

Condition-Dependent Nocturnal Hypothermia in Garden Warblers *Sylvia borin* at a Spring Stopover Site

Authors: Cianchetti Benedetti, Marco, Fusani, Leonida, Bonanni, Roberto, Cardinale, Massimiliano, and Carere, Claudio

Source: *Ardea*, 101(2) : 113-119

Published By: Netherlands Ornithologists' Union

URL: <https://doi.org/10.5253/078.101.0206>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Condition-dependent nocturnal hypothermia in Garden Warblers *Sylvia borin* at a spring stopover site

Marco Cianchetti Benedetti¹, Leonida Fusani², Roberto Bonanni³,
Massimiliano Cardinale⁴ & Claudio Carere^{5,*}

Cianchetti Benedetti M., Fusani L., Bonanni R., Cardinale M. & Carere C. 2013. Condition-dependent nocturnal hypothermia in Garden Warblers *Sylvia borin* at a spring stopover site. *Ardea* 101: 113–119.



Migratory birds have evolved physiological and behavioural adaptations for crossing large ecological barriers through the accumulation of large amounts of fat and protein during the pre-migratory phase. Nevertheless, most migrant passerines usually need several stopovers *en route* to replenish their energy reserves and to rest. Migratory decisions at a stopover site strongly depend on body condition at arrival. Previous studies showed that lean birds prolong their stopover compared with fat birds that leave after a very short time. During the stopover, lean birds may reduce their metabolic costs by lowering body temperature (adaptive hypothermia hypothesis). However, it is not clear whether hypothermia can be an active economising strategy or just an unavoidable consequence of bad condition to avoid starvation. We used temperature loggers to measure skin temperature of 19 Garden Warblers *Sylvia borin* caught at a spring stopover site (Ponza Island, Tyrrhenian Sea) and kept overnight in cotton bags. We found that both body condition and activity were positively correlated with skin temperature during the night. The data showed a gradual nocturnal temperature drop of more than 3°C in lean birds, particularly in the central part of the night, followed by a recovery to normothermic levels. Overall, birds in worse physical condition lost more body mass during the night than birds in better condition, but this was especially true for birds that lowered their body temperature the least. These results indicate that hypothermia is associated with low body condition and that it may be functional by reducing body mass loss during migration.

Key words: body temperature, hypothermia, spring migration, condition, energy saving, stopover

¹Department of Biology and Biotechnology “Charles Darwin”, University of Rome Sapienza, Italy; ²Department of Life Sciences and Biotechnologies, University of Ferrara, Italy; ³Department of Neuroscience, University of Parma, Italy; ⁴Swedish University of Agricultural Sciences, Department of Aquatic Resources, Institute for Marine Research, Lysekil, Sweden; ⁵Department of Ecological and Biological Sciences, University of Tuscia, Borgo Le Saline 01016 Tarquinia (Vt), Italy;

*corresponding author (claudiocarere@unitus.it)

Migratory birds require specific physiological adaptations to cover large distances and cross ecological barriers with non-stop flights and prolonged fasting (Gwinner 1990, Berthold *et al.* 2000, McWilliams *et al.* 2004, Costantini *et al.* 2007, Bauchinger *et al.* 2005, Piersma *et al.* 2005, Bauchinger *et al.* 2011). Birds obtain energy from fat and protein stores accumulated in the pre-migratory phase (Pilastro & Spina 1997, Berthold 2001). Nevertheless, for most migratory

species the energy needed to cover the distance between their breeding and wintering grounds exceeds the amount they can store and carry. Therefore, most migrants make several stopovers to replenish their energy stores for the next flight (Schaub & Jenni 2000). During migration, most diurnal birds change their activity rhythm to fly at night (Berthold 1996). At stopovers, they return to diurnality (Berthold 1996), and may maintain it for several days, until restored

energy reserves are sufficient to resume flight (Biebach *et al.* 1986). Stopover sites are used for resting and/or feeding; in fact most of the time spent during migration, and of the energy devoted to migration, is spent at stopovers (Wikelski *et al.* 2003, Bowlin *et al.* 2005). Many factors influence the decision of staying at or leaving a stopover site, among which: weather conditions, predation risk, food availability, competition, energy reserves and endogenous programs (e.g. Jenni & Schaub 2003, Fusani *et al.* 2009, Fusani *et al.* 2010, Arizaga *et al.* 2011). Birds with sufficient energy reserves usually leave the stopover site on the evening of the arrival day, whereas birds with depleted reserves might interrupt migration for a period ranging from one day to several weeks (Bairlein 1985, Biebach 1985, Biebach *et al.* 1986, Goymann *et al.* 2010).

