Title: Ambient temperature effects on stress-induced hyperthermia in Svalbard ptarmigan

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Running head: Stress-induced hyperthermia in the world's northernmost land bird

ABSTRACT

Stress-induced hyperthermia (SIH), which apparently involves elevated set point temperature, is a commonly observed response to handling in a range of animals. However, in small birds, handling in cold environments typically elicits hypothermia. It is unclear whether this indicates that SIH is differently regulated in birds, or if it is due to size (small birds being more likely to suffer higher heat loss rates when handled), because thermal responses to handling in low temperature have not been measured in birds > 0.03 kg. We studied SIH in the intermediate-sized (0.5-1.0 kg) Svalbard ptarmigan (*Lagopus muta hyperborea*) in 0 °C and -20 °C, in winter and spring. Handling consistently caused back skin vasoconstriction and elevated T_c. T_c increased less and back skin temperature decreased more in -20 °C than in 0 °C, probably because of higher heat loss rate in the cold. Our study confirms the generality of the thermal responses to stress in endotherms, and suggests that body size and thermal environment must be taken into account when evaluating SIH in birds.

Keywords: Arctic, body temperature, handling, stress, stress-induced hyperthermia, thermoregulation

INTRODUCTION

Stress-induced hyperthermia (SIH), is a ubiquitous feature of the body's response to acute stressors, such as restraint or an altered social context, in mammals and birds (e.g. Briese and Cabanac, 1991; Cabanac and Briese, 1992; Carere and Van Oers, 2004; Gray et al., 2008; Korhonen et al., 2000; Meyer et al., 2008). It is believed that the increase in core body temperature (T_c) during SIH represents a sympathetically mediated elevation of the hypothalamic set point, i.e. an 'active hyperthermia' resembling pathogen-induced fevers (Briese and Cabanac, 1991; Kluger et al., 1987; Oka et al., 2001; Vinkers et al., 2009). Hence, SIH is sometimes referred to as 'stress fever' or 'psychogenic fever' (e.g. IUPS Thermal Commission, 2003), although several studies suggest it employs different neural pathways (Gray et al., 2008; Vinkers et al., 2009). Thermal responses leading to elevated T_c during SIH include cutaneous vasoconstriction and shivering thermogenesis (e.g. Briese and Cabanac, 1991; Herborn et al. 2015; Jerem et al., 2015; Kluger et al., 1987; Oka et al., 2001). The diversion of peripheral blood flow to the core, together with stress-induced tachycardia and increased ventilation rate (Cabanac and Aizawa, 2000; Cabanac and Guillemette, 2001; Greenacre and Lusby, 2004; Mans et al., 2012), probably prepares the animal for escape or interaction (i.e., a "fight or flight" response), at the same time as centralization of the blood pool could minimize blood loss in the event of injury.

Because SIH probably reflects set point change it is predicted that, for a given stressor, T_c changes should be independent of the ambient temperature (T_a) under which stress is perceived. This prediction is supported by laboratory studies of rodents (e.g. Briese and Cabanac, 1991; Kluger et al., 1987; Long et al., 1990). However, studies of birds have revealed remarkable variation in the thermal responses to restraint or handling at different T_a's. Specifically, handling in thermoneutral conditions sometimes invokes SIH (Cabanac and Aizawa, 2000;

Cabanac and Guillemette, 2001; Carere and Van Oers, 2004; Herborn et al., 2015), sometimes hypothermia (Carere and Van Oers, 2004; Maggini et al., 2018; Møller, 2010), and sometimes seem to leave T_c unaltered (Lewden et al., 2017), whereas handling below thermoneutrality consistently seems to elicit hypothermia without any co-occurring signs of shock such as lack of muscle tonus (Lewden et al., 2017; Udvardy, 1955; Andreasson, Nord and Nilsson, in review).

Cooling rather than warming of the core need not mean that birds have differentially regulated stress responses to handling. Rather, because the cooling phenomenon seems confined to small (< 30 g) species with inherently higher thermal conductance, it is likely that stress-associated *hypothermia* results from changes to the rate and avenues of heat transfer caused by the handling *per se*. For example, a small bird enclosed by a hand is subject to a substantial increase in the proportion of surface area amenable for conductive heat transfer, suffers reduced insulation when the plumage is compressed, and probably conducts heat over a considerably steeper thermal gradient (as a consequence of the handling-induced reduction in plumage depth). This explanation remains speculative, though, because body temperature responses to handling in larger, better insulated, birds have never been recorded in low T_a (e.g. Cabanac and Aizawa, 2000; Cabanac and Guillemette, 2001; Herborn et al., 2015). In addition, there are no continuous data from birds on the relationship between temperature changes in the periphery and the core during stress, which further complicates our understanding of the regulatory processes involved in situations where 'atypical' thermal responses are observed. Thus, additional data from large and well-insulated birds measured in low T_a are required to better understand why this taxon displays such variable stress-induced body temperature responses.

