ± 0.08 mm) than those forming the cold group (5.67 ± 0.07 mm, treatment: $F_{1,22} = 5.65$, $p = 0.027$), a finding also apparent in muscle scores (treatment: $F_{1,22} = 7.07$, $p = 0.014$, cold: 2.14 ± 0.06, thermoneutral: 2.5 ± 0.08). Pectoral muscles did not change over time (time: $p > 0.09$ in both cases), however, and the interaction was also not significant (treatment*time: $p = 0.5$ in both cases). In contrast, sparrows of both thermal treatments grew their thigh muscles by 15.2% over the 8 days of the experiment (time: $F_{2,46} = 14.29$, $p < 0.0001$; treatment: $p = 0.6$, Fig. 2A). Snow buntings lost 7.1% of their pectoral muscles over the 8 days as measured by ultrasound (time: $F_{2,42} = 5.77$, $p = 0.006$, treatment: $p = 0.09$, Fig 2B) and this was also apparent in muscle scores (time: $F_{2,41} = 8.55$, $p < 0.001$; treatment: $p = 0.9$, Fig. 2C). However, we could not detect any changes in thigh muscle size (time: $p = 0.4$; treatment: $p = 0.6$).

Food intake

Within the first 4 days of being exposed to the cold, chickadees increased their total food intake by 32.5% while no significant changes were observed in those kept at thermoneutrality (treatment*time: $F_{2,47} = 8.97$, $p < 0.001$). Sunflower seeds consumption followed the same trend as birds ate 42.5% more sunflower seeds after 4 days when exposed to the cold while no changes were observed at thermoneutrality (treatment*time: $F_{2,43} = 5.06$, $p = 0.011$, Fig. 3A). Chickadees acclimating to both treatments also increased their consumption of insect mash in the first 4 days of the experiment and remained stable thereafter (time: $F_{2,48} = 4.11$, $p = 0.023$, Fig. 3D) with those living in the cold nevertheless eating 40.7% more on average (0.065 ± 0.004 g/h) than those kept at 28°C (0,046 ± 0.004 g/h, treatment: $F_{1,24} = 4.84$, $p = 0.038$). White-throated sparrows showed a similar pattern. Birds exposed to the cold increased their total food consumption by 115.8% within the first 4 days while those at thermoneutrality showed no significant changes, despite an increasing trend (treatment*time: $F_{2,44} = 9.69$, $p < 0.0005$). Likewise, sunflower seed consumption increased by 151.4% within the same period in the cold group while the thermoneutral group tended to increase its consumption, albeit not significantly (treatment*time: $F_{2,44} =12.02$, $p < 0.0001$, Fig. 3B). Although the interaction was not was quite significant (treatment*time: $F_{2,44} = 3.14$, $p = 0.053$), the trend was similar for the mixed seeds intake. Post hoc Tukey test nevertheless showed that sparrows form the cold treatment increased their intake of mixed seeds by 86.0% to reach a plateau in the first 4 days while birds at thermoneutrality showed a non-significant increase in seed consumption (Fig. 3E). Snow buntings kept in the cold increased their total food intake throughout the experiment with no apparent plateau. On the 8th day, the birds were consuming 92.5% more food than on day 0 (treatment*time: $F_{2,40} = 8.53$, $p < 0.001$). This however was not apparent in birds kept at thermoneutrality. The same pattern was visible for sunflower seed consumption, with birds kept in the cold eating 124.1% more on average on the 8th day compared to day 0 (treatment*time: $F_{2,40} = 8.15$, $p = 0.001$, Fig. 3C). Consumption of mixed seeds increased in both treatments by 43.4% between day 4 and day 8 (time: $F_{2,42} = 6.04$, $p = 0.005$; treatment: $p = 0.3$, Fig. 3F).

Metabolic parameters

Within the 8 days of the experiment, all species showed changes in parameters of metabolic performance but the patterns differed among species. In black-capped chickadees, body size was not related to any metabolic parameter (> 0.7 in all cases). BMR was not affected by thermal treatments ($p = 0.7$) but increased over time, reaching a level on day 8 that was 12.3% higher than on day 0 (time: $F_{2,48} = 6.85$, $p < 0.005$, Fig. 4A). M_{sum} also changed with time and independently from thermal treatment (time: $F_{2,47} = 3.51$, $p = 0.038$; treatment $p = 0.2$). It increased by 7.1% between day 4 and day 8 but this effect was not strong enough for a post-hoc Tukey test to find a significant difference among days (Fig. 4B). MMR remained independent from thermal treatments and did not change significantly over time (time: $p = 0.8$; treatment: $p = 0.7$).

Body size did not influence metabolic parameters in sparrows (> 0.1 in all cases) but metabolic performance nevertheless changed over time with patterns that depended on temperature. Indeed, BMR varied in interaction with time and treatment ($F_{2,40} = 8.39$, $p < 0.001$, Fig. 5A), increasing in the cold by 7.8% over 8 days and decreasing by 6.8% over the same period at thermoneutrality (Fig. 5B). However, this effect was not strong enough for a post-hoc Tukey test to detect significant differences between days and treatments (Fig. 5A). M_{sum} followed a similar pattern (treatment*time: $F_{2,42} = 8.13$, $p = 0.001$, Fig. 5C). Birds kept at thermoneutrality showed a significant 7.5% decline in M_{sum} between day 0 and day 8 while individuals maintained at -5°C increased their thermogenic capacity by 4.3% over the same period (Fig. 5D), although this latter change was not significant (Fig. 5C). Thermal treatment on its own also influenced M_{sum} ($F_{1,22} = 6.06$, $p = 0.022$), with birds kept in the cold expressing a M_{sum} 7.5% higher (2.04 ± 0.02 W) on average than those experiencing thermoneutrality (1.83 ± 0.03 W). White-throated sparrows also showed a general decline in MMR over time (time: $F_{2,44} = 3.50$, $p = 0.039$) with a time effect that varied with treatment (treatment*time: $F_{2,44} = 4.95$, $p = 0.012$). Indeed, birds maintained at

28°C showed a 14.8% decline in MMR between day 0 and day 8 while no significant changes were observed in birds kept at -5°C (0.9% increase, Fig. 5E and 5F).

Despite using a constant photoperiod regime (see Material and Methods), sixteen snow buntings molted part of their feathers during the experience. We therefore quantified molt intensity (body plumage as well as wing and tail feathers, see Material and Methods) and considered the potential effect of molt on metabolic parameters by including these variables as covariates in models. BMR decreased by 9.9% in snow buntings between day 0 and day 8 (time: $F_{2,34} = 3.68$, $p = 0.036$, Fig. 6A) and this effect was independent from thermal treatments ($p = 0.7$), body size ($p = 0.6$), and molt (wing and tail: $p = 0.9$; breast: $p = 0.7$). Time and thermal treatment did not influence size-corrected M_{sum} in buntings (size: $F_{1,13} = 9.62$, $p = 0.008$; time: $p = 0.1$; treatment: $p = 0.8$), which was also not influenced by molt (wing and tail: $p = 0.6$; body: $p = 0.4$). In contrast, MMR was down-regulated by 14.2% in the first 4 days in birds from both treatments (time: $F_{2,40} = 15.13$, $p < 0.0001$; treatment: $p = 0.3$; size: $p = 0.6$, Fig. 6B). Molt also influenced MMR, with birds either not molting or molting only partially their wing and tail feathers showing higher MMR (wing and tail: $F_{1,37} = 5.40$, $p = 0.026$; body: $p = 0.9$), presumably because molting individuals were less active in the hop-flutter wheel than non-molting birds.

Neither total, sunflower seed, insect mash or seed mix intakes were related to BMR in black-capped chickadees and white-throated sparrows when considered as covariates ($p > 0.1$ in all cases for both species). In snow buntings, when considering the significant effect of time, both total food intake and sunflower seed intake were significantly and positively related to BMR (total intake: $F_{1,59} = 4.05$, $p = 0.049$, time: $F_{2,35} = 5.68$, $p = 0.007$; sunflower seed intake: $F_{1,60} = 7.34$, $p = 0.009$, time: $F_{2,35} = 3.63$, $p < 0.005$; seed mix intake $p = 0.6$). Pectoral and thigh muscle size were not significantly related to either M_{sum} or MMR in sparrows and buntings ($p > 0.2$ in all cases) but the size of thigh muscles significantly and positively varied with M_{sum} and MMR in black-capped chickadees (M_{sum}: $F_{1,49} = 4.67$, $p = 0.036$, MMR: $F_{1.49} = 4.43$, $p = 0.04$) while considering the effect of time ($F_{2,47} = 3.84$, $p = 0.029$). MMR also tended to vary positively with pectoral muscle thickness ($F_{1,71} = 3.30$, $p = 0.073$) but this trend was not found for M_{sum} ($p = 0.3$).