Particularly in small migrants, individuals with small energy reserves may economize resources by a strategic reduction of energy expenditure (Biebach 1977) obtained by diurnal and/or nocturnal hypothermia. Rest-phase hypothermia is a state where core temperature is below its range specified for the normal active state of the species. According to the definition of rest-phase hypothermia, body temperature (hereafter T_b) would be lowered by 3–10°C (IUPS Thermal Commission 2001, Wojciechowski & Pinshow 2009). Hypothermia can serve as a mechanism of energy saving, known both in nestlings and adults of some avian species (Biebach 1977, Graf *et al.* 1989, Schleucher 2001, 2004, McKechnie & Lovegrove 2002, Dolby *et al.* 2004). Under normal conditions, T_b reaches highest values in the afternoon and lowest values at night, between 2:00 and 4:00 (Binkley *et al.* 1971, Langman 1973, Prinzinger *et al.* 1991, Rashotte *et al.* 1995). T_b reductions below normothermic levels during the rest phase have been documented in several avian taxa (Biebach 1977, Graf *et al.* 1989, Schleucher 2001, Vezina *et al.* 2007). A reduction in T_b is associated with a decrease in metabolic rate (Daan *et al.* 1989, Rashotte *et al.* 1995). It has been estimated that a reduction of about 4°C may correspond with a more than 50% reduction in energy consumption (McKechnie & Lovegrove 2002). Hypothermic Blackcaps *Sylvia atricapilla* at a stopover site showed a 30% lower energy expenditure compared with normothermic birds (Wojciechowski & Pinshow 2009). Because the energy saved due to hypothermia slows down the depletion of energy reserves and can potentially be used for foraging, hypothermia may accelerate the rate of fuel accumulation during a stopover.

Studies on the role of rest-phase T_b in body mass gain at stopover sites suggest that hypothermic abilities

may be crucial for birds in poor body condition (Gannes 2002, Wojciechowski & Pinshow 2009, Bauchinger *et al.* 2011). However, empirical support for a link with body mass loss is indirect and based on a small sample: intraperitoneally implanted temperature loggers in Blackcaps revealed marked hypothermia, especially at night, restricted to individuals with low weight, however body mass was not measured the evening before (Wojciechowski & Pinshow 2009). Hypothermia during spring migration was also documented in newly arrived Garden Warblers and Icterine Warblers *Hippolais polyglotta* lowering T_b by 10°C below daytime levels at night (Carere *et al.* 2010). Here, no clear correlation between hypothermia and condition was found, probably because most of the birds sampled were in poor condition while nocturnal body mass variation was not measured.

We studied nocturnal hypothermia in migratory Garden Warblers and its relation with initial body condition, body mass variation and nocturnal activity. We recorded the nocturnal pattern of skin temperature (T_s) with temperature loggers at a Mediterranean stopover site during spring migration from Africa to Europe. We sampled individuals that had just arrived after a long flight and were kept overnight. We predict that (i) birds with initial poor body condition would substantially decrease T_s during the night; (ii) hypothermia would be associated with a reduction in nocturnal activity levels, because a positive correlation between condition and nocturnal restlessness has been shown in this species during spring stopover (Fusani *et al.* 2009); (iii) hypothermia would be associated with reduced body mass loss during the night.

METHODS

Species and sampling area

The Garden Warbler is a well-studied species in migration ecology and ecophysiology (e.g. Gwinner *et al.* 1985, Klaassen & Biebach 1994, Totzke *et al.* 1999, Totzke *et al.* 2000, Fusani *et al.* 2010). Its winter grounds are located in trans-Saharan Africa and one major pathway of migration to Europe involves crossing the Mediterranean Sea (Grattarola *et al.* 1999).

Our study was carried out during spring migration on Ponza, an island of 9.87 km² about 50 km off the Tyrrhenian coast of Italy (40°50' N, 12°58' E). A ringing station is active on the island since 2002 (www.inanellamentoponza.it). Birds were trapped using mist nets, which are continuously monitored during the ringing period. The low number of recaptures at Ponza

(less than 5% of trapped birds, M. Cardinale, pers. obs.) as well as a recent radiotracking study on Garden Warblers on the neighbour island of Ventotene (Goymann *et al.* 2010), indicates that most birds spend less than one day and usually only a few hours on the island. Massive arrivals are concentrated in the mid-late morning (Carere *et al.* 2010). Estimates done on Ventotene suggest that birds had completed a 14–16 h non-stop flight that included the early morning hours (Pilastro *et al.* 1995, Grattarola *et al.* 1999, Schwilch *et al.* 2002).