We measured the thermal responses to handling in the Svalbard ptarmigan (*Lagopus muta hyperborea* Sundevall). This 0.5 to 1.0 kg bird is endemic to the high-arctic Svalbard archipelago (76-81 °N), where it is exposed to T_a ranging ca. -40 to +20 °C and a photoperiod varying 24 h over the course of the year. Its thermal conductance varies accordingly, being the lowest in winter when it is dark and cold and birds are in prime body condition, and the highest in summer when birds are at their leanest and have molted into a less insulating plumage (Mortensen and Blix 1986; Nord & Folkow 2018). These properties make the Svalbard ptarmigan a good model for studying how body temperatures of a relatively large bird respond to handling, and if these responses differ in different thermal environments and in line with variation in insulation. Accordingly, we measured temperature changes both peripherally and in the body core when handling Svalbard ptarmigan at thermoneutrality (0 °C) and far below thermoneutrality (-20 °C) (Mortensen and Blix, 1986; Nord and Folkow, 2018), both in winter when insulation peaked, and in in spring when insulation was declining. If the normal SIH response in birds is an increase in T_c, and the reduced T_c during handling in small birds is, in fact, a consequence of plumage disturbances enhancing heat loss rate rather than representing a differentially regulated response, we predict that the large and well-insulated Svalbard ptarmigan would show an elevation of T_c that would be qualitatively similar at thermoneutral and very low T_a's, and that this would be preceded by reduced peripheral temperature (reflecting cutaneous vasoconstriction). Because the Svalbard ptarmigan has low thermal conductance compared to other species, even at its leanest in summer (Mortensen & Blix 1986), we also predict that any seasonal effect on the thermal responses to handling should be minor.

MATERIALS AND METHODS

Birds and housing

Twelve male Svalbard ptarmigan were used. Six were captured as chicks near Longyearbyen, Svalbard (78°13' N, 15°38' E), 16 to 17 months before the start of the experiment, and the other six were captive bred at the University of Tromsø – the Arctic University of Norway. All birds were kept in thermoneutrality under simulated Longyearbyen photoperiod. The morphological and physiological changes associated with winter acclimation do not differ between captive and wild-caught Svalbard ptarmigan as long as the birds are maintained in natural photoperiod (Lindgård and Stokkan, 1989; Stokkan et al., 1986). Housing conditions followed Nord and Folkow (2018).

Measurement of body temperature and experimental protocol

All birds were physically mature (i.e., older than 1 year). Studies were undertaken under polar night conditions in early winter (DD) (07 December 2015 to 17 January 2016), when body condition peaked (body mass: 1064.2 ± 33.0 g (SD); dissectible fat: 261.5 ± 16.7 g) and in spring (03 May to 03 June 2016) in continuous light (LL) when body condition was declining (body mass: 828.1 ± 18.1 g; dissectible fat: 142.0 ± 9.2 g). Data were collected in 0 °C (T_a = -0.1 ± 0.6 °C (SD), which is within the thermoneutral zone, and in -20 °C (-19.9 ± 0.5 °C), which is far below thermoneutrality (Mortensen and Blix, 1986; Nord and Folkow, 2018). We used 11 birds in winter, of which 10 were measured in 0 °C and five also in -20 °C. One additional bird was measured only in -20 °C. Seven of the 11 winter birds, and one additional bird, were measured in spring (i.e., 0 °C: n = 8 birds; -20 °C: n = 5 birds, of which 4 had been measured in -20 °C also in winter). In winter, 7 birds were first measured in 0 °C, and 4 birds were first measured in -20 °C. In spring, all birds were first measured in 0 °C and then in -20 °C, to maximize the larger T_a = 0 °C data set before birds were allocated to the on-site breeding program by the end of May.

