

## Peer Review Information

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**Journal:** Nature Ecology & Evolution

**Manuscript Title:** Migratory lifestyle carries no added overall energy cost in a partial migratory songbird

**Corresponding author name(s):** Nils Linek

### Editorial Notes:

## Reviewer Comments & Decisions:



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2  
3 **Decision Letter, initial version:**

4 7th March 2024

5 \*Please ensure you delete the link to your author homepage in this e-mail if you wish to forward it  
6 to your co-authors.

7  
8 Dear Dr Linek,

9  
10 Your manuscript entitled "Migratory lifestyle carries no energy cost in songbirds" has now been  
11 seen by 3 reviewers, whose comments are attached. The reviewers have raised a number of  
12 concerns which will need to be addressed before we can offer publication in Nature Ecology &  
13 Evolution. We will therefore need to see your responses to the criticisms raised and to some  
14 editorial concerns, along with a revised manuscript, before we can reach a final decision regarding  
15 publication.

16  
17 We are committed to providing a fair and constructive peer-review process. Do not hesitate to  
18 contact us if there are specific requests from the reviewers that you believe are technically  
19 impossible or unlikely to yield a meaningful outcome.

20  
21 When revising your manuscript:

22  
23 \* Include a "Response to reviewers" document detailing, point-by-point, how you addressed each  
24 reviewer comment. If no action was taken to address a point, you must provide a compelling  
25 argument. This response will be sent back to the reviewers along with the revised manuscript.

26  
27 \* If you have not done so already please begin to revise your manuscript so that it conforms to our  
28 Article format instructions at <http://www.nature.com/natecolevol/info/final-submission>. Refer also  
29 to any guidelines provided in this letter.

30  
31 \* Include a revised version of any required reporting checklist. It will be available to referees (and,  
32 potentially, statisticians) to aid in their evaluation if the manuscript goes back for peer review. A  
33 revised checklist is essential for re-review of the paper.

34  
35 Please use the link below to submit your revised manuscript and related files:

36  
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38  
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42  
43 We hope to receive your revised manuscript within four to eight weeks. If you cannot send it within  
44 this time, please let us know. We will be happy to consider your revision so long as nothing similar  
45 has been accepted for publication at Nature Ecology & Evolution or published elsewhere.

46  
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49 on published papers create and link their Open Researcher and Contributor Identifier (ORCID) with  
50 their account on the Manuscript Tracking System (MTS), prior to acceptance. ORCID helps the  
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52 and link your ORCID from the home page of the MTS by clicking on 'Modify my Springer Nature  
53 account'. For more information please visit please visit [www.springernature.com/orcid](http://www.springernature.com/orcid).

54  
55 Please do not hesitate to contact me if you have any questions or would like to discuss these  
56 revisions further.

57  
58 We look forward to seeing the revised manuscript and thank you for the opportunity to review your  
59 work.

60  
61 **[REDACTED]**

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64 Reviewers' comments:

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66 Reviewer #2 (Remarks to the Author):

67  
68 General

69 This study represents a landmark in the study of migratory birds. Collecting many months of heart  
70 rate and body temperature data in migrant and resident individual songbirds is a first, and there  
71 are some very important insights in the paper. That said, we feel that the most exciting parts of  
72 the dataset are physiological, and that more care needs to be made when extending the results of  
73 heart rate and body temperature to energy expenditure (modelled) and to fitness and the evolution  
74 of migratory strategies and tactics. There are clear physiological differences between the migrants  
75 and non-migrants, but how closely do those equate to energy and fitness?

76  
77 One important potential factor that is not considered is whether seasonal, migration-related  
78 changes in heart size could decouple the heart rate from O<sub>2</sub> consumption and energy expenditure.  
79 Other studies show that heart size can increase during migration. This can affect ventricle volume  
80 and thus stroke volume, so a bird could possibly pump more blood per heart beat and thus a lower  
81 heart rate could equate to the same energy expenditure. It's unfortunate that we do not know  
82 what is going on with heart size in this population, but it could confound the results throughout the  
83 entire year. One message of the paper could be that more detailed physiological studies on the  
84 resident and migrant winter ranges should be done.

85  
86 Fig 1b is a bit misleading because at first glance it makes the reader think these are the locations  
87 of birds in the study. So the figure legend could be clearer. Moreover, if you don't know where  
88 exactly they went, how do you know the ambient temperature at the wintering area? There are  
89 many things happening here in the estimation of ambient temperature on the migrant's wintering  
90 area that could affect the results. Why did the authors choose to use a single wintering range for  
91 weather rather than estimating the distance each individual travelled from flight duration and a  
92 bearing to the centroid of the known wintering area? Why not put a line southwest from the  
93 breeding site, use flight duration to estimate winter location for each bird, and then get the  
94 weather data from there?

95  
96 We think that the migration HRT and T<sub>b</sub> results are actually more interesting than the estimated  
97 winter energy expenditures from modelling, which could be flawed either due to the model being  
98 unrealistic or other physiological changes in body composition happening. Here you have excellent  
99 evidence of the anticipatory physiological adjustments that individuals make many weeks in  
100 advance of migratory departure. This shows that "decision" to be a migrant this year and the gene  
101 expression, hormonal, metabolic, and behavioural adjustments are made well in advance by some  
102 individuals in a population without a cue like photoperiod. There is a paragraph in the discussion  
103 sort of addressing this but the overall message of the paper is about fitness differences and more  
104 ultimate causation based on fitness which is not actually what was measured.

4



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105  
106 The authors don't really discuss the fact that residents dropped Tb more in winter than migrants or  
107 the fact that there is a seasonal decrease at all. This Tb and HRT data in itself is very interesting  
108 and relates to how these resident birds are coping with surviving winter, but it is not discussed.  
109

110 The blackbird partial migrant system is great and many insights may be gained. However, we feel  
111 that the authors may be overemphasizing the results from a short distance migrant. Would these  
112 be enhanced or absent in a long-distance migrants? There could be very different mechanisms.  
113

114 The title needs to be changed to better reflect the actual study. To say that "Migratory lifestyle  
115 carries no energy cost in songbirds" is inaccurate and misleading. First, all activities have an  
116 energy cost. Second, this title is generalizing to all songbirds from a short distance partially  
117 migratory species of fairly large body size. It is far from the final word on the topic. Maybe what  
118 would be more appropriate would be that "Migration energy costs are compensated by reduced  
119 thermoregulatory costs in a partial migrant songbird population". Of course, emphasizing  
120 "individual-level anticipatory physiological changes weeks before departure in a partially migrant  
121 songbird" would also be a contender.  
122

123 Perhaps the ultimate causation of partial migration should be answered by measuring survival and  
124 reproduction and making a life table. Trying to do it with physiology alone may not make sense,  
125 although the physiology adds a very interesting dimension to the story.  
126

127 Below we review in the order introduction, methods, results, discussion.  
128

129 Specific:

130 1) Line 12: I can't help but visualize many exceptions from this general statement which really only  
131 applies to bird migration from high to low latitudes. So you either need to specify that or be more  
132 generic, like "Seasonal bird migration may provide energetic benefits associated with moving to  
133 areas with less physiologically challenging climates or increased food availability, but migration  
134 itself can carry high costs".  
135

136 2) L 15-16: I think you need to also include that you relied on physiological modelling here:  
137 "...paired with automated radio telemetry and physiological modelling..." Or you could say energetic  
138 modelling.  
139

140 3) L17: Delete "surprisingly" and replace "birds" with "blackbirds". I think your results are very  
141 interesting, but whether they can already be generalized to all birds may be premature without  
142 further study.  
143

144 4) L19: I think here you need to specify that the model you have predicts energy expenditure  
145 would be decreased enough to compensate for migration costs. So, maybe change to "...departure,  
146 which modelling suggests will dwarf the energy costs...".  
147

148 5)L 19-20: Change to "...migrants did not appear to decrease total daily energy expenditure..."  
149

150 6) L26-27: I suggest changing evolved to evolves since it is believed to be an ongoing process.  
151

152 7) L31: delete temporary and replace the colon with "through".  
153

154 8) L34: Is this what theory predicts? Doesn't theory generally focus on maximizing fitness or some  
155 reasonable correlate of fitness (Lifetime Reproductive Success or the product of survival and  
156 reproduction)? I don't think LRS is necessarily the same as energy expenditure. An animal could  
157 move to a less energetically costly place, but have lower fitness due to other factors like amount of