Sampling procedure

We sampled 19 individuals of unknown sex (the species is monomorphic) between 11 and 19 May 2011, with a maximum of 5 birds per day. Measurements of T_s started at 21:00 and finished at 06:00 the following day. Birds were caught between 19:30 and 20:30 and a single observer scored subcutaneous fat on a 0–8 scale, the size of the pectoral muscles on a 0–3 scale (Bairlein 1994) and weighed them (BM_1). The observer also recorded the length of the third outermost primary wing feather ('third primary length' henceforth) that was used as a measure of structural body size (e.g. Goymann *et al.* 2010). We attached a temperature logger (Thermochron DS 1921H, range -40 to 85°C in 0.125°C steps, 1.5 g, 11 mm diameter, 6 mm height) on the lower part of the rump, in the space between the vertex of first tertials with closed wings. We took care that the sensor was in contact with the skin of each bird using Sauer skin glue, after having cut the feathers to a length of 2 mm. The procedure took about two min after which the bird was individually kept in a cotton bag. The bags were hung in a quiet room at ambient temperature (mean 21°C). The loggers recorded T_s every two min from 21:00 to 6:00. In order to correlate T_s and T_b , T_b was measured in 15 Garden Warblers in the morning using a probe inserted in the throat via the beak (see Carere *et al.* 2010). These birds were caught during spring 2012 and were not used in this experiment. This comparison yielded a significantly positive correlation ($r = 0.61$, $P = 0.016$). Nocturnal activity was estimated by video-recording the bags with a night vision camera (Sony DCR-HC30 Camcorder) for 90 min between 23:30 and 01:00. At 06:00 the loggers were removed using a scalpel, taking care to completely remove all the glue from the skin. The birds were then weighed (BM_2) and released. All birds flew away immediately after release. During the sampling period atmospheric conditions were stable and ambient temperature ranged from 24°C during daytime to 15°C at night.

Data collection and analysis

T_s data were downloaded using One-Wire Viewer. We calculated the average temperature per hour. We also calculated minimum T_s values every 10 min. We visually scanned the 90 min video-recordings and scored the relative frequency of movements by sampling every 1 min, using this as an index of activity. Note that activity could be recorded for 17 out of the 19 sampled birds. Since we expected that our predictor variables (i.e. initial body mass, fat score, muscle score, third primary length and nocturnal activity) were correlated, we ran a principal component analysis (PCA) in order to replace them with new uncorrelated component variables. We named the first factor of the PCA "CONDITION", following Fusani *et al.* 2009, and the second factor "THIRD PRIMARY" (see results). Subsequently, we used a general linear model (GLM), with backward stepwise procedure, to test the effect of the first two factors of the PCA on T_{\min} . We also used a GLM, with backward stepwise procedure, to test the effect of CONDITION, T_{\min} , and their interaction term, on the change in body mass of each bird from time of capture to time of release ($BM_1 - BM_2$). Model residuals were tested for normality using the Kolmogorov–Smirnov test. Next, we used Pearson correlation coefficients to test associations between CONDITION and T_s for each hour during the night, as well as between T_{\min} and the difference between T_{\max} and T_{\min} (ΔT_s). Statistics were performed with Statistica Release 8 (StatSoft Inc., Tulsa, OK, USA).

RESULTS

Average T_s was $33.5 \pm 0.3^\circ\text{C}$ ($T_{\max} = 36.6^\circ\text{C}$; $T_{\min} = 29.4^\circ\text{C}$), average ΔT_s was $2.3 \pm 0.22^\circ\text{C}$ ($\Delta T_{\max} = 4.5^\circ\text{C}$; $\Delta T_{\min} = 1.0^\circ\text{C}$). The first factor of the PCA (CONDITION) explained 55.2% of the total variance in the data and correlated strongly with measures of physical condition (BM_1 , 0.90; fat score, 0.88; muscle score, 0.85), it moderately correlated with nocturnal activity ($r = 0.60$), and weakly with third primary length ($r = -0.33$). This means that birds with high positive scores on this factor were in better physical condition and were also more active during the night. Conversely, the second factor of the PCA (THIRD PRIMARY LENGTH), explaining 20.5% of the total variance in the data, was strongly positively correlated with third primary length ($r = 0.87$) and moderately positively correlated with activity ($r = 0.50$), whereas it weakly correlated with the other variables ($r < 0.12$). So, birds with high positive score on this factor were characterized by larger