Starting at 10:06 am ± 30 min (SD) (GMT +1), birds were weighed and fitted with 36-gauge type T (copper-constantan) thermocouples (Omega Engineering, Stamford, CT, USA) for measurement of T_c (70 mm into the colon), back skin temperature (T_{back}) between the wings, and head skin temperature (T_{head}) on the scalp following Nord & Folkow (2018). Skin thermocouples were attached using a small amount of cyanoacrylate glue (Loctite® Power Easy Gel, Henkel, Düsseldorf, Germany) and taking care not to cover the thermocouple junction. This glue does not cause any skin damage or irritation in Svalbard ptarmigan (AN, LPF, pers. obs.). Thermocouples were calibrated at 0 °C (Ice point drywell model 5115) and 40 °C (High precision bath model 6025, both Fluke Calibration, American Fork, UT, USA) prior to use.

Before the handling experiments, we first measured resting metabolic rate (using flow-through respirometry) and body temperatures in a climatic chamber during 1 h 44 min ± 13 min (SD), as part of a different study. After completion of metabolic measurements, we opened the metabolic chamber, side-pinned (terminology *sensu* Herborn et al., 2015) the bird, and administered an immune challenge (100 µl 1 mg kg^{-1} intramuscular LPS), also as part of a different study that is not reported here. Instead, here we report the changes in body temperatures that were recorded during and after this handling period, which lasted, on average, 3.2 ± 0.6 min (SD) (range: 2.5 to 5.3 min) and did not differ between seasons or T_a's (season × T_a, season, T_a: all $P \geq 0.3$). Because the metabolic chamber was fully open when birds were handled, metabolic rate could not be measured during this part of the study.

During winter measurements, the climatic chamber was always dark (except for illumination with dim red light, << 1 lx, to allow video inspection) to simulate polar night, whereas it was always fully illuminated by full spectrum white light bulbs in spring. All but three birds had been subjected to a similar handling- and measurement protocol on 2 to 8 instances before the

start of the study (mean ± SD: 6 ± 2). Data were recorded at 10 samples/s, and were digitized from raw signals using a ML796 PowerLab/16SP A-D converter (ADInstruments, Sydney, Australia).

Ethical approval was issued by the Norwegian Food Safety Authority (permit no. 6640). Live capture of Svalbard ptarmigan chicks was under permissions issued by the Governor of Svalbard (permit no. 2014/00290-2 a.522-01) and the Norwegian Food Safety Authority (permit no. 2014/150134).

Data analyses

We only used data from periods where the birds were at full rest (standing or walking but not moving vigorously, or perched with ptiloerection) immediately before handling. This criterion was met in 24 of 31 instances (winter, 0 °C: 8 of 10; winter, -20 °C: 6 of 7; spring, 0 °C: 7 of 9; spring, -20 °C: 3 of 5). We also dismissed data from T_{head} thermocouples that fell off or broke (winter, -20 °C: 1; spring, 0 °C: 2; spring, -20 °C: 1). T_c and T_{back} data were complete.

Pre-handling data were collected during 2 min immediately before handling. Handling and post-handling data were then collected during 20 min after the end of this stressor, i.e., a period sufficient to encompass the body temperature response to acute stress in other Galliformes (Herborn et al., 2015), but not long enough to include any thermal or metabolic effects of LPS (Marais et al., 2011). We binned data in 5 s (i.e., 50 samples) averages, partitioned in pre-handling, handling, and post-handling, periods. We then calculated: ‘response amplitude’ as the maximum or minimum body temperature attained during handling; ‘duration of response’ as the first time point where a 30 s running mean for each body temperature had returned to, or intersected, pre-handling values once the stressor had been removed; and ‘response magnitude’

as mean body temperature change (relative to pre-handling values) over the duration of the response. If a given body temperature had not returned to pre-handling levels by the end of the focal period, we set 'duration of response' to 20 min (i.e. the length of the post-handling observation period), and calculated 'response magnitude' based on this period.

Statistics were done using R 3.4.3 for Windows (R Core Team, 2018). We analyzed all response variables in tissue-specific mixed effect models fitted with maximum likelihood (lmer function in the lme4 package) (Bates et al., 2015), with season and T_a and their interaction as factors, and 'bird id' as a random intercept to account for repeated measurements. Final models were derived by sequentially excluding terms with the highest *P*-values based on likelihood ratio tests for the original and alternative models, starting with the interactions, until only significant ($P \leq 0.05$) variables remained. We then refitted the final model using restricted maximum likelihood (Zuur et al., 2009) and calculated predicted means ± SE using the lsmeans package (Lenth 2016).