Using least square regressions to investigate relationships between changes in parameters from day 0 to day 8, food intake and BMR were not related in black-capped chickadees and snow buntings ($p > 0.1$ in all cases) but white-throated sparrows showed a positive relationship between the change in all food intake variables and the change in BMR (total food intake: $r^2 = 0.27$, $n = 21$, $p = 0.017$; sunflower seed intake: $r^2 = 0.22$, $n = 21$, $p = 0.033$; seed mix intake: $r^2 = 0.22$, $n = 21$, $p = 0.031$). One bird from the thermoneutral treatment appeared as an outlier, showing a relatively large increase in food intake associated with a decrease in BMR. Removing this individual from analyses substantially increased the fit of relationships (total food intake: $r^2 = 0.51$, $n = 20$, $p = 0.004$; sunflower seed intake: $r^2 = 0.43$, $n = 20$, $p = 0.002$; seed mix intake: $r^2 = 0.46$, $n = 20$, $p = 0.001$, Fig. 7A). Investigating relationships between changes in muscle size and maximal metabolic rates, regressions were not significant for any species when considering thigh muscles ($p > 0.2$ in all cases). When considering pectoral muscles, we also found no relationships ($p > 0.1$ in all cases) but, here again, one individual snow bunting appeared as an outlier, expressing one of the largest increase in muscle size and the largest decline in M_{sum}. Removing this individual from the analysis revealed a positive relationship between the change in pectoral muscles and the change in M_{sum} in this species ($r^2 = 0.29$, $n = 17$, $p = 0.026$, Fig. 7B).

4. Discussion

Using three passerine species from contrasting natural thermal environments, our aims in this study were (1) to determine the pattern of variation in metabolic performance after an acute change in ambient temperature, (2) to investigate whether components of metabolic performance vary at comparable rates during thermal acclimation, and (3) to determine whether rates of change in metabolic performance differ during exposure to warm and cold environments. Our results showed significant phenotypic adjustments in the first 8 days following a 15-18°C temperature change in all species. They also showed that these adjustments differed among species.

Energy balance

Regardless of thermal treatment, all species lost body mass in the first 4 days of the experiment to reach a lower and apparently stable mass between day 4 and day 8. This was paralleled by a decline in fat score in the first 4 days in cold acclimating chickadees and in sparrows of both treatments, while all buntings lost fat reserves throughout the experiment. We could not detect significant changes through time in chickadee muscle size measured by muscle scores or ultrasound (but see Royer-Boutin et al. (2015) for a discussion on the limit of precision in measurement by ultrasound in this species). Similarly, although birds acclimating to cold maintained smaller pectoral muscles on average than those kept at thermoneutrality (based on ultrasound measures), white-throated sparrows kept the size of their pectoral muscles constant throughout the experiment. In contrast, snow buntings acclimating to both thermoneutrality and cold showed a continuous decline in pectoral muscle score and thickness. Therefore, despite a 33-115% increase in total food consumption in birds acclimating to cold, it appears that individuals from all species, whether they were facing cold or thermoneutral temperatures, were in negative energy balance in the first half of the experiment.

The loss of mass and fat reserves in birds acclimating to cold is not surprising given the added thermoregulation cost. These birds compensated by increasing their daily energy intake but the expenses likely outweighed the energy income in the first half of the experiment, leading to a loss of mass, fat reserves and, in snow buntings, a loss of muscles. However, the finding of a negative energy balance in birds being alleviated from thermoregulatory requirements came as a surprise given that these individuals did not change their daily food consumption. Birds wintering in cold environments typically maintain a heavier body mass, larger fat reserves and pectoral muscles than during summer (Blem, 1976; Liknes and Swanson, 2011b; Petit et al., 2014). It is therefore expected that individuals undergoing a reduction of thermostatic costs would decrease the size of these body components to reduce locomotion costs and maintain maneuverability (Dietz et al., 2007; Krams, 2002; Kullberg et al., 1996; Lind et al., 1999). However, the mechanism by which this change may have happened in captive birds maintaining constant energy intake is not clear and will require further investigation.

White-throated sparrows were the only birds showing significant positive changes in body components, increasing the size of their thigh muscle from day 0 to day 8 in both cold and thermoneutral treatments. We believe, however, that this unexpected muscle growth results from a training effect caused by the MMR trials. Sparrows hopped to a greater extent than the other species during trials (pers. obs.). Chickadees tended to spend more time fluttering in the center of the wheel while snow buntings were much less active and needed a motivation measure (ping-pong balls) to stimulate locomotion. Therefore, it is likely that the increase in thigh muscle size recorded in sparrows has been provoked by the MMR trials, a finding consistent with the positive effect of daily flight training on pectoral muscles thickness in house sparrows (*Passer domesticus*) (Zhang et al., 2015).

Patterns of variation in metabolic performance

Because seasonal acclimatization to winter at northern latitudes leads to elevated metabolic performance (Marsh and Dawson, 1989; Swanson, 2010; Swanson and Vézina, 2015), we expected to find an increase in BMR and M_{sum} in birds exposed to the cold and a reverse pattern in birds acclimating to thermoneutrality. Although white-throated sparrows did show the expected pattern, black-capped chickadees and snow buntings showed variations in metabolic rate that were inconsistent with our predictions.

Chickadees acclimating to both cold and thermoneutrality showed the same response, a 12% increase in BMR over 8 days, a moderate, but non-significant, 7% increase in M_{sum} between day 4 and day 8 and no changes in MMR over time. The causes for these changes in chickadees are not obvious. In birds, BMR variations are expected to reflect changes in size and activity of internal organs (Barcelo et al., 2009; Cavieres and Sabat, 2008; Kersten and Piersma, 1987; Maldonado et al., 2009; McKechnie, 2008; Petit et al., 2014; Piersma et al., 1996) and, in birds acclimating to cold, organs associated with energy acquisition are thought to play an important role in BMR changes (Liu and Li, 2006; Sabat et al., 2009; Tieleman et al., 2003; Williams and Tieleman, 2000; Zheng et al., 2008).

However, the lack of relationship between daily food intake and BMR in chickadees suggests that the adjustments in digestive organs that may have occurred over the 8 days of acclimation had little influence on maintenance energy expenditure. Using body composition analyses from dissections, Petit et al. (2014) also found little support for the influence of digestive organs on BMR variations in free-living wintering black-capped chickadees. The reasons for the increase in BMR observed here therefore remains unexplained.

Variations in M_{sum} and MMR are expected to relate positively with muscle size (Chappell et al., 1999; Hammond et al., 2000; Petit and Vezina, 2014; Swanson and Vézina, 2015; Swanson et al., 2013). We could not detect changes over time in pectoral or thigh muscle size in chickadees using either muscles scores or ultrasonography. However, our finding of a significant influence of thigh muscles on M_{sum} and MMR and nearly significant effect of pectoral muscles on MMR does bring support to the role of muscles in driving maximal metabolic rates. Our results therefore add on to comparable observations made in this and other species (Petit et al., 2014; Swanson et al., 2014a; Swanson and Vézina, 2015; Swanson et al., 2013).

In snow buntings, irrespective of thermal treatment, BMR declined by 10% and MMR decreased by 14% between day 0 and day 8. Of the three species, buntings experienced the greatest relative loss of mass (15%). They also lost 7% of their pectoral muscles based on thickness measurement. Assuming that the loss of pectoral muscles reflects an overall decrease in lean mass, negative changes in lean body component presumably drove the observed decline in BMR (Scott and Evans, 1992). However, in contrast with observations in chickadees, we also found that food consumption was positively correlated with BMR in this species. Therefore, these data are consistent with the expected influence of digestive functions on maintenance costs in cold acclimated birds (Liu and Li, 2006; Sabat et al., 2009; Williams and Tieleman, 2000; Zheng et al., 2008) and suggest that this effect may therefore differ between species. Given that both M_{sum} and MMR reflect active aerobic metabolism of skeletal muscles (Chappell et al., 1999; Hammond et al., 2000; Petit and Vezina, 2014; Swanson et al., 2013), the observed decrease in muscle size likely drove the changes in maximal metabolic performance. We could not detect an effect of time on M_{sum} per say, but the positive relationship across treatments between the change in M_{sum} and the change in pectoral muscle thickness between day 0 and day 8 nevertheless supports this hypothesis.