structural body size and were more active during the night, although they were not necessarily in better condition. In other words, variation in body size was not correlated with variation in physical condition. Moreover, the second factor also represented the portion of variation in birds' nocturnal activity that was not correlated with physical condition. We found that only CONDITION had a significant and positive effect on T_{min} ($t = 3.37, P = 0.004$). This means that birds in worse physical condition, and that were also less active, had lower T_{min} during the night (Figure 1). So, variation in structural body size (THIRD PRIMARY), as well as variation in nocturnal activity that was not correlated to physical condition, had no significant effect on T_{min} ($t = -1.21, P = 0.25$). Note that T_{min} was negatively correlated with ΔT_s ($r = -0.72, n = 17, P = 0.001$), so birds with lower T_{min} during the night were also those experiencing greater reductions in T_s . CONDITION was significantly correlated with T_s at all hours of the night except at 5:00, although correlation coefficients were higher in the central hours of the night (23:00–3:00, Table 1). In Figure 2 we show the nocturnal T_s profile of a normothermic and a hypothermic individual.

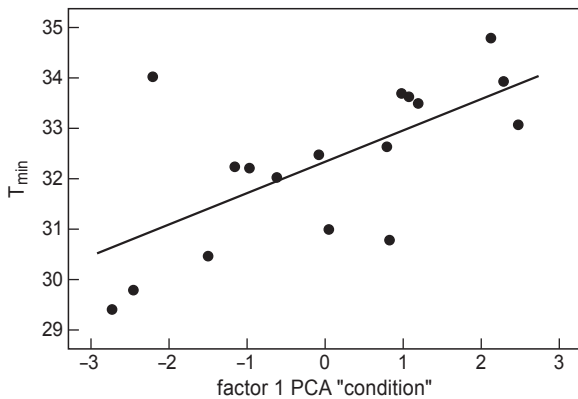


Figure 1. Scatter plot of minimum skin temperature recorded at night (T_{min}) versus the first factor of the PCA "CONDITION". Higher positive values on the PCA factor indicate better body condition and higher nocturnal activity.

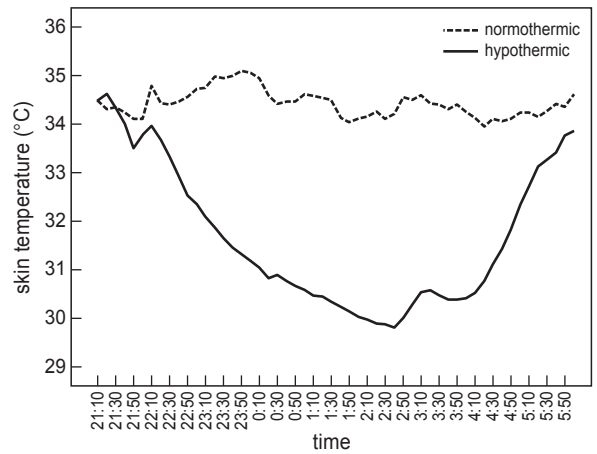


Figure 2. Profile of nocturnal skin temperature (at 10 min intervals) in one lean individual (rated at fat = 0, muscle = 1), marked as hypothermic, and one individual in good condition (fat = 2, muscle = 2), marked as normothermic.

The change in body mass was significantly affected only by the interaction effect of T_{min} and CONDITION ($t = -2.85, P = 0.01$). Specifically, body mass decreased with decreasing CONDITION in birds with higher T_{min} , but not in birds with lower T_{min} (Figure 3).

DISCUSSION

The results indicate that at a stopover site, few hours after a prolonged flight, Garden Warblers with low energy reserves tend to become inactive during the night and to become hypothermic, reducing T_s by up to 4.5°C. By contrast, birds in good condition tend to remain active and normothermic.

The results show that T_s was influenced by a linear combination of condition and activity, and it was related to condition especially between 23:00 and 03:00. Birds with worse body condition, and those that were less active, had lower T_{min} (Figure 1), and dropped their temperature more than individuals in better condition

Table 1. Correlations (Pearson coefficients and P -values) between hourly skin temperature (22:00–05:00) and PCA Factor 1 "CONDITION" (see text for details).