RESULTS

Parameter estimates and test statistics are reported in Table S1.

All T_c responses to handling were positive and attenuated in -20 °C compared to in 0 °C. Accordingly, birds reached 0.19 ± 0.06 °C greater maximum T_c in 0 °C (ΔT_c = 0.52 ± 0.04 °C) than in -20 °C (ΔT_c = 0.32 ± 0.05 °C) (P = 0.009, Fig. 1). Response duration, i.e. the time taken for T_c to return to pre-handling levels for at least 30 s once the stressor had been removed, was longer in 0 °C (13.4 ± 1.1 min) than in -20 °C (5.6 ± 1.4 min) by 7.8 ± 1.8 min (+138 %) (P < 0.001, Fig. 1). The response magnitude, i.e. the mean deviation from pre-handling T_c during the

response, was larger when birds were measured in thermoneutrality (0.29 ± 0.03 °C) than when they were measured in -20 °C (0.17 ± 0.04 °C), by 0.12 ± 0.04 °C (P = 0.016). The modifying effect of T_a was always uniform across seasons (season × T_a: all $P \geq 0.22$), and there was no difference in mean responses between winter and spring ($P \geq 0.43$ in all cases; Table S1).

T_{back} decreased on average during handling. However, one bird showed increased T_{back} in three out of four measurement sessions, and two additional birds showed positive response when measured in thermoneutrality in spring (Fig 1). In all but one of these cases, positive responses were initiated by a slight T_{back} decrease (Fig. 1B). The strongest ΔT_{back} response was 1.38 ± 0.44 °C below pre-handling levels. There was a tendency for a stronger maximum response at -20 °C (-2.03 ± 0.77 °C) than at 0 °C (-1.01 ± 0.53 °C) (P = 0.092; Fig. 1). Birds had recovered this decrease within 10.5 ± 1.3 min, but tended to take longer to do so at -20 °C (12.0 ± 2.2 min) than at 0 °C (7.2 ± 1.8 min) (P = 0.098; Fig. 1). Average response magnitude was uniform, at 0.45 ± 0.16 °C below pre-handling T_{back}, across T_a's. Neither season nor the season-by-T_a interaction affected the T_{back} response to handling (all $P \geq 0.12$; Table S1).

The maximum ΔT_{head} response was positive on average (+0.67 ± 0.35 °C) (Fig. 1). This increase subsided within 7.5 ± 0.4 min after removal of the stressor (Fig. 1). The response magnitude index showed that ΔT_{head} was elevated, on average by 0.45 ± 0.16 °C, during this time. Season, T_a, and their interaction, did not affect any T_{head} metric (all $P \geq 0.1$; Table S1).

DISCUSSION

Handling of Svalbard ptarmigan was associated with increased T_c and T_{head} and decreased T_{back} that lasted, on average, 6.6 to 9.7 min after the stressor had been removed (Fig. 1). The

maximum T_c response was small but distinct and within the range of those recorded over similar time periods in other bird species of comparable body sizes but at higher T_a (Bittencourt et al., 2015; Cabanac and Aizawa, 2000; Cabanac and Guillemette, 2001; Gray et al., 2008). Both the maximum increase in T_c and the T_c response magnitude were more pronounced in 0 °C than in -20 °C (Fig. 1; Table S1). This probably reflects that low T_a blunted the rate of increase in T_c. Thus, since the stressor was of fixed duration and probably too short to allow the birds to reach a new set-point, T_c did not have time to increase as much in -20 °C as it did in 0 °C. T_{back}, moreover, tended to decrease about twice as much in -20 °C than in 0 °C (Fig. 1). This could suggest that a stronger peripheral vasoconstrictor response was employed to elevate T_c when T_a was lower, but more likely reflects that the drop in skin temperature when cutaneous blood flow was diminished in the cold, was larger in the lower T_a due to a more rapid heat loss rate. Thus, the difference in response strength in the two T_a's most likely reflected that higher heat loss rate in the cold slowed and blunted the T_c response, and increased T_{back} change, relative to changes in the milder T_a.

In some cases (5 of 24), birds responded to handling by vasodilation of back skin (reflected by increased T_{back}; Fig. 1), but this was preceded by an initial T_{back} decrease in all but one of these instances. This suggests that also those few birds that displayed positive T_{back} change at least initially met the stressful stimulus with the expected cutaneous vasoconstrictor response, but then, for some reason, rapidly switched to vasodilation. Our data do not allow us to determine the proximate explanation for this result, which could be related to skin thermocouple placement in relation to vascular structures, or that the thermal state of these particular birds caused them to revert to heat dissipation because a new set-point temperature was reached more rapidly. In this latter context, we noted that pre-handling T_{back} was higher (by 1.05 °C) in these birds.