Of the three species, white-throated sparrows were the only birds showing the expected pattern of variation in metabolic parameters. Indeed, these birds showed a general response where BMR and M_{sum} were found to be up to 8% higher after 8 days of cold acclimation while an opposite pattern was found in birds kept at thermoneutrality (up to 8% loss). MMR also changed in these birds. However, the only clear effect in this case was observed at thermoneutrality, where birds lost 15% of their maximal metabolic capacity over the course of the experiment. Therefore, although changes over 8 days may be moderate relative to seasonal variations observed in other species (e.g. 5% to 50% for BMR and M_{sum}, Cooper and Swanson, 1994; Liknes et al., 2002; Liknes and Swanson, 1996; Petit et al., 2013) , these findings demonstrate that metabolic parameters associated with thermal acclimation responded within days to changes in ambient temperature in white-throated sparrows. As far as we are aware, this is the first demonstration of such rapid response in metabolic performance in the context of thermal acclimation in birds.

As in snow buntings, we also found evidence that daily food consumption, and presumably physiological adjustments for digestion (Liu and Li, 2006; Sabat et al., 2009; Williams and Tieleman, 2000; Zheng et al., 2008), had an influence on maintenance energy costs in sparrows (Fig. 7A). However, although M_{sum} seemingly began to increase in cold acclimating birds (non-significant 4% increase), muscle thickness did not vary significantly over the 8 days of the experiment. In fact, pectoral muscles were smaller on average in the cold group than in the thermoneutral group but the latter showed a significant decrease of both M_{sum} and MMR. This therefore suggests that variations in M_{sum} and MMR were not the sole result of muscle size variations in this species. Studies have demonstrated that cellular metabolic activity can parallel winter increments of thermogenic capacity and be directly correlated to M_{sum} (Marsh and Dawson, 1989; Swanson, 2010), although not in all cases (Liknes and Swanson, 2011a; Pena-Villalobos et al., 2014; Swanson et al., 2014a;

Swanson et al., 2014b; Swanson et al., 2013). Consequently, although an increase of skeletal muscle mass may be required to improve maximal metabolic rate in birds (Swanson and Vézina, 2015), a loss of metabolic capacity at the cell level, in response to thermoneutral conditions, could perhaps result in a decrease in whole animal performance before one can detect notable changes in muscle size. Accordingly, muscle atrophy typically results from a reduction in cell size, mainly caused by the loss of organelles (including mitochondria), proteins and cytoplasm (Sandri, 2008), and decreases in contractile function of muscle can occur within a few days (Fitts et al., 2000).

Rate of change in metabolic parameters

Considering percent changes relative to day 0, our white-throated sparrow data suggest that BMR responds faster to a decrease in ambient temperature than maximal metabolic rate measured as M_{sum} or MMR. Indeed, over the 8 days of experiment, birds acclimating to -5°C showed a significant 8% increase in BMR, no change in MMR (<1%) and a 4% gain of M_{sum} that was not significant when considered within treatment (Fig. 5C and 5D). Although metabolic performance in chickadees did not respond to thermal treatment, similar findings were obtained, with a significant 12% increase of BMR, a non-significant elevation (7%) of M_{sum} (Fig. 4B) and no changes in MMR over time. Interestingly, the increase in BMR found in chickadees is greater than the interseasonal mass corrected variation observed in our source population (6%) (Petit et al., 2013). It is also comparable to the seasonal variation observed by others in whole BMR (13-18% in chickadees from South Dakota, Cooper and Swanson, 1994). Therefore, independent of temperature, chickadees showed as much amplitude of variation in their BMR within a week than within a year, while short-term variation in maximal metabolic rates was much more limited (7% increase in M_{sum} relative to 32% in our source population, Petit et al., 2013). Taken together, these results suggest that BMR can change quite rapidly and potentially faster than maximal metabolic rate.

Our findings therefore suggest that the rates of change in BMR and M_{sum}/MMR may be constrained by different mechanisms when birds have to adjust their metabolic phenotype (Petit et al., 2013; Swanson et al., 2012; Vézina et al., 2011) and recent findings by Bauchinger and McWilliams (2010a, b) seem to support to this hypothesis. These authors demonstrated that the rate of change in avian organ mass is determined by tissue-specific protein turnover rates. They showed that, among body components, the intestines, liver and kidneys, which are large and often found to influence BMR in cold acclimated birds (Liknes and Swanson, 2011b; Liu and Li, 2006; Petit et al., 2014; Williams and Tieleman, 2000; Zheng et al., 2008), have the highest rate of turnover while flight and leg muscles, which are associated with maximal metabolic performance (Marsh and Dawson, 1989; Petit and Vezina, 2014; Swanson et al., 2014a; Swanson et al., 2013; Vézina et al., 2006; Vézina et al., 2007; Wiersma et al., 2007), have the lowest rate of tissue turnover. Therefore, assuming that changes in basal and maximal metabolic rates such as those observed in white-throated sparrows during cold acclimation primarily reflect size changes in these specific organs, our finding that BMR respond faster and to a greater extent than M_{sum} and MMR to a sudden decrease in temperature likely highlights intrinsic limitations in organ growth rate. Consequently, 8 days may be insufficient for small birds to upregulate their maximal metabolic performance by relative amounts comparable to that observed between seasons in species wintering in cold environments.

Tissue turnover rate is assumed to explain both anabolic and catabolic processes involved in organ remodeling, meaning that fast growing organs are also expected to be fast regressing organs (Bauchinger and McWilliams, 2010a). The rate of change in organ mass therefore does not easily explain why, in sparrows and buntings maintained at thermoneutrality, M_{sum} and MMR declined at rates comparable or faster than those of BMR. However, we found evidence for an influence of digestive function on BMR in both these species and individuals at thermoneutrality tended to maintain their food consumption constant over time. It is therefore possible that body components may not all have changed at the same rate or in the same direction in response to thermoneutrality compared to cold temperatures. As BMR variations should be influenced by total lean body mass, while M_{sum} and MMR should vary with muscle size (Marsh and Dawson, 1989; Petit and Vezina, 2014; Swanson et al., 2014a; Swanson et al., 2013; Vézina et al., 2006; Vézina et al., 2007;

Wiersma et al., 2007), in absence of the need for active thermoregulation, muscle maximal performance could thus have declined faster than the overall resting energy consumption. An alternative but non-exclusive hypothesis is that maximal metabolic rate could also be influenced to a greater extent by variations in cellular metabolic pathways than basal metabolic rate. For example, a downregulation in the activity of specific enzymes, either by changes in protein levels or allosteric regulation, would be expected to have a greater effect on M_{sum}/MMR, where enzymes are operating closer to their maximal capacities, than on BMR, where enzymes should operate at much lower levels of activity (Swanson, 2010; Vézina and Williams, 2005).

Rate of change in metabolic parameters between temperatures

Barcelo et al. (2009) studied BMR variations in captive rufous-collared sparrows during acclimation to either cold or warm temperatures. They found that, compared to initial values measured at 22°C, birds acclimating to 15°C had increased their BMR by 22% over 4 weeks, while those experiencing a temperature of 30°C had decreased their BMR by only 13% over the same time period. Similarly, using three acclimation temperatures (10°C, 22°C, and 35°C), McKechnie et al. (2007) found in laughing doves (*Streptopelia senegalensis*), not only the expected negative relationship between BMR and air temperature, but also that for a given amount of time (21 days), the magnitude of change in BMR was greater when these birds faced colder than warmer temperatures (see Fig. 5 in McKechnie et al., 2007). These studies therefore suggest that birds adjust their BMR faster when experiencing a cooling rather than a warming environment.

The only species for which we could compare the rate of change in metabolic parameters in relation to temperature is the white-throated sparrow. In contrast with findings by Barcelo et al. (2009) and (McKechnie et al., 2007), BMR varied at comparable rates between treatments (+8% in the cold and -7% at thermoneutrality, Fig. 5B), which is consistent with organ growth and shrinkage progressing at the same rate (Bauchinger and McWilliams, 2010a). One important difference between our study and those cited above, however, is the time span between measurements. McKechnie et al. (2007) and Barcelo et al. (2009) acclimated birds for periods ranging from 21 days to 4 weeks before re-measuring individual BMR, while our measures were spaced in time by only 4 days. It is not possible to determine whether BMR had already attained stability at the time of second measure in these previous studies. However, considering the rates of change documented here, it is reasonable to assume that BMR progressed at comparable rates in both thermal treatments, therefore reaching stability in a shorter time period during warm than cold exposure. Additional research is required to determine whether this pattern is generalizable to other species.