		22:00	23:00	0:00	1:00	2:00	3:00	4:00	5:00
CONDITION	r	0.60	0.72	0.68	0.68	0.68	0.64	0.51	0.36
	P	0.011	0.001	0.003	0.003	0.003	0.006	0.036	0.16

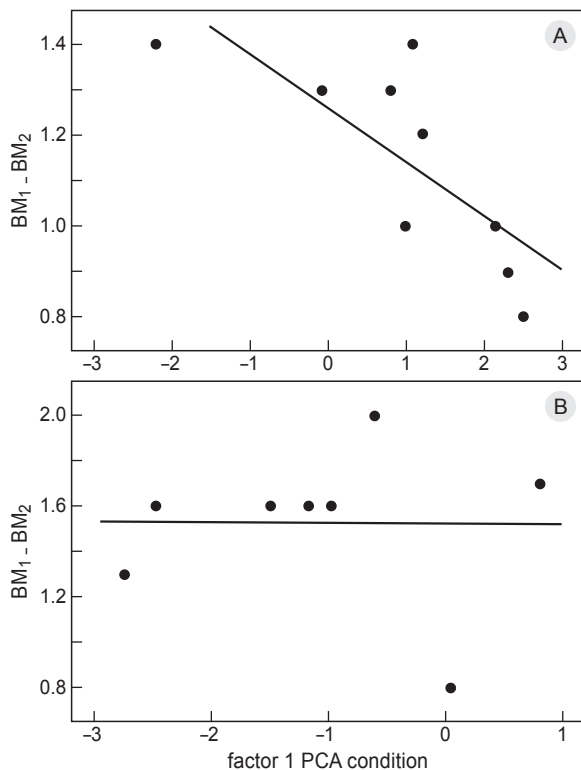


Figure 3. Scatter plots of the difference between initial and final body mass ($BM_1 - BM_2$) versus Factor 1 PCA “CONDITION”, for birds whose T_{min} recorded during the night was higher than mean T_{min} (A), and for birds whose T_{min} was lower than mean T_{min} (B). Higher values for $BM_1 - BM_2$ indicate greater reductions in body mass during the night. Higher values for Factor 1 PCA “CONDITION” indicate better initial body condition and higher nocturnal activity. Pearson correlations are: (A) $r = -0.76$, $P = 0.017$; (B) $r = -0.01$, $P = 0.99$.

and that were more active (Figure 1, 2). Notably, this effect was independent of structural body size estimated as third primary length. Six individuals showed a decrease in temperature of more than 3°C, i.e. rest-phase hypothermia by definition (Wojciechowski & Pinshow 2009). Hypothermic birds were less active than the others. We acknowledge that our measurement of activity is rough compared to classical measurements of *Zugunruhe* obtained in infrared or video equipped cages (e.g. Berthold *et al.* 2000, Fusani *et al.* 2009), however, the results are in line with the expectations, and suggest that hypothermic birds were asleep, as documented in a previous study in which birds were handled for night T_b measurements (Carere *et al.* 2010). The analysis also showed that hypothermia could not be explained by reduced activity alone, because some individuals that were not in bad physical condition hardly reduced T_s although they were not

active at night. Furthermore, we found that worse condition and lower activity resulted in higher body mass loss, which was contrary to our initial expectation. However, this decrease in body mass with decreasing physical condition and activity was found only in birds with relatively high T_{min} during the night (Figure 3). Conversely, in birds with lower T_{min} there was no relationship between CONDITION and body mass loss, although overall they tended to lose more mass than birds with higher T_{min} (Figure 3). A possible explanation for these results is the existence of a threshold in T_{min} below which body mass and energy loss in lean birds are effectively slowed down. Future studies should follow the birds on subsequent nights and record the temporal dynamics of the variables of interest.

Hypothermia has been recently discovered in passerines during migration. Wojciechowski & Pinshow (2009) documented marked hypothermia in Blackcaps temporarily kept in captivity with intraperitoneally implanted temperature loggers. Carere *et al.* (2010) measured T_b with a probe inserted in the throat in Garden Warblers and Icterine Warblers and found a decrease in nocturnal T_b of up to 10°C at 01:00. We cannot exclude that being restrained in a bag for several hours could have enhanced the hypothermic response especially in the lean individuals, though the observations on caged Blackcaps (Wojciechowski & Pinshow 2009), as well as new data from Ponza on Garden Warblers, Robins *Erythacus rubecula*, Whinchats *Saxicola rubetra* and Common Redstarts *Phenicurus phenicurus* kept in cages at night with temperature loggers, show similar patterns (Machado Tahamtani 2012).