- 158 food, competition for food, or predation risk. Specifically regarding partial migration, isn't it thought  
159 to be either a mixed ESS where migrants and non-migrants get the same fitness, or a best of a bad  
160 job where residents achieve greater fitness than migrants and migrants switch to residents if  
161 possible? What is the case in blackbirds? Does your data suggest at least for energy the costs are  
162 about equal between tactics?  
163
- 164 9) L 38: We suggest rephrasing from "conclusive theory" to something like "greater understanding  
165 of the energetic trade-offs of migration".  
166
- 167 10) L40: Singular/plural don't agree. Change to "The Common blackbird is a wide-ranging  
168 species..."
- 169 11) L45: Perhaps be more specific about what you mean by conditions getting too harsh. Do you  
170 mean declining temperatures, decreasing food availability, high snowfall?  
171
- 172 12) L 46: I think the figure legend of Fig 1b needs to be more explicit that these wintering locations  
173 are not those of the birds in the current study, but those of birds from an earlier geolocator study.  
174 When a reader first looks at the figure they may easily assume that these are the known wintering  
175 locations of study birds.  
176
- 177 13) L 51, 56, 135, 189, 200, 617 and elsewhere: Change energetic to energy. Energetics is a field  
178 of study, but grammatically "energetic" also is a modifier. So I think it is better to say what is  
179 being expended: energy.  
180
- 181 14) L57: Perhaps change to "...would on average exhibit..."  
182
- 183 15) L 445, 449, 452: gram, g, gr – be consistent in notation.  
184
- 185 16) L 452: The total weight of the logger (3.3g) and radio tag (2.6g) does not add up 4.9g. It  
186 should be 6.2g or 6.9% of a 90g bird. Perhaps you can make a point that part of the possible  
187 energy/survival costs of external tags is the aerodynamic effects they can have rather than just  
188 extra mass. So, the 3.3 g implanted tag likely has less of a negative cost to the bird's activities,  
189 and you have compared return rates of blackbirds with loggers and tags to those with tags only  
190 (L458). Also, for the future, there are lighter (1g) radio tags available that could have met your  
191 needs for tag life.  
192
- 193 17) L 454: ad libitum should be italics.  
194
- 195 18) L 491: change to loggers.  
196
- 197 19) L 515: If there was only a data quality issue with the heart rate data, why did you end up with  
198 more heart rate measurements than Tb when they were taken at the same rate (every 30 min)?  
199
- 200 20) L 526: Is this 97.4% or only 0.974 %?  
201
- 202 21) L 527-528: If you could estimate flight durations and stopovers, why not create an estimate of  
203 total migration distance along the known southwest migration route of your previously studied  
204 birds? See me general comment about this. If effect maybe you could have estimated a wintering  
205 area and done a better job at estimating the temperature conditions individuals experienced rather  
206 than using a single estimated temperature regime.  
207
- 208 22) L 604: I think you could be clearer here that temperatures were measured in the resident  
209 wintering area, but predicted for the migrants by assuming they were somewhere in the range of  
210 known wintering areas.



211  
212 23) L 612: Change to "...from geolocator-based estimates of winter range from previously-studied  
213 birds..."

214  
215 24) L 73: What is meant by higher movement expenses here? Do you mean energy expended on  
216 movement as inferred from HRT data? Because you follow this by saying that heart rate did not  
217 differ. Please be more specific.

218  
219 25) L 82-83: Does the higher Tb confer other benefits such as better immune function?  
220

221 26) L 90-94: Another interpretation is that the model predictions are wrong and may be based on  
222 too many assumptions. Physiological changes in body composition (organ and shivering muscle  
223 sizes) or mitochondria could also happen that explain why a simple model predicts a difference in  
224 energy expenditure, while heart rate data do not. Again larger or smaller hearts could pump  
225 different amounts of blood per beat. In any case I think there should be a case made for more  
226 detailed physiological studies of the two types.

227  
228 27) L 96-126: To me this is the most exciting finding of the study. It's a missed opportunity that  
229 you start be emphasizing how organ sizes could change, but then do not consider previous  
230 literature that shows that heart size and thus stroke volume could increase during this  
231 premigration phase. This would decouple heart rate from oxygen consumption (energy  
232 expenditure) to some degree. Never the less the data speaks for itself. It clearly suggests that  
233 metabolic rate (Tb and HRT) at night is decreased in individuals that are preparing to migrate.

234  
235 28) L 171-173: Could the nocturnal temperatures at the wintering area have been warmer during  
236 the spring premigration preparation phase than they were during the fall premigration phase?  
237 Perhaps it was just warmer and so it wasn't possible for birds to drop Tb and HRT?

238  
239 29) L 187: Please be specific that this was estimated from the thermoregulation model, which  
240 could be flawed. How about "According to the metabolic simulation model we used, on average..."

241  
242 30) L 196-199: Why not estimate the energy costs of the migratory flights from allometric  
243 equations or the "FLIGHT" program. If you know how long they fly then you should be able to  
244 calculate an approximate number of kJ expended on migratory flight to compare with the  
245 thermoregulation savings. For example, to fly 800 km at 10m/sec would take 80,000 sec. Using  
246 the equation in Bishop and Butler 2015  $y=52.6M^{0.74}$  (M in kg) a 90 thrush expends 8.9 W (J/s),  
247 so the flights would require 712 kJ. That's only 4% of the thermoregulatory difference.

248  
249 31) L 230: Missing second parenthesis )

250  
251 32) L 235: Change to "energy allocation"

252  
253 33) Fig 2 – letters should align with relative position of each subfigure: a above c,d,e.

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257 Reviewer #3 (Remarks to the Author):

258  
259 This manuscript reports a study that incorporated implanted heart rate and temperature data  
260 logger and automated radio telemetry to understand the physiology of migratory birds, making use  
261 of a partially migratory species – the European blackbirds (*Turdus merula*). By means of these  
262 technologies, the authors were able to examine the metabolic rates (using heart rate as a proxy)  
263 and thermoregulation (using body temperature as an indicator) of migratory and non-migratory

7



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264 individuals, from after breeding to wintering, including both stages of autumnal and vernal  
265 migrations. The obtained data showed internal differences in heart rates and body temperature  
266 between migrants and residents, being most pronounced in certain life-history stages of a year.  
267 More importantly, despite the 5-8 °C higher temperature experienced by the migrants in the  
268 wintering grounds and therefore lower energetic demands for thermoregulation, the physiological  
269 data do not show uni-directional differences between migrants and residents. The complex  
270 differences post a challenge for the authors to interpret the data, yet probably reveal part of the  
271 complex system animal ecologists are routinely dealing with.

272  
273 I personally admire this study. The methods the authors used (the combination of implanted data  
274 logger and automated radio telemetry) and the data they obtained are absolutely amazing. The  
275 fact that the authors were able to identify migratory versus non-migratory individuals within a  
276 partially migratory population is already rarely achieved to my knowledge, let alone obtaining  
277 longitudinal physiological data at fine temporal scales. The data obtained by this study are  
278 therefore extremely valuable and must be made known to the scientific community, especially for  
279 animal ecologists who study migration ecology and physiology.

280  
281 That being said, I do have some suggestions for the authors to consider, by which I sincerely hope  
282 that my comments would be considered constructive. Mostly, my comments are questions from a  
283 fellow scientist who is also studying migration physiology in birds. I sincerely hope that my  
284 comments represent the questions that readers may also have and might help the authors to see  
285 some blind spots that may exist in the manuscript.

286  
287 Major comments:

288 The major comments I have are about the interpretation and also the presentation of the data,  
289 which are related to each other. For some data, I am wondering whether there might be alternative  
290 explanation. As for the data presentation, although I assumed that the authors had hierarchical  
291 data at both between- and within-individual levels at hands, the figures are unclear to me whether  
292 the trends were observed at which level. Let me elaborate my concerns/questions below:

293  
294 1. Lines 77-83: In this paragraph, the authors stated that, despite higher ambient temperature  
295 ( $T_a$ ) in the wintering grounds (Fig. 1c), migrants did not realise "an overall metabolic benefit"  
296 (Lines 77-78). This was the authors' interpretation to the lack of clear difference in heart rates  
297 between migrants and residents throughout the year (particularly in winter). The authors explained  
298 that this might be due in part to the higher body temperature ( $T_b$ ) in the migrants (Lines 78-79,  
299 Fig. 2b and 2j) and this "challenges the assumption that migrants realise a thermoregulatory  
300 benefit of overwintering in warmer areas or if they simply expend equivalent energy to maintain  
301 slightly higher  $T_b$ ."

302  
303 I do not outright disagree with the authors' interpretation on the data. However, I was wondering,  
304 could this result actually reveal the thermoregulatory benefits the migrants have enjoyed in a  
305 warmer wintering area?

306  
307 We know that heat loss increases when the difference of  $T_b$  and  $T_a$  increases. Therefore, in a  
308 colder region, maintaining a slightly higher  $T_b$  would require more energy and increases heat loss.  
309 Therefore, maintaining a slightly higher  $T_b$  might only be affordable in a relatively warmer region.  
310 The question is whether maintaining a slightly higher  $T_b$  confers any physiological or survival  
311 benefits to the migrants so that they would spend the energy they could otherwise spare in the  
312 warmer wintering grounds to maintain a slightly higher  $T_b$ .

313  
314 2. Fig. 3: These are amazing data, without a doubt, but I do not fully understand what data the  
315 authors were actually presenting. It would be great if the authors could clarify. This will also help  
316 readers to understand your findings.





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First of all, since you have to recapture the birds to retrieve the implanted data logger, I suppose you have very fine within-individual recordings. Did you use them to calculate and obtain a single data point per individual? If so, I may have missed such a description.

Second, if you did not calculate a single data point per individual and instead included the repeated recordings per individual in your analysis (which might be so since you mentioned using hierarchical GAMs), this figure apparently did not represent that kind of data.