As far as we know, this is the first study to measure the rate of change in M_{sum}/MMR over less than 8 days in response to temperature. For both MMR and M_{sum}, metabolic capacity was lost by as much as 15% over 8 days in birds kept at thermoneutrality, while the cold treatment induced, at best, moderate and non significant increases in metabolic performance (1-4%). As stated above, muscle protein turnover (Bauchinger and McWilliams, 2010a, b) might limit the rate of increase in maximal metabolic capacity in birds acclimating to cold while cellular changes could potentially explain the rapid decline of metabolic capacity at thermoneutrality (Fitts et al., 2000; Swanson, 2010). In a context where temperature stochasticity is expected to increase at northern latitudes (Easterling et al., 2000; IPCC, 2013; Katz et al., 2005), a rapid decline of thermogenic capacity during warm winter days could be detrimental if birds are slow to readjust their phenotype with the return of cold. Documentation of such an effect, however, will require further investigation.

5. List of abbreviations

BMR: basal metabolic rate

M_{sum}: summit metabolic rate (maximal thermogenic capacity)

MMR: maximal metabolic rate

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9. Figures legends

Figure 1. Changes in body mass and fat reserves during thermal acclimation.

Data are presented as least square means of body mass (top) and fat score (bottom) in black-capped chickadees, white-throated sparrows, and snow buntings measured on day 0 (before temperature change) and on days 4 and 8 of thermal acclimation. In (D), open circles represent birds from the cold treatment (-5°C) and filled circles represent birds from the thermoneutral treatment (28°C). Different letters indicate significant differences.

Figure 2. Changes in muscle size during thermal acclimation.

Data are least square means of pectoral muscle score and pectoral and thigh muscle thickness measured by ultrasonography in white-throated sparrows (A) and snow buntings (B and C). Data are presented for day 0 (before temperature change) and for day 4 and 8 of thermal acclimation. Different letters indicate significant differences.

Figure 3. Changes in food intake during thermal acclimation.

Data are least square means of sunflower seed intake (top) and either insect mash or mixed seed intake (bottom) for black-capped chickadees, white-throated sparrows, and snow buntings. Data are presented for day 0 (before temperature change) and for day 4 and 8 of thermal acclimation. Open circles represent birds from the cold treatment (-5°C) and filled circles represent birds from the thermoneutral treatment (28°C). Different letters indicate significant differences.

Figure 4. Changes in BMR and M_{sum} in black-capped chickadees during thermal acclimation.

Data are least square means of BMR (A) and M_{sum} (B) presented for day 0 (before the temperature change) and for day 4 and 8 of thermal acclimation. Different letters indicate significant differences.

Figure 5. Changes in BMR, M_{sum}, and MMR in white-throated sparrows during thermal acclimation.

Left panel show least square means of BMR (top), M_{sum} (middle) and MMR (bottom) on day 0 (before the temperature change) and on day 4 and 8 of thermal acclimation. Right panels show the same data expressed as percent change relative to values measured on day 0. Open circles represent birds from the cold treatment (-5°C) and filled circles represent birds from the thermoneutral treatment (28°C). Different letters indicate significant differences.

Figure 6. Changes in BMR and MMR in snow buntings during thermal acclimation. Data are least square means of BMR (A) and MMR (B) presented for day 0 (before the temperature change) and for day 4 and 8 of thermal acclimation. Different letters indicate significant differences.

Figure 7. Influence of food consumption and muscle size on parameters of metabolic performance during thermal acclimation.
Figure (A) shows the relationship between the change in total food intake and the change in BMR in white-throated sparrows. Figure (B) shows the relationship between the change in pectoral muscle thickness and the change M_{sum} in snow buntings. Changes are calculated as the differences between values measured on day 8 of thermal acclimation and on day 0, before the temperature change. Open circles represent birds from the cold treatment (-5°C) and filled circles represent birds from the thermoneutral treatment (28°C). Open and filled squares were used to label outliers accordingly. Regression lines represent analyses excluding outliers.

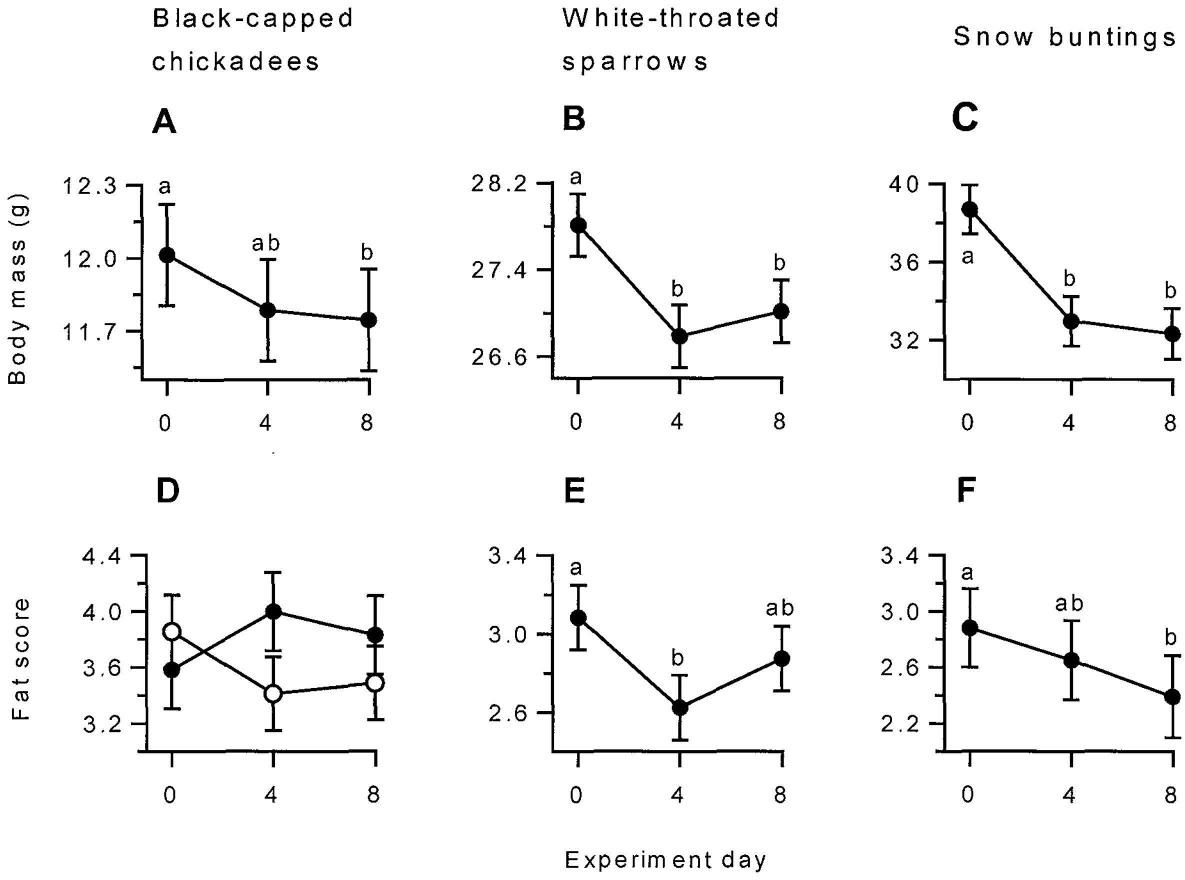
Black-capped chickadees
White-throated sparrows
Snow buntings
A
B
C
Body mass (g)
12.3
12.0
11.7
a
ab
b
28.2
27.4
26.6
a
b
b
40
36
32
a
b
b
0
4
8
D
E
F
Fat score
4.4
4.0
3.6
3.2
3.4
3.0
2.6
a
b
ab
3.4
3.0
2.6
2.2
a
ab
b
Experiment day