T_{head} on the scalp increased in response to handling, but only after a short-lasting drop that implied rapid vasoconstriction (Fig. 1). Thus, cutaneous T_{head} initially followed predictions for peripheral temperature change during acute stress, but rapidly reverted to the opposite response. The temperature increase was probably a combined effect of increased delivery of internal heat to the head in conjunction with the rise in $T_{c,}$ and increased blood flow to the brain in response to the stressor (Hasler et al., 2007; Wang et al., 2005) that together outweighed any reduced supply of heat due to constriction of the cutaneous head vasculature. Increased blood delivery to the brain likely prompted higher attentiveness and increased cognitive ability that would aid the animal in decision-making in a threatening situation. Physiologically, increased temperature in the poorly insulated head (cf. Nord & Folkow 2018), lasting several minutes after removal of the stressor, probably contributed to reversal of the T_c response due to its effects on central thermoreceptors, even if the ultimate explanation for T_{head} change in our study was not related to heat dissipation as such. It, therefore, appears that this response, together with birds' general heat loss rate, was sufficient to regain thermal balance in the relatively low T_a's applied in this study. This could also explain why we mostly did not record any corresponding compensatory peripheral temperature increase in back skin as T_c returned to normothermia (Fig. 1B). This is in contrast to previous studies of the body temperature responses to handling conducted in considerably milder T_a, e.g. in the cold-tolerant common eider (*Somateria mollissima*) (Cabanac and Guillemette, 2001).

CONCLUSIONS

The Svalbard ptarmigan, like other medium-sized to large birds, displayed a rapid cutaneous vasoconstrictor response and an increase in T_c during handling, indicative of SIH. These responses did not vary between seasons despite higher overall heat loss rate in spring (Nord &

Folkow 2018) that should allow more rapid return to pre-handling T_c. Moreover, even when insulation was close to its annual minimum in late spring, handling in T_a far below thermoneutrality did not cause hypothermic T_c. This is in stark contrast to data from the considerably smaller cold-tolerant black-capped chickadee (*Poecile atricapillus*) (Lewden et al. 2017) and great tit (*Parus major*) (Andreasson et al., in review), in which handling in the cold results in T_c dropping several degrees C below normothermic values. Thus, our data from cold exposure in the substantially larger Svalbard ptarmigan support the argument that stress-related *hypothermia* in small birds handled below thermoneutrality does not reflect a regulated process but more likely is due to increased heat loss rate following mechanical distortion of insulation during handling, or reduced heat production if handling elicits tonic immobility (cf. Hohtola 1981). Yet, thermal responses to handling in our birds were still modified by T_a, particularly in the core but to some extent also peripherally on the back. Hence, our study suggests that when interpreting the body temperature responses to handling, one must take into account both body size of the model and the thermal environment in which measurements are undertaken.

ACKNOWLEDGEMENTS

Hans Lian, Hans Arne Solvang and Renate Thorvaldsen assisted with bird maintenance. Comments from Katherine Herborn and Paul Jerem improved a previous version of the manuscript.

COMPETING INTERESTS

We declare no conflicting or financial interests.

FUNDING

AN was supported by the Swedish Research Council (grant no. 637-2013-7442), the Carl Trygger Foundation for Scientific Research (grant no. 14:347), the Birgit and Hellmuth Hertz Foundation / The Royal Physiographic Society of Lund (grant no. 2017-39034) and the Längman Cultural Foundation.

AUTHOR CONTRIBUTION

AN conceived the idea, AN and LPF developed methodology and AN collected the data. AN analyzed the data and wrote the first draft, which was critically edited by LPF. Both authors approved the final version of the manuscript and agreed to be accountable for all contents. AN administered the project and acquired the funding.

DATA AVAILABILITY

Data will be deposited in figshare.