I am not criticizing this. My point is, what do the data points on this figure represent? It is now unclear to me whether each of the data points represents one individual at the departure time from the breeding site.

At last, the above questions matter in terms of the interpretation of your results. Although I may have misunderstood the figure, I am highly intrigued whether the reduction of heart rate and body temperature in migrants was observed across individuals or within individuals?

If each data point represents one individual, this pattern could be driven by a correlation between heart rate and departure time, e.g., if late goers have lower heart rates and body temperature than early goers, but this correlation wasn't clear in residents (since they do not go). Could this be a possibility?

3. Overall, I have some concerns about how the authors reached the main conclusion as claimed in the title "Migratory lifestyle carries no energy cost in songbirds." I am not saying that I consider the data insufficient to support this conclusion. My concern is, how this conclusion was reached was unclear to me. After reading this manuscript, I saw the amazing data that showed differences in heart rates and Tb between migrants and residents, and also the lack of differences between the two groups of individuals. However, do these results suggest that migratory lifestyle carries no energy cost in the migrants? Perhaps, but the reasoning and deduction was unclear to me.

Beside my major comments, below are a few minor comments for the authors to consider:

1. Line 90 "Fig. 4": If you reported and cited this figure earlier, why wasn't it "Fig. 3"?
2. Line 150 "Fig. 3c": should this be "3d" since it is about Tb?
3. Lines 174-175: Here I have a minor question about the interpretation. If you attributed the Tb increase of the residents to seasonal changes, why did the migrants lack such a seasonal change?
4. Line 206: would a reference for the Extended POL be needed here?
5. Line 384 in the legend of Fig. 1 "an implanted and temperature logger": should it be "an implanted temperature logger" or "an implanted heart rate and temperature logger"?
6. Lines 451-452: Yet, the internal data logger also adds another 3.3g. Does that not need to be taken into account because it is internal? I am sure that it is still within the weight limit a blackbird can carry without apparent negative impact, but it would be great to clarify whether the weight of an internal data logger needs to be taken into account., e.g., for animal welfare consideration.
7. Lines 457-458: I was exactly curious about the survival and return or recapture rates of the birds that were installed with a data logger. Was that reported in the Results? I did not see it. I would suggest reporting these results, at least in the Extended Data, if not yet.
8. Lines 495-496: That was an amazingly high recapture rate that made this system and the data rare and highly valuable!
9. Lines 584-588: I do not fully understand how you avoided pseudoreplication this way. Could you elaborate this?

Reviewer #4 (Remarks to the Author):

9



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This is a novel and important study that provides new insights into the energetics of short-range avian migration. However, several of the major conclusions depend heavily on estimates of energy expenditure from a biophysical model about which very little detail is provided. At the very least, the authors need to provide full details (most likely in supplementary materials) of the values used to parameterize the NicheMapR model, the source for each value and assumptions, including those about where the birds were roosting, whether digestion-associated thermogenesis substitutes for thermoregulatory heat production, etc.

I am also concerned that the species-specific NicheMapR model that provides the basis for all the estimates of metabolic rate upon which the major conclusions of the study are based was not validated against empirical, species-specific metabolic rate and body temperature data (along the lines of Conradie et al. 2023 JEB doi:10.1242/jeb.245066, in the context of hotter conditions). The NicheMapR endotherm model is still new, and has not, to the best of my knowledge, been properly validated in the context of shallow reductions in rest-phase body temperature. The energy savings associated with small reductions in body temperature can be substantially larger than expected based on the magnitude of hypothermia, and so I am wary about accepting the authors' estimates of thermoregulatory energy expenditure at face value.

Just to be clear, heart rate data were not converted to metabolic rates? It might be worth adding a sentence or two explaining why not, since this has often been done in previous studies.

Clarification is needed on the combined mass of the Star Oddi loggers and backpack-mounted transmitters. In line 445, the mass of each logger is given as 3.3 g, and in line 449 the mass of the backpack transmitters as  $\leq 2.6$  g. This is a combined mass of 5.9 g, equivalent to 6.6 % of the blackbirds' 90-g body mass, not 4.9 g and 5.4 % as currently stated in line 452. The generally accepted upper limit for attached devices on birds is 5 % of body mass, and I think the authors need to carefully consider whether their data and variables like migration speed or duration may have been influenced?

The title overstates the significance of the study to the point of being misleading. The study involved one species of European partial migrant in which some individuals migrate 800 km, but the title makes it sound like you have shown a lack of an energetic cost for a migratory lifestyle among migratory passerines in general, some of which fly many thousands of kilometers.

Abstract: please remove adjectives like "solid" and "critical"... this is not good scientific writing style.

Lines 40-45: Is there any information available on how the proportion of blackbirds migrating has changed in recent decades with factors like urbanization and climate warming? If there is, please add a sentence or two here.

\*\*\*\*\*END\*\*\*\*\*

## Author Rebuttal to Initial comments

416  
417

## Referee 1:



418

419 This study represents a landmark in the study of migratory birds. Collecting many  
420 months of heart rate and body temperature data in migrant and resident individual  
421 songbirds is a first, and there are some very important insights in the paper. That  
422 said, we feel that the most exciting parts of the dataset are physiological, and that  
423 more care needs to be made when extending the results of heart rate and body  
424 temperature to energy expenditure (modelled) and to fitness and the evolution of  
425 migratory strategies and tactics. There are clear physiological differences between  
426 the migrants and non-migrants, but how closely do those equate to energy and  
427 fitness?

428 ***Thank you for commenting on our manuscript and referencing the novelties and***  
429 ***uniqueness of our study. We agree that the most interesting parts are the newly***  
430 ***gathered data. With the help of your valuable feedback on other potential***  
431 ***causes for the physiological differences found between migratory strategies, we***  
432 ***concentrated more on those aspects of our findings. We made the model more***  
433 ***transparent to clarify its uncertainty. The revised version is considerably more***  
434 ***careful in drawing conclusions about energy and fitness differences between***  
435 ***the two migratory strategies.***

436 One important potential factor that is not considered is whether seasonal,  
437 migration-related changes in heart size could decouple the heart rate from O<sub>2</sub>  
438 consumption and energy expenditure. Other studies show that heart size can  
439 increase during migration. This can affect ventricle volume and thus stroke volume,  
440 so a bird could possibly pump more blood per heart beat and thus a lower heart rate  
441 could equate to the same energy expenditure. It's unfortunate that we do not know  
442 what is going on with heart size in this population, but it could confound the results  
443 throughout the entire year. One message of the paper could be that more detailed  
444 physiological studies on the resident and migrant winter ranges should be done.

445 ***Thank you very much for this comment. In the revised version, we included***  
446 ***corresponding literature (lines 120,128) showing the potential effect of***  
447 ***physiological changes in heart rate size in relation to a migratory lifestyle.***  
448 ***Additionally, we added a paragraph highlighting the uncertainty of our drawn***  
449 ***conclusions (line 248-254) and suggest more morpho- and physiological***  
450 ***measurements in the field as a future line of research (lines 219-224, 254).***

11



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451 Fig 1b is a bit misleading because at first glance it makes the reader think these are  
452 the locations of birds in the study. So the figure legend could be clearer. Moreover, if  
453 you don't know where exactly they went, how do you know the ambient temperature  
454 at the wintering area? There are many things happening here in the estimation of  
455 ambient temperature on the migrant's wintering area that could affect the results.  
456 Why did the authors choose to use a single wintering range for weather rather than  
457 estimating the distance each individual travelled from flight duration and a bearing  
458 to the centroid of the known wintering area? Why not put a line southwest from the  
459 breeding site, use flight duration to estimate winter location for each bird, and then  
460 get the weather data from there?

461 ***You are absolutely right about the inaccuracy of the text in the legend. We***  
462 ***rewrote the figure legend to clarify the data's origin (line 522-532). Regarding the***  
463 ***estimation of ambient temperature at the wintering sites of migratory***  
464 ***blackbirds, we have chosen the current approach since the migration direction***  
465 ***of blackbirds (from several populations) is quite variable, even within***  
466 ***populations. To illustrate this, we have attached a figure of blackbird migration***  
467 ***tracks we recorded from all over Europe in the last two years (see Fig. RL1***  
468 ***below). We feel that this approach better guarantees that we estimate ambient***  
469 ***temperature from observed overwintering locations rather than simulating***  
470 ***migratory movements themselves, which could result in predicted***  
471 ***overwintering locations with no empirical validation.***