Figure 1

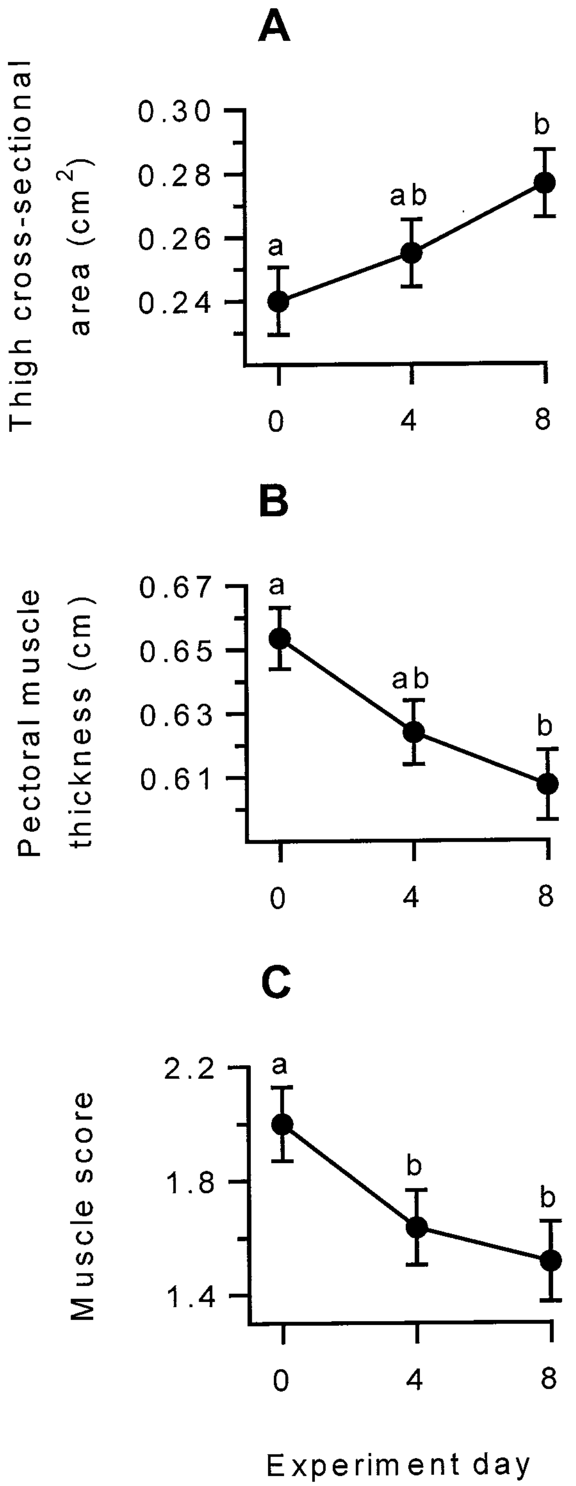
A
Thigh cross-sectional area (cm^2)
0.30
0.28
0.26
0.24
a
ab
b
0
4
8
B
Pectoral muscle thickness (cm)
0.67
0.65
0.63
0.61
a
ab
b
0
4
8
C
Muscle score
2.2
1.8
1.4
a
b
b
0
4
8
Experiment day

Figure 2

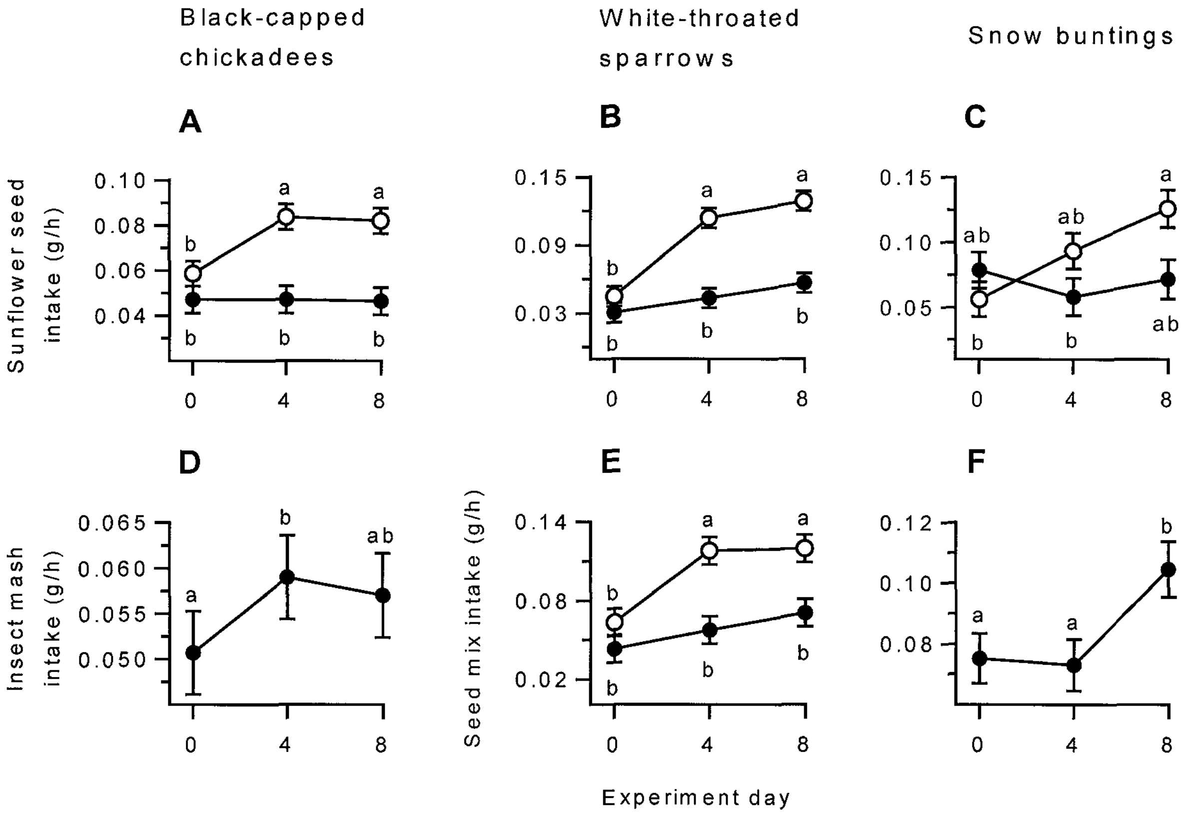
Black-capped chickadees
White-throated sparrows
Snow buntings
A
B
C
Sunflower seed intake (g/h)
0.10
0.08
0.06
0.04
0.15
0.09
0.03
0.15
0.10
0.05
a
b
0
4
8
D
E
F
Insect mash intake (g/h)
0.065
0.060
0.055
0.050
Seed mix intake (g/h)
0.14
0.08
0.02
0.12
0.10
0.08
ab
Experiment day

Figure 3

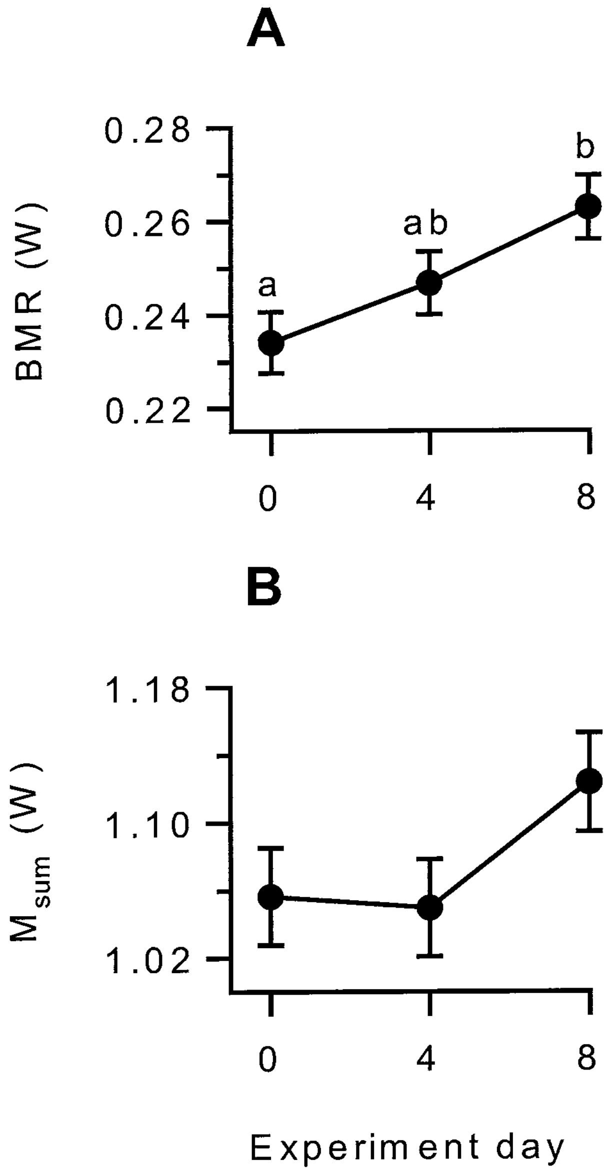
A
0.28
0.26
0.24
0.22
BMR (W)
a
ab
b
0
4
8
B
1.18
1.10
1.02
M_{sum} (W)
0
4
8
Experiment day