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FIGURES

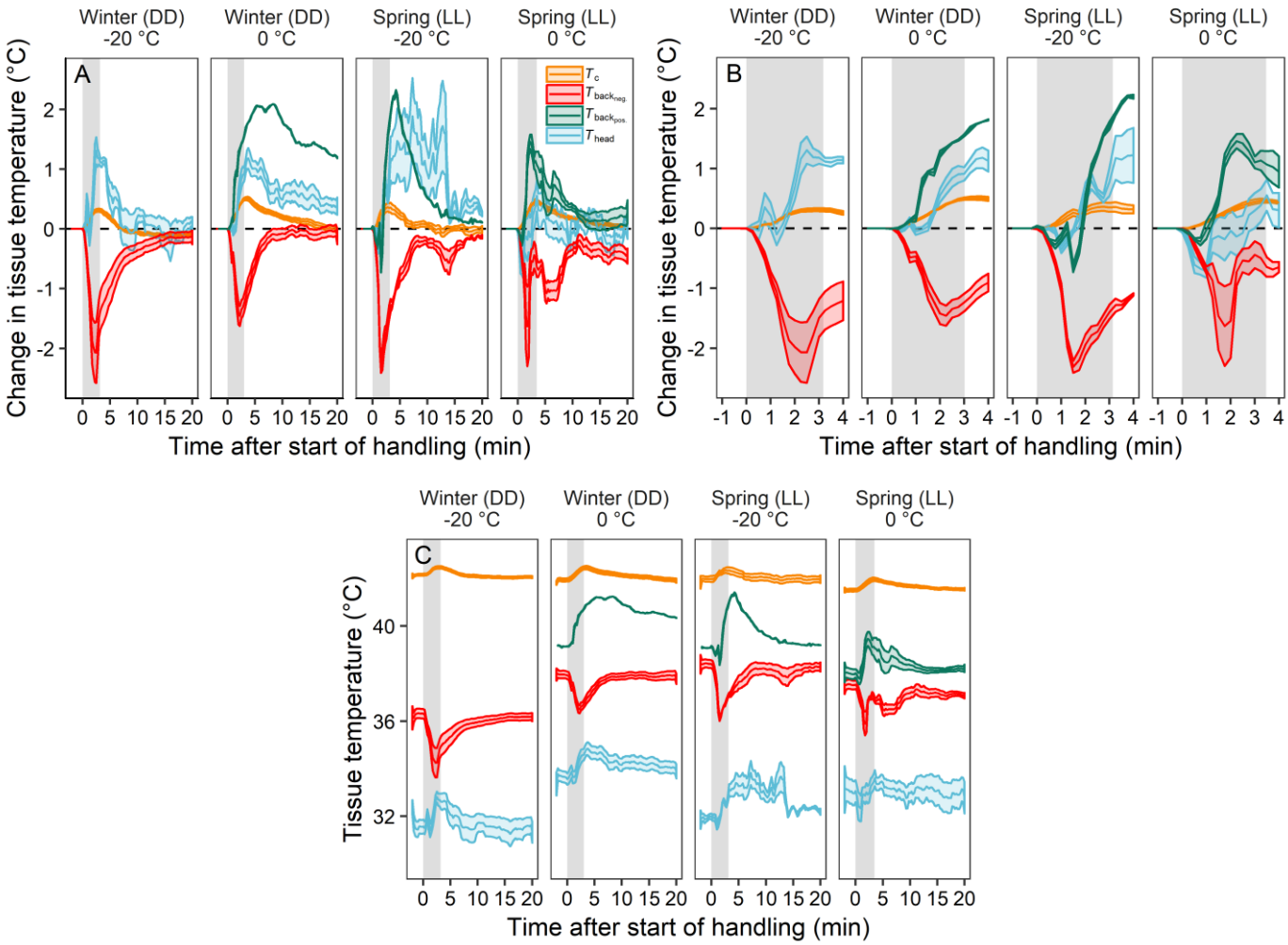

Fig. 1. Mean ± SE changes in cloacal temperature (T_c), back skin temperature (T_{back}), and head skin temperature (T_{head}) during handling in Svalbard ptarmigan. Panels show the response over: (A) the 22 min observation period relative to pre-handling temperature; (B) the response during the handling event ± 1 min relative to pre-handling temperature; and (C) mean ± SE absolute body temperatures during the observation period (C). Data were collected in thermoneutrality (0°C) and below thermoneutrality (-20°C) in continuous darkness (DD) in winter and continuous light (LL) in spring. The vertical grey bars show periods of handling. T_{back} change is presented separately for birds showing negative and positive averages responses, of which the latter occurred in three birds in three different measurement conditions. Data were binned in 30 s (A, C) or 15 s (B) intervals before plotting.