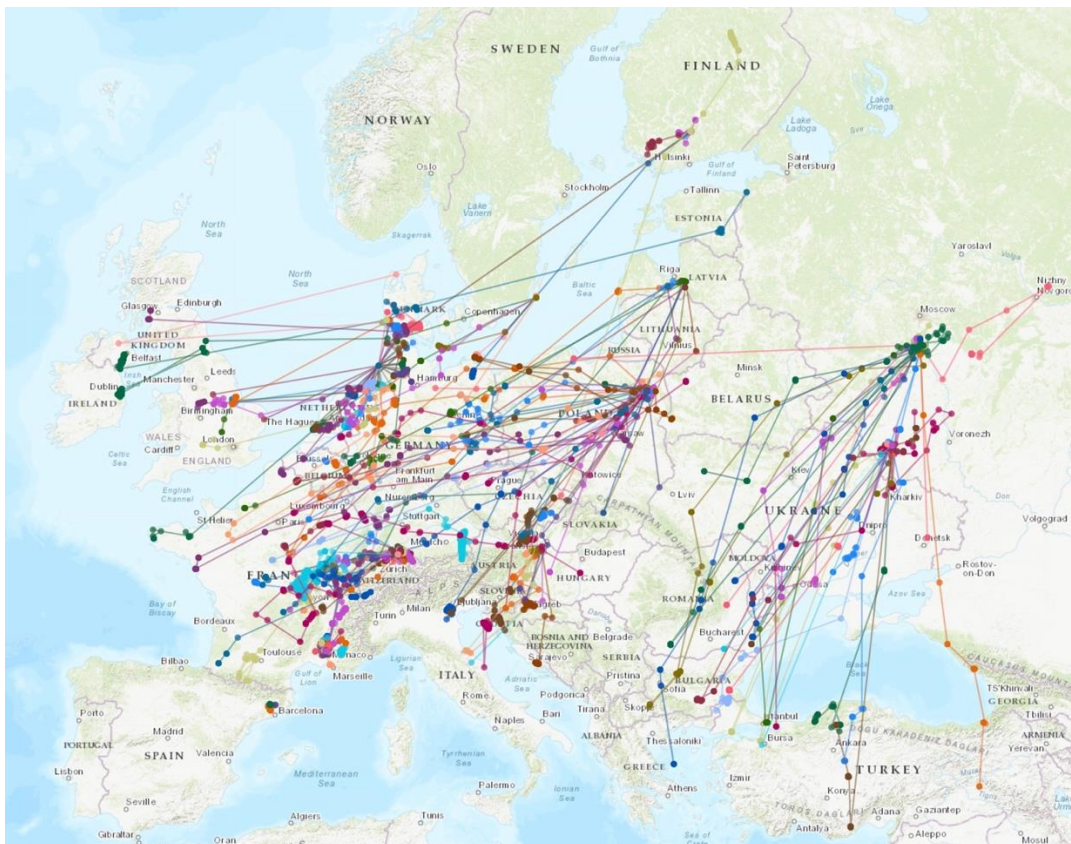
472  
473 ***Using flight durations quantified with heart rate data is an interesting approach,***  
474 ***but we feel again that it may be unlikely to improve the accuracy of the***  
475 ***estimated ambient temperatures at the wintering sites. The migration direction***  
476 ***for individual birds is unknown in this study (and could range between 270***  
477 ***degrees west and 180 degrees south). Also, factors that could influence***  
478 ***direction and rate of travel (e.g., wind support) cannot be suitably estimated.***

479 ***Overall, we still think, that the ambient temperature values we used are the***  
480 ***among-individual mean temperatures (where individual temperatures are***  
481 ***recorded at known wintering locations from a prior study on the same***  
482 ***population) most accurate.***

483 ***The reason why we intended to include such estimates of ambient temperature***  
484 ***from winter sites of migratory blackbirds even if not exact in this study is two-***  
485 ***fold. First to get an idea how much warmer wintering sites of migrants may be***



486 **compared to the sites of their resident conspecifics. And second, to estimate**  
 487 **strategy-specific thermoregulatory energy expenditures using the endotherm**  
 488 **models. Due to the potential inaccuracy of the estimates of ambient**  
 489 **temperature, we run also models including ambient temperatures at the**  
 490 **wintering and breeding sites 1 and 2 °C warmer and cooler as the used**  
 491 **estimates and found our conclusions were robust to bias in estimates of winter**  
 492 **ambient temperatures. This has also been included in the supplementary**  
 493 **(Extended Data Fig. 4). Additionally, we want to highlight that these estimates of**  
 494 **the ambient temperature of winter sites were not used for any analyses of heart**  
 495 **rate or body temperature.**



496  
 497  
 498 **Fig. RL1 | Migration tracks and positions of common blackbirds in Europe. The map illustrates the**  
 499 **migration paths of blackbirds tracked across Europe over the years 2022 and 2023. Each line**  
 500 **represents the track of individual birds, showcasing their diverse routes and stopover points.**

501  
 502 We think that the migration HRT and Tb results are actually more interesting than the



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503 estimated winter energy expenditures from modelling, which could be flawed either  
504 due to the model being unrealistic or other physiological changes in body  
505 composition happening. Here you have excellent evidence of the anticipatory  
506 physiological adjustments that individuals make many weeks in advance of  
507 migratory departure. This shows that “decision” to be a migrant this year and the  
508 gene expression, hormonal, metabolic, and behavioural adjustments are made well  
509 in advance by some individuals in a population without a cue like photoperiod. There  
510 is a paragraph in the discussion sort of addressing this but the overall message of  
511 the paper is about fitness differences and more ultimate causation based on fitness  
512 which is not actually what was measured.

513

514 ***Thank you for your comment. We fully agree with the reviewer’s suggestion to***  
515 ***put a stronger focus on the physiological outcomes of the heart rate and body***  
516 ***temperature data. We have reduced emphasis on the model results throughout***  
517 ***the manuscript and focused more on the physiological findings, including***  
518 ***moving the results earlier in the manuscript (lines 80-98) and introducing the***  
519 ***simulation model later (line 207-224). We also stronger highlighted the***  
520 ***anticipatory nature of these physiological adjustments (lines 109-143). Both the***  
521 ***physiological data and the model results show that migrants realise the***  
522 ***thermoregulatory benefits of higher Body temperature. The model’s primary***  
523 ***purpose is to define the expected differences in energy expenditure due to***  
524 ***thermoregulation and show support for our initial hypothesis (that migrants***  
525 ***expend less energy on thermoregulation). We agree that the model relies on***  
526 ***many assumptions, and we have changed many parts of the manuscript to***  
527 ***clarify and emphasise these assumptions. However, the results found from a***  
528 ***previous study<sup>1</sup> and the model simulations go in the same direction as our***  
529 ***trustworthy physical measurements, which we now emphasise more in the***  
530 ***revised version.***

531 The authors don’t really discuss the fact that residents dropped Tb more in winter  
532 than migrants or the fact that there is a seasonal decrease at all. This Tb and HRT  
533 data in itself is very interesting and relates to how these resident birds are coping  
534 with surviving winter, but it is not discussed.

535 ***In the revised version, we now point out more clearly that the reduction of body***  
536 ***temperature and seasonal pattern of body temperature and heart rate data is***



537 ***the main scope of our earlier work, already published<sup>1</sup> (lines 168, 193).***

538 The blackbird partial migrant system is great and many insights may be gained.  
539 However, we feel that the authors may be overemphasizing the results from a short  
540 distance migrant. Would these be enhanced or absent in a long-distance migrants?  
541 There could be very different mechanisms.

542 ***Thank you for this question. We, of course, can only speculate about the***  
543 ***implications for a long-distance migrant. However, we did a preliminary sub-***  
544 ***analysis of the data in this study where we compared the physiological***  
545 ***adjustments between migrants with more and migrants with fewer migration***  
546 ***nights (a coarse proxy for travel distance). However, no significant differences***  
547 ***were found between the groups, although this may, of course, be due to the***  
548 ***smaller sample size. Throughout the discussion, we revised the text to be more***  
549 ***careful in our interpretation of the results and changed the title accordingly.***

550 The title needs to be changed to better reflect the actual study. To say that  
551 “Migratory lifestyle carries no energy cost in songbirds” is inaccurate and  
552 misleading. First, all activities have an energy cost. Second, this title is generalizing  
553 to all songbirds from a short distance partially migratory species of fairly large body  
554 size. It is far from the final word on the topic. Maybe what would be more appropriate  
555 would be that “Migration energy costs are compensated by reduced  
556 thermoregulatory costs in a partial migrant songbird population”. Of course,  
557 emphasizing “individual-level anticipatory physiological changes weeks before  
558 departure in a partially migrant songbird” would also be a contender.

559 ***We agree that the previous title might have sounded like we overstated our***  
560 ***conclusions. We previously tried to highlight our intention by using the phrase***  
561 ***“net” energy costs in the manuscript. However, to further clarify and avoid any***  
562 ***confusion for the reader, we changed the title to “Migratory lifestyle carries no***  
563 ***overall energy cost in a partial migratory songbird” and want to thank you for the***  
564 ***valuable suggestions on this matter. Also see the previous comment.***

565 Perhaps the ultimate causation of partial migration should be answered by  
566 measuring survival and reproduction and making a life table. Trying to do it with  
567 physiology alone may not make sense, although the physiology adds a very  
568 interesting dimension to the story.



569 ***We agree that physiology can only be a part of the story of why partial migration***  
570 ***evolved. Many other factors, like survival<sup>2</sup> and reproductive fitness, are crucial.***  
571 ***The latter (reproduction) is still missing for this species, largely owing to high***  
572 ***predation rates. Here, our findings imply an energy benefit to migrants that may***  
573 ***have life history implications – we have revised our discussions to clarify the***  
574 ***hypotheses generated by our findings as a useful future course of study (lines***  
575 ***257-272, 294-299).***

576

577 1. Line 12: I can't help but visualize many exceptions from this general  
578 statement which really only applies to bird migration from high to low  
579 latitudes. So you either need to specify that or be more generic, like  
580 "Seasonal bird migration may provide energetic benefits associated with  
581 moving to areas with less physiologically challenging climates or  
582 increased food availability, but migration itself can carry high costs".