Migrants usually arrive on Ponza in the late morning after a non-stop flight of about 14–16 hours (Pilastro *et al.* 1995; Grattarola *et al.* 1999, Schwilch *et al.* 2002). Based on their condition, they decide whether to stay or leave the following night, as suggested by measurements on *Zugunruhe* (Bairlein 1985, Biebach 1985, Biebach *et al.* 1986, Fusani *et al.* 2009), and by a radiotelemetry study (Goymann *et al.* 2010). Our data provide evidence for another proximate factor related to this behavioural decision, the possibility to go into hypothermia. Moreover, in the same individuals the levels of nocturnal activity were positively correlated with body condition and T_s , supporting the hypothesis that birds in good condition and remaining normothermic would be on nocturnal flight if not confined. Activity and radiotelemetry data show that individuals not departing during the night are leaner (Fusani *et al.* 2009, Goymann *et al.* 2010). For these birds it may be convenient to become inactive and to

lower T_b to save energy. For example, hummingbirds can use torpor to conserve energy stored for later use on migration (Carpenter & Hixon 1988).

Hypothermia could entail a cost in terms of decreased flight ability and increased risk of predation (Reinertsen & Haftorn 1986, Pravosudov & Grubb 1995, Carr & Lima 2013), since hypothermic individuals are less responsive to external stimuli than non-hypothermic ones (Reinertsen 1996). On the other hand, this process could have the advantage of favouring accumulation of energy reserves quicker allowing an earlier departure from the stopover site, as shown by body mass changes across several nights of hypothermia (Wojciechowski & Pinshow 2009).

In sum, we found that: (i) birds in poor condition decreased nocturnal T_s more than birds in good condition; (ii) overall, worse condition and lower activity resulted in higher body mass loss, although this was restricted to birds with relatively high T_{min} ; and that (iii) hypothermic birds reduced nocturnal activity levels. We conclude that hypothermia during stopover may indeed be an active, economising strategy aimed at minimizing body mass loss.

ACKNOWLEDGEMENTS

The ringing station of Ponza is operating within the long-term ringing project 'Piccole Isole' coordinated by Dr. F. Spina (Istituto Superiore per la Protezione e Ricerca Ambientale). ISPRA and the Regione Lazio authorized all procedures with respect to Italian laws. We thank Sara Lupi, Gloria Guberti and Wolfgang Goymann for feedback and assistance during the field work, the volunteers of CISCA for helping during the ringing activities and David Costantini for critical reading of an earlier draft. Popko Wiersma gave important suggestions on data analysis and interpretation in the revision phase.

REFERENCES

- Arizaga J., Schmaljohann H. & Bairlein F. 2011. Stopover behaviour and dominance: a case study of the Northern Wheatear *Oenanthe oenanthe*. *Ardea* 99: 157–165.
- Bairlein F. 1985. Body weights and fat deposition of Palaearctic passerine migrants in the central Sahara. *Oecologia* 66: 141–146.
- Bairlein F. 1994. Manual of Field Methods. European-African Songbird Migration Network, Wilhelmshaven.
- Bauchinger U., Wohlmann A. & Biebach H. 2005. Flexible remodeling of organ size during spring migration of the garden warbler (*Sylvia borin*). *Zoology* 108: 97–106.
- Bauchinger U., McWilliams S.R. & Pinshow, B. 2011. Reduced body mass gain in small passerines during migratory stopover under simulated heat wave conditions. *Comp. Biochem. Physiol. A* 158: 374–381.
- Berthold P. 1996. Control of Bird Migration. Chapman & Hall, London.
- Berthold P., Fiedler W. & Querner U. 2000. Migratory restlessness or Zugunruhe in birds – a description based on video recordings under infrared illumination. *J. Ornithol.* 141: 285–299.
- Berthold P. 2001. Bird Migration: A General Survey. Oxford University Press, Oxford.
- Biebach H. 1977. Reduktion des energiestoffwechsels und der korper Temperatur hungernder Amseln (*Turdus merula*). *J. Ornithol.* 118: 294–300.
- Biebach H. 1985. Sahara stopover in migratory flycatchers: fat and food affect the time program. *Experientia* 41: 695–697.
- Biebach H., Friedrich W. & Heine G. 1986. Interaction of body mass fat foraging and stopover period in trans-Sahara migrating passerine birds. *Oecologia* 69: 370–379.
- Binkley S., Kluth E., & Menaker M. 1971. Pineal functions in sparrows: circadian rhythms and body temperature. *Science* 174: 311–314.
- Bowlin M.S., Cochran W.W. & Wikelski M.C. 2005. Biotelemetry of New World thrushes during migration: physiology, energetics and orientation in the wild. *Integr. Comp. Biol.* 45: 295–304.
- Carere C., Costantini D., Fusani L., Alleva E. & Cardinale M. 2010. Hypothermic abilities of migratory songbirds at a stopover site. *Rend. Fis. Acc. Lincei* 21: 323–334.
- Carpenter F.L. & Hixon M.A. 1988. A new function for torpor: fat conservation in a wild migrant hummingbird. *Condor* 73: 373–378.
- Carr J.M. & Lima S.L. 2013. Nocturnal hypothermia impairs flight ability in birds: a cost of being cool. *Proc. R. Soc. B* 280: 1846.
- Costantini D., Cardinale M. & Carere C. 2007. Oxidative damage and anti-oxidant capacity in two migratory bird species at a stop-over site. *Comp. Biochem. Physiol. C* 144: 363–371.
- Daan S., Masman D., Strijkstra A. & Verhulst S. 1989. Intraspecific allometry of basal metabolic rate: relations with body size temperature composition and circadian phase in the kestrel *Falco tinnunculus*. *J. Biol. Rhythms* 4: 267–283.
- Dolby A.S., Temple J.G., Williams L.E., Dilger E.K. Stechler K.M. & Davis V.S. 2004. Facultative rest-phase hypothermia in free-ranging white-throated sparrows. *Condor* 106: 386–390.
- Fusani L., Cardinale M., Carere C. & Goymann, W. 2009. Stopover decision during migration: physiological conditions predict nocturnal restlessness in wild passerines. *Biol. Lett.* 5: 302–305.
- Fusani L., Cardinale M., Schwabl I. & Goymann, W. 2010. Food availability and not melatonin affects nocturnal restlessness in a wild migrating passerine. *Horm. Behav.* 59: 187–192.
- Gannes L.Z. 2002. Mass change pattern of blackcaps refuelling during spring migration: evidence for physiological limitations to food assimilation. *Condor* 104: 231–239.
- Goymann W., Spina F., Ferri A. & Fusani L. 2010. Body fat influences departure from stopover sites in migratory birds: evidence from whole island telemetry. *Biol. Lett.* 6: 478–481.
- Graf R., Krishna S. & Heller H.C. 1989. Regulated nocturnal hypothermia induced in pigeons by food deprivation. *Am. J. Physiol.* 256: R733–R738.