Figure 4

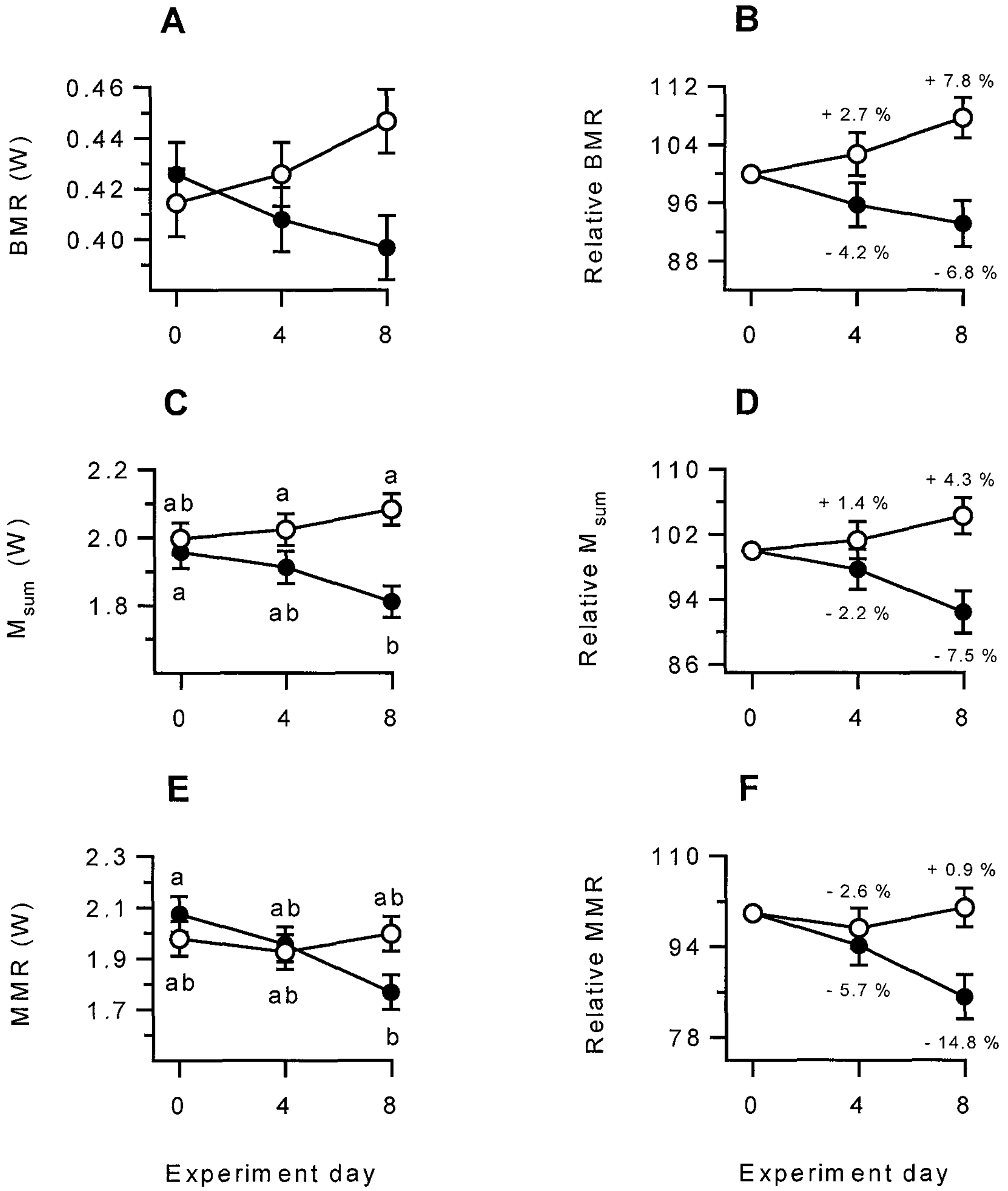
A
BMR (W)
0.46
0.44
0.42
0.40
0
4
8
B
Relative BMR
112
104
96
88
+ 7.8 %
+ 2.7 %
- 4.2 %
- 6.8 %
0
4
8
C
M_{sum} (W)
2.2
2.0
1.8
ab
a
a
a
ab
b
0
4
8
D
Relative M_{sum}
110
102
94
86
+ 4.3 %
+ 1.4 %
- 2.2 %
- 7.5 %
0
4
8
E
MMR (W)
2.3
2.1
1.9
1.7
a
ab
ab
ab
ab
b
0
4
8
Experiment day
F
Relative MMR
110
94
78
+ 0.9 %
- 2.6 %
- 5.7 %
- 14.8 %
0
4
8
Experiment day

Figure 5

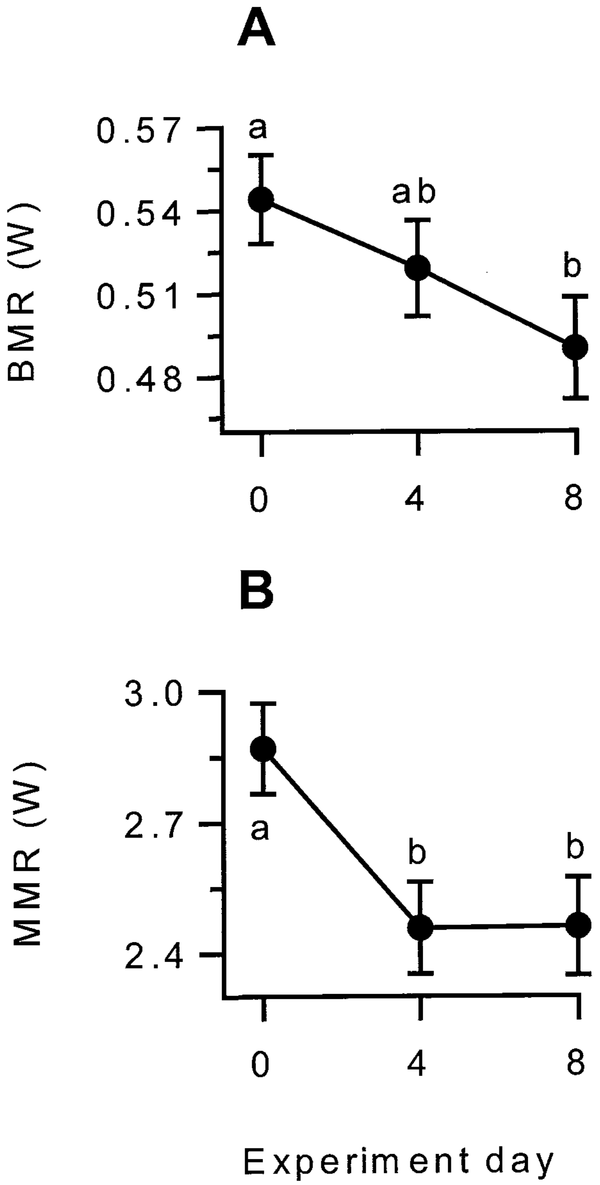
A
0.57
0.54
0.51
0.48
BMR (W)
a
ab
b
0
4
8
B
3.0
2.7
2.4
MMR (W)
a
b
b
0
4
8
Experiment day

Figure 6

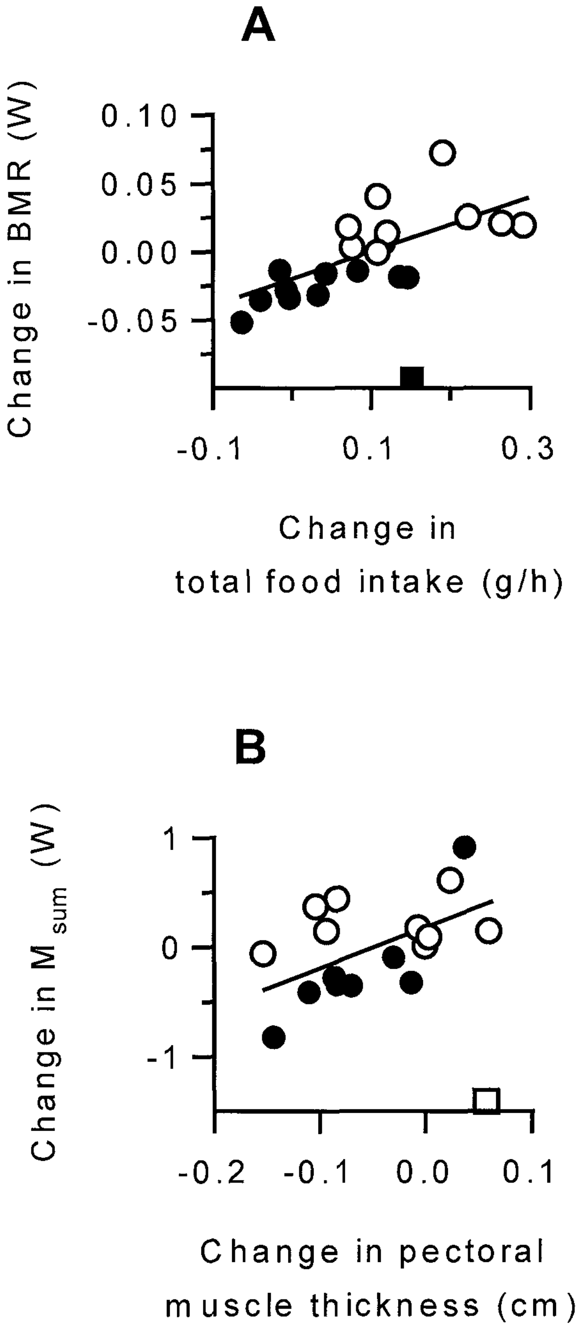
A
Change in BMR (W)
0.10
0.05
0.00
-0.05
-0.1
0.1
0.3
Change in
total food intake (g/h)
B
Change in M_{sum} (W)
1
0
-1
-0.2
-0.1
0.0
0.1
Change in pectoral
muscle thickness (cm)