583 ***We agree and changed it according to your suggestion (line 13).***

584

585 2. L 15-16: I think you need to also include that you relied on physiological modelling  
586 here: "...paired with automated radio telemetry and physiological modelling..." Or  
587 you could say energetic modelling.

588 ***We agree and added "energetic modelling" to be more specific from the***  
589 ***start (line 19).***

590

591 3. L17: Delete "surprisingly" and replace "birds" with "blackbirds". I think your results  
592 are very interesting, but whether they can already be generalized to all birds may be  
593 premature without further study.

594 ***Thank you for spotting these imprecisions. We changed it according to your***  
595 ***suggestions (lines 13-27).***

596

597 4. L19: I think here you need to specify that the model you have predicts energy





598 expenditure would be decreased enough to compensate for migration costs. So,  
599 maybe change to “...departure, which modelling suggests will dwarf the energy  
600 costs...”.

601

602 ***Thank you for your comment. However, our model does not quantify the amounts of***  
603 ***energy saved through premigratory energy conservation. While our results clearly***  
604 ***show a decrease in heart rate during this period, indicating energy savings, we did***  
605 ***not directly compare these potential savings to the actual flight costs or later***  
606 ***energy amounts from thermoregulatory benefits. We have revised the sentence to***  
607 ***clarify this point and to emphasise the uncertainty regarding the extent to which***  
608 ***these savings balance against the subsequent costs (line 21).***

609

610 5. L 19-20: Change to “...migrants did not appear to decrease total daily energy  
611 expenditure...”

612 ***Thank you for your comment. We changed the wording (line 22).***

613

614 6. L26-27: I suggest changing evolved to evolves since it is believed to be an  
615 ongoing process.

616

617 ***Thank you for your suggestion. We agreed and changed it (line 30).***

618

619 7. L31: delete temporary and replace the colon with “through”.

620

621 ***Thank you for your suggestion. We rewrote the sentence based upon your***  
622 ***suggestion (line 35).***

623

624 8. L34: Is this what theory predicts? Doesn't theory generally focus on maximizing  
625 fitness or some reasonable correlate of fitness (Lifetime Reproductive Success  
626 or the product of survival and reproduction)? I don't think LRS is necessarily the  
627 same as energy expenditure. An animal could move to a less energetically costly  
628 place, but have lower fitness due to other factors like amount of food,  
629 competition for food, or predation risk. Specifically regarding partial migration,



630 isn't it thought to be either a mixed ESS where migrants and non-migrants get  
631 the same fitness, or a best of a bad job where residents achieve greater fitness  
632 than migrants and migrants switch to residents if possible? What is the case in  
633 blackbirds? Does your data suggest at least for energy the costs are about equal  
634 between tactics?

635  
636 ***Thank you for your question and highlighting the crucial distinction between energy***  
637 ***expenditure and fitness outcomes. Our study initially focuses on the energy costs***  
638 ***associated with migration, recognising that these do not directly equate to fitness.***  
639 ***Fitness indeed involves many complex factors, including- but not limited to - energy***  
640 ***expenditure. Here, we started from the energetic perspective to disentangle***  
641 ***migratory behaviour's various drivers and components. For blackbirds, specifically,***  
642 ***our data indicates a balance in the energetic costs between migrants and residents***  
643 ***over winter. This could imply an evolutionary stable strategy, like you already***  
644 ***suggested, where neither group consistently outperforms the other in fitness. We***  
645 ***acknowledge that fitness is the ultimate measure of success. Still, our primary***  
646 ***focus is on understanding whether an energy deficit needs to be overcome through***  
647 ***modifications in life history. If an energy deficit exists, it would imply differential***  
648 ***fitness or differences in life history strategies. We are currently further investigating***  
649 ***repeatability data regarding the wintering strategy and looking deeply into telomere***  
650 ***samples from individuals before and after winter to determine the "actual costs" of***  
651 ***either strategy. However, we are very aware of the fact that reproductive success is***  
652 ***still missing, as mentioned earlier. We appreciate your insightful feedback and have***  
653 ***revised the manuscript in multiple sections better to reflect the complex***  
654 ***relationship between energy expenditure and fitness, ensuring we do not imply***  
655 ***direct fitness conclusions from energetic data alone (e.g., lines 246, 259-272, 274-***  
656 ***289).***

657

658 9. L 38: We suggest rephrasing from "conclusive theory" to something like "greater  
659 understanding of the energetic trade-offs of migration".

660

661 ***Thanks a lot for the comment. During our revision, the sentence including***  
662 ***"conclusive theory" was completely replaced (lines 39-42)***

663

664 10. L40: Singular/plural don't agree. Change to "The Common blackbird is a wide-  
665 ranging species....".

18



666

667

**Thank you for your comment. We corrected the sentence based on your comment (line 44).**

668

669

670

11. L45: Perhaps be more specific about what you mean by conditions getting too harsh. Do you mean declining temperatures, decreasing food availability, high snowfall?

671

672

673

674

**Yes, rapidly declining temperatures leading to ground frost and continuous snowfall covering any feeding spots appear to be the main factor that leads to sudden winter migration. In a past preliminary analysis, we also show some evidence that high snowfall in the breeding region directly correlates to the percentage of blackbirds leaving spontaneously in the middle of the winter (see Fig. RL2 below). We revised the sentence to make what we meant (line 48) clearer.**

675

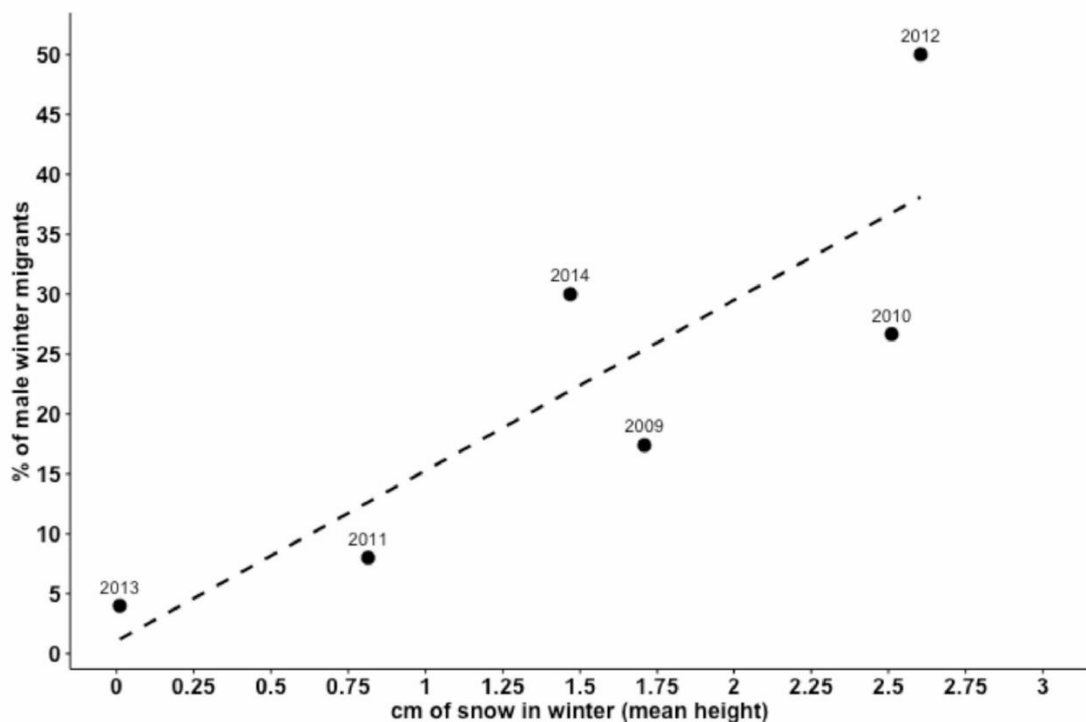
676

677

678

679

680



681

682

683

**Fig. RL2** | Relationship between snow coverage and migration of male blackbirds. This scatter plot depicts the impact of winter snow coverage (measured in centimetres of snow) on the proportion of male blackbirds

19



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684 *that migrate during the same winter. Data points represent different years, illustrating the correlation*  
685 *between increased snow coverage and a higher percentage of migratory male blackbirds.*  
686

687 12. L 46: I think the figure legend of Fig 1b needs to be more explicit that these  
688 wintering locations are not those of the birds in the current study, but those of  
689 birds from an earlier geolocator study. When a reader first looks at the figure  
690 they may easily assume that these are the known wintering locations of study  
691 birds.

692  
693 ***Thank you for your comment. We are sorry if there has been any confusion***  
694 ***about the origin of those wintering locations and glad you pointed it out.***  
695 ***We changed the figure legend to make it clear that the positions belong to***  
696 ***birds of the same breeding population of previous studies but not to the***  
697 ***birds of the current study. We have also revised the method section in this***  
698 ***aspect (lines 521-532, 714).***

699  
700 13. L 51, 56, 135, 189, 200, 617 and elsewhere: Change energetic to energy.  
701 Energetics is a field of study, but grammatically “energetic” also is a modifier.  
702 So I think it is better to say what is being expended: energy.