- Grattarola A., Spina F. & Pilastro A. 1999. Spring migration of the Garden Warbler (*Sylvia borin*) across the Mediterranean sea. *J. Ornithol.* 140: 419–430.
- Gwinner E. 1990. *Bird Migration: Physiology and Ecophysiology*. Springer, Berlin.
- Gwinner E., Biebach H. & Von Kries I. 1985. Food availability affects migratory restlessness in caged garden warblers (*Sylvia borin*). *Naturwissenschaften* 72:51.
- IUPS Thermal Commission. 2001. Glossary of terms for thermal physiology. *Jpn. J. Physiol.* 51: 245–280.
- Jenni L. & Schaub M. 2003. Behavioural and physiological reaction to environmental variation in bird migration: a review. In: Berthold P., Gwinner E. & Sonnenschein E. (eds) *Bird Migration*. Springer, Berlin, pp. 155–171.
- Klaassen M. & Biebach H. 1994. Energetics of fattening and starvation in the long-distance migratory garden warbler, *Sylvia borin*, during the migratory phase. *J. Comp. Physiol. B* 164: 362–371.
- Langman V.A. 1973. Radio-biotelemetry system for monitoring body temperature and activity levels in zebra finch. *Auk* 90: 375–383.
- Machado Tahamtani F. 2012. Adaptive hypothermia strategy in migratory songbirds at a stopover site during spring migration. Master of Science Thesis in Applied Animal Behaviour and Animal Welfare, University of Edinburgh.
- McKechnie A.E. & Lovegrove B.G. 2002. Avian facultative hypothermic responses: a review. *Condor* 104: 705–72.
- McWilliams S.R., Guglielmo C., Pierce B., Klaassen M. 2004. Flying, fasting and feeding in birds during migration: a nutritional and physiological ecology perspective. *J. Avian Biol.* 95: 377–393.
- Piersma T., Perez-Tris, J., Mouritsen H., Bauchinger U. & Bairlein F. 2005. Is there a “migratory syndrome” common to all migrant birds? *Ann. N.Y. Acad. Sci.* 1046: 282–293.
- Pilastro A. & Spina F. 1997. Ecological and morphological correlates of residual fat reserves in passerine migrants at their spring arrival in southern Europe. *J. Avian Biol.* 28: 309–318.
- Pilastro A., Baccetti N., Massi A., Montemaggioli A., Roselli A. & Spina F. 1995. Stima della direzione di migrazione e del consumo di grasso per ora di volo nel beccafico (*Sylvia borin*) durante la migrazione primaverile. *Atti del VII Convegno Italiano di Ornitologia. Suppl. Ric. Biol. Fauna Selv.* 22: 453–463.
- Pravosudov V.V. & Grubb T.C. 1995. Vigilance in the Tufted Titmouse varies independently with air temperature and conspecific group size. *Condor* 97: 1064–1067.
- Prinzinger R., Pressmar A. & Schleucher E. 1991. Body temperature in birds. *Comp. Biochem. Physiol. A* 99: 499–506.
- Rashotte M.E., Basco P.S. & Hendersson, R.P. 1995. Daily cycles in body temperature metabolic rate and substrate utilization in pigeons: influence of amount and timing of food consumption. *Physiol. Behav.* 57: 731–746
- Reinertsen R.E. & Haftorn S. 1986. Different metabolic strategies of northern birds for nocturnal survival. *J. Comp. Physiol. B*, 156: 655–663.
- Reinertsen R. 1996. Physiological and ecological aspects of hypothermia. In: Carey C. (ed.) *Avian energetics and nutritional ecology*. Chapman & Hall, New York, pp. 125–157.
- Schaub M. & Jenni L. 2000. Body mass of six long-distance migrant passerine species along the autumn migration route. *J. Ornithol.* 141: 441–460.
- Schleucher E. 2001. Heterothermia in pigeons and doves reduces energetic costs. *J. Therm. Biol.* 26: 287–293.
- Schleucher E. 2004. Torpor in birds: taxonomy energetics and ecology. *Physiol. Biochem. Zool.* 77: 942–949.
- Schwilch R., Piersma T., Holmgren N.M.A. & Jenni L. 2002. Do migratory birds need a nap after a long non-stop flight? *Ardea* 90: 149–154.
- Totzke U., Hübinger A., Korthaus G. & Bairlein F. 1999. Fasting increases the plasma glucagon response in the migratory garden warbler. *Gen. Comp. Endocr.* 115: 116–121.
- Totzke U., Hübinger A., Dittami J. & Bairlein F. 2000. The autumnal fattening of the long-distance migratory garden warbler (*Sylvia borin*) is stimulated by intermittent fasting. *J. Comp. Physiol. B* 170: 627–631.
- Veza T.F., Jalvingh K.M., Dekinga A. & Piersma T. 2007. Thermogenic side effects to migratory predisposition in shorebirds. *Am. J. Physiol.* 292: R1287–R1297.
- Wikelski M., Tarlow E.M., Raim A., Diehl R.H., Larkin R.P. & Visser G.H. 2003. Costs of migration in free-flying songbirds. *Nature* 423: 704.
- Wojciechowski M.S. & Pinshow B. 2009 Heterothermy in small migrating passerine birds during stopover: use of hypothermia at rest accelerates fuel accumulation. *J. Exp. Biol.* 212: 3068–3075.