Figure 7

CONCLUSION GÉNÉRALE

IMPORTANCE ET IMPLICATION DES RÉSULTATS

Cette étude est la première à caractériser les patrons de flexibilité phénotypique retrouvés chez des espèces aviaires dans les jours suivant un changement rapide de température. Les mésanges à tête noire, les bruants à gorge blanche et les plectrophanes des neiges ont tous modifié leur physiologie à l'intérieur d'une semaine. Les bruants ont démontré une hausse de performance métabolique au froid (-5°C) alors que le patron inverse a été observé à thermoneutralité (28°C), ce qui est en accord avec nos prédictions. Par contre, les mésanges et les plectrophanes ont répondu avec des patrons de variation différents. Dans les deux cas, les traitements de température n'ont pas influencé la performance métabolique. Cependant, les deux espèces ont néanmoins transformé leur phénotype suite aux changements de température, soit avec une hausse (mésanges) ou une baisse (plectrophanes) de performance. Ainsi, il apparaît que les oiseaux soient en mesure d'ajuster rapidement leur phénotype en réponse à un changement de la température ambiante. Ce seul constat est crucial puisqu'il prouve que les espèces aviaires peuvent répondre promptement à de brusques variations environnementales, ce qui n'avait pas été vérifié auparavant.

Un autre constat résultant de notre étude est que les espèces ne réagissent pas toutes de façon similaire à une même perturbation thermique. Cela suggère que certaines espèces pourraient se révéler plus aptes que d'autres à s'acclimater à la hausse prévue de la stochasticité environnementale (Easterling et al., 2000 ; IPCC, 2013 ; Katz et al., 2005). Dans cette optique, les résultats démontrent l'importance de considérer la flexibilité phénotypique dans les modèles visant à prédire les impacts des changements climatiques sur les populations aviaires. Comme celles-ci ont la capacité d'adapter leur physiologie aux contraintes écologiques, il importe de mieux comprendre et de quantifier cette flexibilité afin d'améliorer le pouvoir prédictif des modèles théoriques (Boyles et al., 2011 ; Chown et al., 2010).

Notre étude est l'une des rares à s'être intéressée en même temps aux trois paramètres qui caractérisent la gamme complète de performance métabolique individuelle. Cela nous a permis d'obtenir un rapport complet des changements physiologiques se déroulant lors de l'acclimatation thermique. Chez les bruants et les plectrophanes, nous avons observé des variations du MMR, confirmant que les capacités motrices peuvent être modifiées par les ajustements reliés à l'acclimatation thermique. Cela suggère que la convergence des deux paramètres de la performance métabolique maximale peut être profitable durant la saison froide, en allouant aux oiseaux, non seulement une meilleure endurance au froid, mais aussi une meilleure endurance physique pour des activités basées sur la locomotion, telles la quête alimentaire. Lorsque les efforts de thermorégulation sont réduits, la diminution de la taille et/ou de l'intensité métabolique musculaire qui s'ensuit illustre l'influence de la température ambiante sur cette composante corporelle. Elle permettrait également, en parallèle à la perte de masse corporelle, de maintenir la manœuvrabilité en abaissant les coûts énergétiques de déplacement (Dietz et al., 2007 ; Krams, 2002 ; Lind et al., 1999).

Nous avons également pu mettre en évidence, pour la première fois, que les taux métaboliques ne varient pas tous à la même vitesse pour une espèce donnée pendant la période d'acclimatation. En effet, pour deux des trois espèces, les oiseaux ont démontré des taux d'ajustement plus rapides pour le BMR que pour le M_{sum} et le MMR. Ces observations suggèrent que les variations de ces paramètres seraient dépendantes de mécanismes différents lors de l'acclimatation, ce qui ajoute du poids aux arguments réfutant la théorie du lien fonctionnel entre le BMR et le M_{sum}/MMR (Petit et al., 2013 ; Swanson et al., 2012 ; Vézina et al., 2006). La vitesse de remodelage des composantes corporelles serait principalement limitée par le taux de renouvellement des protéines et il a été démontré que ce taux diffère entre les organes (Bauchinger et McWilliams, 2010a,b), avec des changements rapides observés dans les organes digestifs, qui influenceraient le BMR (Liu et Li, 2006 ; Sabat et al., 2009 ; Williams et Tieleman, 2000 ; Zheng et al., 2008) et des changements relativement plus lents dans les muscles, reconnus comme les organes effecteurs du M_{sum} et du MMR (Petit et Vézina, 2014 ; Swanson et Vézina, 2015 ; Swanson et al., 2013).

Nous avons également été en mesure de confirmer que la vitesse d'ajustement des paramètres de la performance métabolique diffère entre les traitements de température. Cependant, seuls les bruants ont présenté des réponses distinctes entre les groupes soumis à l'environnement froid ou thermoneutre. Il n'est donc pas possible, à partir de cette seule étude de généraliser nos observations à plus d'une espèce. Chez les bruants à gorge blanche, la vitesse de changement du BMR était comparable pour les deux traitements de température, alors que le M_{sum} et le MMR ont changé moins rapidement dans l'environnement froid qu'à thermoneutralité. Compte tenu de l'influence supposée de la machinerie digestive sur les variations de BMR (Liu et Li, 2006 ; Sabat et al., 2009 ; Williams et Tieleman, 2000 ; Zheng et al., 2008), les changements comparables de BMR dans les deux traitements est probablement le résultat d'un taux de synthèse et de dégradation similaire (Bauchinger et McWilliams, 2010a) de ces organes en fonction du niveau de consommation de nourriture. Dans le cas du M_{sum}/MMR, une hausse de la masse des muscles squelettiques, limitée par le taux de synthèse protéique, est probablement nécessaire afin d'augmenter les taux métaboliques au froid. À thermoneutralité, notre hypothèse est que la diminution de la performance serait due à une baisse de la capacité métabolique à l'échelle cellulaire (Marsh et Dawson, 1989 ; Swanson, 2010), un phénomène possiblement rapide et précédant les changements visibles de taille des muscles.

LIMITATIONS DE L'ÉTUDE

Les oiseaux impliqués dans l'étude ont tous démontré une perte significative de masse corporelle dans les premiers jours de l'expérience, et ce peu importe le traitement de température. Bien que cette baisse de masse puisse facilement être comprise au froid compte tenu de l'augmentation des coûts de thermorégulation, elle est moins évidente à thermoneutralité. Compte tenu du fait que les oiseaux sont généralement moins lourds en été ou dans un environnement thermique peu contraignant, la perte de masse à thermoneutralité pourrait provenir d'une réduction de la taille de certaines composantes corporelles dans le but de diminuer les efforts requis pour la locomotion (Dietz et al., 2007 ; Krams, 2002 ; Kullberg et al., 1996 ; Lind et al., 1999). Le mécanisme par lequel ce changement a pu survenir chez des oiseaux captifs dont la consommation alimentaire est demeurée constante reste cependant à éclaircir. Par contre, il n'est pas exclu que cette réponse ait été provoquée par notre approche expérimentale. En effet, lors du changement de température, les oiseaux étaient transférés de leur salle programmée à 10°C vers une seconde salle dans laquelle la température était fixée à -5°C ou 28°C. Ainsi, bien qu'ils aient été de courte durée, le transfert et l'adaptation subséquente au nouvel environnement auraient pu avoir un impact sur le comportement des oiseaux ou leur niveau de stress. Cependant, les salles étant identiques et les oiseaux habitués à la manipulation, il est probable que cet impact ait été somme toute minime. Les études subséquentes utilisant un protocole similaires devraient au préalable tester l'effet potentiel d'un transfert de salle sur la masse des oiseaux.