703  
704 ***Thank you for your comment. We corrected it throughout the manuscript***  
705 ***based on your valuable suggestion.***

706  
707 14. L57: Perhaps change to “...would on average exhibit...”.

708  
709 ***Thank you for your comment. We changed the wording to be more precise***  
710 ***(line 66).***

711  
712 15. L 445, 449, 452: gram, g, gr – be consistent in notation.

713  
714 ***Thank you for pointing out the inconsistency in the notation regarding the***  
715 ***measurement units for weight. The notation for grams has been***



716 ***standardised to 'g' throughout the manuscript.***

717

718 16. L 452: The total weight of the logger (3.3g) and radio tag (2.6g) does not add up  
719 4.9g. It should be 6.2g or 6.9% of a 90g bird. Perhaps you can make a point that  
720 part of the possible energy/survival costs of external tags is the aerodynamic  
721 effects they can have rather than just extra mass. So, the 3.3 g implanted tag  
722 likely has less of a negative cost to the bird's activities, and you have compared  
723 return rates of blackbirds with loggers and tags to those with tags only (L458).  
724 Also, in the future, lighter (1g) radio tags will be available to meet your needs for  
725 tag life.

726

727 ***Thank you for your comment and for identifying the discrepancy in our***  
728 ***weight calculations. Indeed, the combined weight of the logger (3.3g) and***  
729 ***radio tag (2.6g) should total 5.9g, which equates to 6.56% of a 90g bird. We***  
730 ***double-checked and corrected these numbers (line 594) in the revised***  
731 ***manuscript. We want to point out that the weight of the transmitter varied***  
732 ***from around 1.8g to 2.6g and we ensured that the heavier birds got the***  
733 ***heavier tags of any batch, which mitigates the relative burden. In the***  
734 ***revised manuscript, we acknowledge that besides the mass, the***  
735 ***aerodynamic effects of external tags could impact bird activities. By their***  
736 ***location within the body, the implanted loggers likely have reduced***  
737 ***aerodynamic influence, contributing to lesser negative impacts on the***  
738 ***birds. This factor has been crucial in comparing return rates between***  
739 ***blackbirds with only transmitter backpacks and those with additional***  
740 ***implanted loggers.***

741

742 L 454: ad libitum should be italics.

743

744 ***Thank you for this comment. We changed it (601).***

745

746 17. L 491: change to loggers.

747



748 ***Thank you for this comment. We did so (line 643).***

749

750 18. L 515: If there was only a data quality issue with the heart rate data, why did you  
751 end up with more heart rate measurements than Tb when they were taken at the  
752 same rate (every 30 min)?

753

754 ***Thank you for spotting this discrepancy. The order of the two numbers was wrong.***  
755 ***We corrected it in the revised version (line 666).***

756

757 19. L 526: Is this 97.4% or only 0.974 %?

758

759 ***Thank you for spotting this error. Really, the Classification AUC 0.977 reflects a***  
760 ***match of 97.7%. We corrected it (line 677).***

761

762 20. L 527-528: If you could estimate flight durations and stopovers, why not create  
763 an estimate of total migration distance along the known southwest migration  
764 route of your previously studied birds? See me general comment about this. If  
765 effect maybe you could have estimated a wintering area and done a better job at  
766 estimating the temperature conditions individuals experienced rather than using  
767 a single estimated temperature regime.

768

769 ***Thank you for your insights. We acknowledge the potential advantages of***  
770 ***the method you proposed for estimating total migration distance and***  
771 ***consequent wintering area temperatures. However, as detailed in our***  
772 ***general response to your comment (above), the extensive variation in***  
773 ***migration directions, even within the same population, led us to adopt a***  
774 ***different approach. By averaging the ambient temperatures of all known***  
775 ***centroids of wintering locations, we aimed to minimise the error that***  
776 ***might arise from assuming a single migration route or stopover for each***  
777 ***bird. Additionally, our method mitigates the potential inclusion of non-***  
778 ***representative areas that are equidistant but not ecologically relevant to***



779 ***the blackbirds. We believe that this approach provides a reliable average***  
780 ***estimate that captures the typical conditions the population encounters.***  
781 ***We also recognise the merit of exploring alternative methods and will***  
782 ***consider these for future analyses to compare their precision and***  
783 ***applicability.***  
784

785 21. L 604: I think you could be clearer here that temperatures were measured in the  
786 resident wintering area, but predicted for the migrants by assuming they were  
787 somewhere in the range of known wintering areas.

788  
789 ***We rewrote the sentence to clarify the origin of the temperature data (line***  
790 ***769).***  
791

792 22. L 612: Change to “...from geolocator-based estimates of winter range from  
793 previously-studied birds...”  
794

795 ***Thank you for this comment. We added your suggestion in the revised version (line***  
796 ***779).***  
797

798 23. L 73: What is meant by higher movement expenses here? Do you mean energy  
799 expended on movement as inferred from HRT data? Because you follow this by  
800 saying that heart rate did not differ. Please be more specific.

801  
802 ***We revised this section to refer to the actual energy expenses (derived***  
803 ***from heart rate) more accurately during migration (Fig. 3c, Extended Data***  
804 ***Fig. 3) (line 93). Furthermore, in the revised version, we clearly emphasise***  
805 ***that although the heart rates differ temporarily in different migration***  
806 ***stages, no differences can be found overall (e.g., lines 81, 95).***  
807

808 24. L 82-83: Does the higher Tb confer other benefits such as better immune  
809 function?  
810



811 ***Thank you for this question. Increased immune functions and higher predator***  
812 ***avoidance capabilities are among the first benefits we thought of. We added this in***  
813 ***our manuscript to elaborate on the benefits (lines 215-219).***  
814

815 25. L 90-94: Another interpretation is that the model predictions are wrong and may  
816 be based on too many assumptions. Physiological changes in body composition  
817 (organ and shivering muscle sizes) or mitochondria could also happen that  
818 explain why a simple model predicts a difference in energy expenditure, while  
819 heart rate data do not. Again larger or smaller hearts could pump different  
820 amounts of blood per beat. In any case I think there should be a case made for  
821 more detailed physiological studies of the two types.

822  
823 ***Thank you for your comment. We fully agree that other changes in body or***  
824 ***organ composition not analysed here could influence their total energy***  
825 ***consumption. Instead, the model is based solely on body temperature***  
826 ***and ambient temperature. We have stressed this throughout the***  
827 ***manuscript's revised version (e.g., lines 210, 563). We have also followed***  
828 ***your suggestion and highlighted the necessity of more detailed***  
829 ***physiological studies (e.g. measuring body compositions of migrants on***  
830 ***their wintering sites) (lines 219-224,248-254).***  
831

832 26. L 96-126: To me this is the most exciting finding of the study. It's a missed  
833 opportunity that you start be emphasizing how organ sizes could change, but  
834 then do not consider previous literature that shows that heart size and thus  
835 stroke volume could increase during this premigration phase. This would  
836 decouple heart rate from oxygen consumption (energy expenditure) to some  
837 degree. Never the less the data speaks for itself. It clearly suggests that  
838 metabolic rate (Tb and HRT) at night is decreased in individuals that are  
839 preparing to migrate.

840  
841 ***Thank you for your comment. We agree that this previously unknown***  
842 ***downregulation of heart rate and body temperature before migration is of great***  
843 ***importance. To give more weight to this finding and to address physiological***  
844 ***changes more in line with your suggestion, we included more existing literature***





845 *about morphological adaptations in organ size in the revised version (lines 128-130,*  
846 *but also see previous comment)*  
847

848 27. L 171-173: Could the nocturnal temperatures at the wintering area have been  
849 warmer during the spring premigration preparation phase than they were during  
850 the fall premigration phase? Perhaps it was just warmer and so it wasn't  
851 possible for birds to drop Tb and HRT?

852  
853 *Thank you for your question. Yes, that could very well be the case. Additionally, it*  
854 *could also very well be that the whole physiological system is already in a different*  
855 *mode in spring than in fall, with the reproductive apparatus starting to be active to*  
856 *be fully ready as soon as the birds arrive back at their breeding site <sup>3</sup> and have to*  
857 *compete with resident individuals for the same territories <sup>4</sup>. We added these points*  
858 *in the revised paragraph version (lines 193-196).*  
859

860 28. L 187: Please be specific that this was estimated from the thermoregulation  
861 model, which could be flawed. How about "According to the metabolic  
862 simulation model we used, on average..."

863  
864 *We changed the sentence according to your suggestion (line 227).*  
865

866 29. L 196-199: Why not estimate the energy costs of the migratory flights from  
867 allometric equations or the "FLIGHT" program. If you know how long they fly  
868 then you should be able to calculate an approximate number of kJ expended on  
869 migratory flight to compare with the thermoregulation savings. For example, to  
870 fly 800 km at 10m/sec would take 80,000 sec. Using the equation in Bishop and  
871 Butler 2015  $y=52.6M^{0.74}$  (M in kg) a 90 thrush expends 8.9 W (J/s), so the flights  
872 would require 712 kJ. That's only 4% of the thermoregulatory difference.