SAMENVATTING

Trekvogels zijn fysiologisch en gedragsmatig aangepast om grote ecologische barrières te overbruggen. Zo slaan ze, voordat ze aan de trek beginnen, vet en eiwitten op. Desondanks onderbreken de meeste zangvogels de trek om hun energievoorraad aan te vullen. Eerdere studies hebben laten zien dat magere vogels hun tussenstop verlengen in tegenstelling tot vogels in een betere conditie die al na korte tijd verder vliegen. Tijdens zo'n tussenstop kunnen magere vogels hun energie-uitgave beperken door de lichaamstemperatuur te verlagen (adaptieve hypothermie hypothese). Het is echter niet duidelijk of trekvogels hypothermie als een energiebesparende strategie inzetten of dat het een onoverkomelijk gevolg is van een slechte lichaamsconditie die slechts dient om verhogering te voorkomen. De auteurs gebruikten temperatuurloggers om de huidtemperatuur van 19 Tuinfluiters *Sylvia borin* te meten die in het voorjaar waren gevangen tijdens een tussenstop op het eiland Ponza in de Tyrreen Zee (Italië). Tijdens de nacht ware lichaamsconditie en activiteit positief gecorreleerd met de huidtemperatuur van de vogels. In magere vogels nam de lichaamstemperatuur geleidelijk af met 3°C (de afname was het sterkst halverwege de nacht), waarna er een herstel was naar de normale lichaamstemperatuur. Vogels in een slechte conditie verloren 's nachts meer gewicht dan vogels in een goede conditie. De afname in lichaamsgewicht was het sterkst bij vogels die hun temperatuur het minst verlaagden. Deze metingen laten zien dat hypothermie samengaat met een slechte lichaamsconditie en dat hypothermie functioneel kan zijn om gewichtsverlies op de trek te beperken. (PW)

Corresponding editor: Popko Wiersma

Received 10 October 2012; accepted 28 October 2013