Bien que nous ayons maintenu tous les oiseaux en conditions contrôlées et à photopériode fixe, une part importante de notre groupe de plectrophanes des neiges était en mue pendant l'expérience. Puisque la mue peut être associée à une hausse parfois importantes du taux métabolique de base et pourrait influencer l'isolation du plumage (Dietz et al., 1992 ; Klaassen, 1995 ; Lindström et al., 1993 ; Vézina et al., 2009), il importe de rester prudent dans l'interprétation de nos résultats. Cependant, l'absence d'effet significatif des variables associés à la mue lors des analyses suggère que l'influence de la mue sur les patrons observés est toutefois relativement faible.

Les observations précédentes nous incitent à proposer une solution qui, à défaut d'avoir été appliquée dans cette étude, aurait permis d'isoler avec plus d'assurance l'effet du changement de température des effets potentiels de la manipulation ou de la mue sur la physiologie des oiseaux. Pour ce faire, il aurait été pertinent d'inclure un groupe contrôle pour chaque espèce dans le plan d'échantillonnage. Ce groupe aurait suivi précisément le même protocole que les autres oiseaux, incluant les transferts de salle, mais n'aurait été soumis à aucun changement de température ambiante et serait donc demeuré à 10°C. Il serait judicieux d'intégrer un groupe contrôle semblable dans les prochaines études afin de faciliter les interprétations subséquentes.

Les valeurs de MMR enregistrées pendant l'étude semblent relativement faibles en comparaison avec celle disponibles dans la littérature. Chez les bruants à gorge blanche les valeurs de MMR mesurées étaient du même ordre (4,6 X BMR) que celles obtenues pour le M_{sum}, (4,7 X BMR) alors qu'en moyenne l'effort durant l'exercice mène à une portée métabolique d'environ 10 X BMR (Marsh et Dawson, 1989 ; Swanson, 2010). Cependant, les valeurs enregistrée sont en accordance avec celles mesurées par (Price et Guglielmo, 2009) chez la même espèce, ce qui suggère que d'avantage de données sont nécessaires sur un plus grand nombre d'espèces avant de tirer des généralités.

Dans cette étude, nous avons utilisé la méthode de l'échographie ainsi qu'un indice visuel pour déterminer la taille des muscles pectoraux et la taille des cuisses des oiseaux. Nous avons aussi utilisé la consommation quotidienne de nourriture comme mesure indirecte pouvant informer sur les ajustements potentiels des organes digestifs. Cependant, des variations significatives de taille des muscles n'ont été observées que chez les bruants et les plectrophanes qui sont de plus grande taille que les mésanges. Une étude récente (Royer-Boutin et al., 2015) suggère que la technique de l'échographie est à sa limite de précision avec des espèces de petite taille comme les mésanges. Bien que l'indice visuel ait produit le même résultat que les mesures en échographie pour les muscles pectoraux, cela suggère que nos observations de variation de taille de muscle pour cette espèce aient été limitées par notre technique de mesure. La pesée des organes digestifs et des muscles à partir de dissections aurait probablement amené des résultats plus précis (Petit et al., 2014). Cependant, cette approche terminale ne permet qu'une mesure par individu à un moment fixe de l'expérience et empêche toute analyse intra-individuelle, indispensable dans le contexte de la flexibilité phénotypique. Notre approche a tout de même permis de détecter dans certains cas les liens attendus entre la prise alimentaire et le BMR ainsi qu'entre la taille des muscles et les taux métaboliques maximaux.

VALIDATIONS NÉCESSAIRES

Les patrons d'ajustement phénotypique observés dans cette étude suggèrent une variabilité interspécifique importante dans la réponse des espèces aviaires aux variations thermiques. Cependant, bien qu'il s'agisse d'un premier pas important, il est difficile de généraliser à partir de nos seules observations. Il serait donc pertinent d'étudier ces patrons chez d'autres espèces de milieux contrastés, notamment chez des espèces provenant d'environnements où les conditions thermiques sont différentes de celles retrouvées aux latitudes nordiques. Par exemple dans les zones tropicales, les oiseaux ont des taux métaboliques généralement plus faibles (Wiersma et al., 2007b) et peuvent même présenter des variations métaboliques saisonnières inverses à celles observées dans l'hémisphère nord, bien que beaucoup plus variables (Lindsay et al., 2009a,b ; McKechnie et al., 2015 ; Smit et McKechnie, 2010). Les patrons de flexibilité phénotypique en réponse à l'environnement thermique pourraient donc être partagés par l'ensemble des espèces aviaires, mais se révéler dépendants des conditions climatiques locales (McKechnie et al., 2015). Certaines évidences à l'échelle intra-spécifique supportent également cette hypothèse (Cavieres et Sabat, 2008).

Notre étude a permis de démontrer que la performance métabolique peut être ajustée en quelques jours suite à un changement de température de l'ordre de 15-18°C. Ceci dit, il est plausible que les patrons de réponse diffèrent en fonction des conditions thermiques initiales. Sachant dans quelle mesure les phénotypes inter- (Swanson, 2010) et intra-saisonniers (Petit et al., 2013) peuvent être modulés, une même variation thermique (e.g. baisse de 15°C) pourrait représenter une contrainte différente selon que les individus sont initialement acclimatés à des conditions hivernales ou estivales. Ainsi, il serait pertinent d'évaluer la vitesse d'acclimatation thermique à partir de différentes températures de départ.

Les évidences récentes suggèrent que la vitesse à laquelle la taille des composantes corporelles puisse être modifiée dépend du taux de renouvellement des protéines propres aux tissus (Bauchinger et McWilliams, 2010a,b), ce qui peut expliquer une part des variations de performance métabolique observées en période d'acclimatation thermique. Cependant, la part des changements métaboliques directement imputable aux modifications de taille des organes représente au plus 40% des variations du BMR et 65% des variations de M_{sum} (Petit et al., 2014). Le contrôle de l'intensité métabolique cellulaire allouerait aux oiseaux la capacité de moduler leur performance sans nécessairement avoir à procéder à des changements morphologiques importants (Swanson, 2010). Ainsi, des variations saisonnières dans l'activité d'enzymes oxydatives mesurée dans les muscles squelettiques et les organes digestifs ont été enregistrées en parallèle aux ajustements métaboliques (Liknes et Swanson, 2011 ; Liu et al., 2008 ; Pena-Villalobos et al., 2014 ; Zheng et al., 2008). L'implication et l'importance de ces mécanismes lors de l'acclimatation thermique à court terme devraient donc être investigués pour obtenir un aperçu complet des ajustements physiologiques responsables des changements de performance individuels.

PERSPECTIVES D'AVENIR

Nos données montrent que les oiseaux des latitudes nordiques démontrent une grande flexibilité phénotypique face à l'environnement thermique, qui se révèle dès les premiers jours suivant des perturbations environnementales. La température ambiante est clairement un paramètre très influent sur la performance métabolique (Swanson et Olmstead, 1999) et ses fluctuations entraînent des réponses rapides de la part des espèces aviaires. Ces organismes semblent donc être en mesure de s'ajuster à une hausse de la variabilité climatique. Cependant, avant de tirer cette conclusion, il reste à déterminer à quel point les réponses enregistrées dans cette étude peuvent être extrapolées à l'ensemble des espèces aviaires et à établir si les populations démontrant une grande flexibilité démontrent aussi une valeur sélective élevée. Par exemple, si les coûts reliés à la réorganisation corporelle rapide dépassent les avantages de tamponner les variations environnementales, il est alors probable qu'une augmentation de la fréquence des fluctuations thermiques puisse être défavorable à long terme. En effet, il est possible que la réponse aux changements de température se produise au détriment immédiat ou futur d'autres besoins énergivores tels que la défense immunitaire et, à plus long terme, la reproduction (Lochmiller et Deerenberg, 2000 ; Zera et Harshman, 2001). La période d'acclimatation pourrait alors entraîner des compromis physiologiques potentiellement dommageables, surtout dans le cas des populations aviaires faisant face à une forte stochasticité environnementale. Dans ce contexte, il importe également de se questionner sur les tendances évolutives façonnant la flexibilité phénotypique chez les différentes populations et espèces d'oiseaux. Par exemple, dans les environnements relativement stables thermiquement, la sélection naturelle favorise-t-elle généralement une amélioration de la réponse directe aux perturbations du milieu ou plutôt une absence de capacité à tamponner l'effet de ces perturbations? Alternativement, occasionne-t-elle sensiblement les mêmes dispositions chez une espèce donnée, en fonction de ses caractéristiques intrinsèques, et ce indépendamment du milieu où on retrouve cette espèce? Les coûts et les bénéfices associés aux divers types de patrons d'ajustement phénotypique dans un environnement donné (ex. réponse lente ou rapide) ainsi que l'occurrence de ces patrons à travers une diversité d'environnements restent donc largement à être investigués.

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