873  
874 *Thank you for this suggestion. While these calculations would be*  
875 *relatively broad considering uncertainties such as actual distances*  
876 *travelled, current location wind conditions, and altitude, we have added*  
877 *this to the revised version (line 242, also see Methods 'Energy expenditure*



878 ***of migratory flights' and Supplementary Data Table 12). This addition***  
879 ***strengthens our argument by providing a more comprehensive***  
880 ***understanding of the energy trade-offs involved in migratory behaviour.***  
881

882 30. L 230: Missing second parenthesis ).

883

884 ***Thank you for spotting the missing parenthesis. We corrected it (line 283).***

885

886 31. L 235: Change to “energy allocation”.

887

888 ***Thank you for this comment. We changed it accordingly (line 288).***

889

890 32. Fig 2 – letters should align with relative position of each subfigure: a above c,d,e.

891

892 ***We initially tried to align the labels in relative order of their mentioning in the main***  
893 ***text but agree that it is confusing for the readers to have them “search” for the***  
894 ***correct figure. We changed the labelling based on their position within the figure***  
895 ***(Fig. 2).***

896

897

898

899



## 900 Referee 2:

901

902 This manuscript reports a study that incorporated implanted heart rate and temperature data  
903 logger and automated radio telemetry to understand the physiology of migratory birds, making  
904 use of a partially migratory species – the European blackbirds (*Turdus merula*). By means of  
905 these technologies, the authors were able to examine the metabolic rates (using heart rate as a  
906 proxy) and thermoregulation (using body temperature as an indicator) of migratory and non-  
907 migratory individuals, from after breeding to wintering, including both stages of autumnal and  
908 vernal migrations. The obtained data showed internal differences in heart rates and body  
909 temperature between migrants and residents, being most pronounced in certain life-history  
910 stages of a year. More importantly, despite the 5-8 °C higher temperature experienced by the  
911 migrants in the wintering grounds and therefore lower energetic demands for thermoregulation,  
912 the physiological data do not show uni-directional differences between migrants and residents.  
913 The complex differences post a challenge for the authors to interpret the data, yet probably  
914 reveal part of the complex system animal ecologists are routinely dealing with.

915

916 I personally admire this study. The methods the authors used (the combination of implanted  
917 data logger and automated radio telemetry) and the data they obtained are absolutely amazing.  
918 The fact that the authors were able to identify migratory versus non-migratory individuals within  
919 a partially migratory population is already rarely achieved to my knowledge, let alone obtaining  
920 longitudinal physiological data at fine temporal scales. The data obtained by this study are  
921 therefore extremely valuable and must be made known to the scientific community, especially  
922 for animal ecologists who study migration ecology and physiology.

923

924 That being said, I do have some suggestions for the authors to consider, by which I sincerely  
925 hope that my comments would be considered constructive. Mostly, my comments are  
926 questions from a fellow scientist who is also studying migration physiology in birds. I sincerely  
927 hope that my comments represent the questions that readers may also have and might help the  
928 authors to see some blind spots that may exist in the manuscript.

929

930 Major comments:

931 The major comments I have are about the interpretation and also the presentation of the data,  
932 which are related to each other. For some data, I am wondering whether there might be  
933 alternative explanation. As for the data presentation, although I assumed that the authors had  
934 hierarchical data at both between- and within-individual levels at hands, the figures are unclear

27



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935 to me whether the trends were observed at which level.  
936

937 ***Thank you for your comments on our manuscript and for pointing out the***  
938 ***innovations and uniqueness of our study. With the help of your valuable feedback,***  
939 ***we have substantially revised several portions of the manuscript. Specifically, we***  
940 ***have clarified in the text and figure captions that most of our analyses refer to***  
941 ***expected within-individual dynamics. We are confident that the manuscript now***  
942 ***provides more clarity about the data shown and offers a more well-rounded***  
943 ***discussion of conclusions that describe alternative explanations for the patterns***  
944 ***we documented.***

945

946 1. Lines 77-83: In this paragraph, the authors stated that, despite higher ambient temperature  
947 ( $T_a$ ) in the wintering grounds (Fig. 1c), migrants did not realise “an overall metabolic  
948 benefit” (Lines 77-78). This was the authors’ interpretation to the lack of clear difference in  
949 heart rates between migrants and residents throughout the year (particularly in winter). The  
950 authors explained that this might be due in part to the higher body temperature ( $T_b$ ) in the  
951 migrants (Lines 78-79, Fig. 2b and 2j) and this “challenges the assumption that migrants  
952 realise a thermoregulatory benefit of overwintering in warmer areas or if they simply expend  
953 equivalent energy to maintain slightly higher  $T_b$ .”

954

955 I do not outright disagree with the authors’ interpretation on the data. However, I was  
956 wondering, could this result actually reveal the thermoregulatory benefits the migrants  
957 have enjoyed in a warmer wintering area?

958

959 We know that heat loss increases when the difference of  $T_b$  and  $T_a$  increases. Therefore, in  
960 a colder region, maintaining a slightly higher  $T_b$  would require more energy and increases  
961 heat loss. Therefore, maintaining a slightly higher  $T_b$  might only be affordable in a relatively  
962 warmer region. The question is whether maintaining a slightly higher  $T_b$  confers any  
963 physiological or survival benefits to the migrants so that they would spend the energy they  
964 could otherwise spare in the warmer wintering grounds to maintain a slightly higher  $T_b$ .

965

966 ***Thank you very much for your comments and input. Yes, we agree that the***  
967 ***thermoregulatory benefits that the migrants realise with apparently similar energy***  
968 ***spending could be one of the drivers of this partial migratory system.***

969 ***Thermoregulatory benefits, expressed here in a higher body temperature, could***  
970 ***have manifold advantages to individuals. Especially in birds, it has been previously***

28



971 ***shown that higher body temperatures can result in increased immune functions and***  
972 ***predator avoidance capabilities. We added examples and references to the revised***  
973 ***manuscript to highlight such benefits (lines 217-219). We also fully agree that the***  
974 ***mechanism behind these thermoregulatory mechanisms could be driven in***  
975 ***significant parts by precisely the concept you described (lines 81-95).***

976

977

978 2. Fig. 3: These are amazing data, without a doubt, but I do not fully understand what data the  
979 authors were actually presenting. It would be great if the authors could clarify. This will also  
980 help readers to understand your findings.

981

982 First of all, since you have to recapture the birds to retrieve the implanted data logger, I  
983 suppose you have very fine within-individual recordings. Did you use them to calculate and  
984 obtain a single data point per individual? If so, I may have missed such a description.

985

986 Second, if you did not calculate a single data point per individual and instead included the  
987 repeated recordings per individual in your analysis (which might be so since you mentioned  
988 using hierarchical GAMs), this figure apparently did not represent that kind of data.

989

990 I am not criticizing this. My point is, what do the data points on this figure represent? It is  
991 now unclear to me whether each of the data points represents one individual at the  
992 departure time from the breeding site.

993

994 At last, the above questions matter in terms of the interpretation of your results. Although I  
995 may have misunderstood the figure, I am highly intrigued whether the reduction of heart  
996 rate and body temperature in migrants was observed across individuals or within  
997 individuals?

998

999 If each data point represents one individual, this pattern could be driven by a correlation  
1000 between heart rate and departure time, e.g., if late goers have lower heart rates and body  
1001 temperature than early goers, but this correlation wasn't clear in residents (since they do  
1002 not go). Could this be a possibility?

1003

1004 ***Thank you for your questions. We are very sorry that our previous figure legend and***  
1005 ***description within the manuscript weren't clear enough. Indeed, for every***  
1006 ***individual, we have single-point measurements on a 30-minute interval of varying***



1007 **quality over the entire study from fall to the following spring. However, as we**  
1008 **collected data over three years and aimed to compare migrants and residents in**  
1009 **different phases of their overwintering cycle, we had to find a way to centre each**  
1010 **measurement on a specific time within the migration cycle. To analyse energetic**  
1011 **differences at various migration stages (Methods section: ‘Definition of seasons and**  
1012 **individual key migratory stages’), we assigned each single heart rate and body**  
1013 **temperature measurement of resident birds to simultaneous single measurements**  
1014 **of migratory individuals of the same sex based on the real-time timestamp. Due to**  
1015 **the complexity of comparing migration phases between the two strategies,**  
1016 **especially with no migration for residents, this approach allowed us to effectively**  
1017 **synchronise and compare the data from both groups. By distributing all**  
1018 **measurements of resident birds (N = 54) from the same sex equally among the**  
1019 **migratory birds (N = 19), every single measurement from a resident was only**  
1020 **referenced once to a specific measurement of a migrant bird. This resulted in every**  
1021 **single measurement of a resident being assigned a “stage of migration”**  
1022 **corresponding to the reference migrant measurement, allowing us to directly**  
1023 **compare the physiological data of residents and migratory blackbirds in relation to**  
1024 **the departure and arrival events of the migrants. Since each resident measurement**  
1025 **was assigned only once, the dataset contains unique occurrences of each**  
1026 **measurement, thereby avoiding any pseudoreplication.**

1027  
1028 **Consequently, Fig. 3 displays the above assigned and centred datasets, with each**  
1029 **point being the mean of measurements of all migrants (N = 19) and all residents (N =**  
1030 **54) as well relative to specific migration stages (e.g. date of departure.**

1031  
1032 **The downregulation of heart rate and body temperature was observed across all**  
1033 **individuals, even though it is present in each individual. It is generally masked by a**  
1034 **high variation of physiological measurements within and across individuals and**  
1035 **time.**

1036  
1037 **In response to your feedback, we have revised the manuscript’s methods section**  
1038 **(lines 741-751) and figure legend (lines 548-557, i.e. Fig.3) to more accurately**  
1039 **describe our approach and the data displayed, ensuring that the physiological**  
1040 **trends of heart rate and body temperature are clearly communicated.**

1041



1042 3. Overall, I have some concerns about how the authors reached the main conclusion as  
1043 claimed in the title “Migratory lifestyle carries no energy cost in songbirds.” I am not saying  
1044 that I consider the data insufficient to support this conclusion. My concern is, how this  
1045 conclusion was reached was unclear to me. After reading this manuscript, I saw the  
1046 amazing data that showed differences in heart rates and Tb between migrants and  
1047 residents, and also the lack of differences between the two groups of individuals. However,  
1048 do these results suggest that migratory lifestyle carries no energy cost in the migrants?  
1049 Perhaps, but the reasoning and deduction was unclear to me.

1050

1051 ***Thank you for your comment. Our original title might have been simplistic. This***  
1052 ***conclusion of course refers to the equivalent overall energy expenditure implied by***  
1053 ***equivalent heart rates. That said, we recognise that other parts of the manuscript do***  
1054 ***indeed show a benefit from, for example, reduced thermoregulatory expense.***  
1055 ***Thus, in the revised manuscript, we changed the title to be more appropriate:***  
1056 ***“Migratory lifestyle carries no overall energy cost in a partial migratory songbird”.***  
1057 ***Additionally, we reworked multiple parts to further elaborate on the limitations of***  
1058 ***our findings (e.g., lines 33, 80-95, 128, 219-224, 248-254)***

1059

1060 4. Line 90 “Fig. 4”: If you reported and cited this figure earlier, why wasn’t it “Fig. 3”? .

1061

1062 ***Thank you for your question. Following a comprehensive revision of significant***  
1063 ***sections of the manuscript, Fig. 4 has now been properly sequenced after Fig. 3 (line***  
1064 ***213).***

1065

1066 5. Line 150 “Fig. 3c”: should this be “3d” since it is about Tb?

1067

1068 ***Yes, we corrected the reference to the Fig. 3d, which is now Fig. 3h (line 167).***

1069

1070 6. Lines 174-175: Here, I have a minor question about the interpretation. If you attributed the  
1071 Tb increase of the residents to seasonal changes, why did the migrants lack such a  
1072 seasonal change?

1073

1074 ***Thank you for your question. Because the migrants overwinter in more southern***  
1075 ***regions with a relatively more stable climate, we expect their weather conditions to***  
1076 ***change less drastically during this time of the year and, therefore, exhibit a more***



1077 **“stable” body temperature<sup>1</sup>. We added this disclaimer information to the sentence**  
1078 **(lines 171-175).**

1079  
1080 7. Line 206: would a reference for the Extended POL be needed here?  
1081

1082 **Thank you for pointing out the missing reference. We added it in the revised version**  
1083 **of the manuscript (line 259).**

1084  
1085 8. Line 384 in the legend of Fig. 1 “an implanted and temperature logger”: should it be “an  
1086 implanted temperature logger” or “an implanted heart rate and temperature logger”?  
1087

1088 **Thank you for spotting the error. The latter was correct, and we added the word**  
1089 **“heart rate” (line 523, i.e. Fig. 1).**

1090  
1091 9. Lines 451-452: Yet, the internal data logger also adds another 3.3g. Does that not need to  
1092 be taken into account because it is internal? I am sure that it is still within the weight limit a  
1093 blackbird can carry without apparent negative impact, but it would be great to clarify  
1094 whether the weight of an internal data logger needs to be taken into account., e.g., for  
1095 animal welfare consideration.  
1096

1097 **Thank you for your comment. The previously stated sum of weight needed to be**  
1098 **corrected, and the combined weight of the logger (3.3g) and radio tag (2.6g) should**  
1099 **total 5.9g, which equates to 6.56% of a 90g bird. The transmitter weight varied from**  
1100 **around 1.8g to 2.6g, and during tagging, we ensured that the heavier birds got the**  
1101 **heavier tags of any batch. We acknowledge that besides the mass, the aerodynamic**  
1102 **effects of external tags could significantly impact bird activities. Because of their**  
1103 **implanted nature, the loggers likely have less of an aerodynamic influence,**  
1104 **contributing to a lesser negative impact on the bird’s flight performance and**  
1105 **mitigating the relative burden. Our comparisons of return rates between blackbirds**  
1106 **with external transmitters only and the combination with an implanted logger have**  
1107 **also shown no signs of a higher impact of the combination of radio-transmitter /**  
1108 **heart rate logger. Although we would not want to make any general statements**  
1109 **about the effect of implanted devices, we can, at least, say that we could not find a**  
1110 **negative influence on the migratory propensity, survival and return rate for our**

32





1111 ***blackbirds with an addition of an implanted logger and an average weight addition of***  
1112 ***a maximum of 6.59%.***

1113  
1114 10. Lines 457-458: I was exactly curious about the survival and return or recapture rates of the  
1115 birds that were installed with a data logger. Was that reported in the Results? I did not see  
1116 it. I would suggest reporting these results, at least in the Extended Data, if not yet.

1117  
1118 ***Thank you for your inquiry. We have added these numbers to the revised Methods***  
1119 ***section (lines 603-609).***

1120  
1121 11. Lines 495-496: That was an amazingly high recapture rate that made this system and the  
1122 data rare and highly valuable!

1123  
1124 ***We appreciate you acknowledging our enormous effort in fieldwork during the***  
1125 ***recapture periods.***

1126  
1127 12. Lines 584-588: I do not fully understand how you avoided pseudoreplication this way.  
1128 Could you elaborate this?

1129  
1130 ***Thank you for your question, and please excuse the inaccuracy of our description of***  
1131 ***this analysis. By assigning each measurement from a resident bird to a unique***  
1132 ***reference measurement of a migrant bird, we did not duplicate any comparisons***  
1133 ***during the analysis. Please see also my response to your comment #2. We revised***  
1134 ***the paragraph of this description in the revised manuscript to better reflect the***  
1135 ***purpose of analysing the data on energetic differences at different migration stages***  
1136 ***and, in particular, between the two phenotypes' overwintering strategies where the***  
1137 ***residents do not show migration behaviour. We also added more detailed***  
1138 ***information on the data preparation (lines 741-760).***



1139 **Referee 3:**

1140

1141 This is a novel and important study that provides new insights into the energetics of short-range  
1142 avian migration. However, several of the major conclusions depend heavily on estimates of  
1143 energy expenditure from a biophysical model about which very little detail is provided. At the  
1144 very least, the authors need to provide full details (most likely in supplementary materials) of the  
1145 values used to parameterize the NicheMapR model, the source for each value and  
1146 assumptions, including those about where the birds were roosting, whether digestion-  
1147 associated thermogenesis substitutes for thermoregulatory heat production, etc.

1148 I am also concerned that the species-specific NicheMapR model that provides the basis for all  
1149 the estimates of metabolic rate upon which the major conclusions of the study are based was  
1150 not validated against empirical, species-specific metabolic rate and body temperature data  
1151 (along the lines of Conradie et al. 2023 JEB doi:10.1242/jeb.245066, in the context of hotter  
1152 conditions). The NicheMapR endotherm model is still new, and has not, to the best of my  
1153 knowledge, been properly validated in the context of shallow reductions in rest-phase body  
1154 temperature. The energy savings associated with small reductions in body temperature can be  
1155 substantially larger than expected based on the magnitude of hypothermia, and so I am wary  
1156 about accepting the authors' estimates of thermoregulatory energy expenditure at face value.

1157

1158 ***Thank you very much for reading our manuscript and highlighting the need for***  
1159 ***greater transparency regarding our use of the NicheMapR model in our study. In***  
1160 ***response to your concerns, we have extensively revised our manuscript by focusing***  
1161 ***more on our physiological data measured by the logger and providing detailed***  
1162 ***descriptions of the parameters used in the model. We are still convinced that our***  
1163 ***model is a valuable contribution to our analysis as it offers an explanation of how***  
1164 ***migrants potentially realise energetic benefits even though the heart rate of***  
1165 ***migrants and resident individuals doesn't differ. Additionally, the model serves as***  
1166 ***an additional analytical dimension to our heart rate measurements and quantifies***  
1167 ***our estimated energy sums while aligning well with our empirically measured***  
1168 ***physiological data. The revised manuscript is now more careful about the***  
1169 ***conclusions drawn from the model calculations, which are meant simply to***  
1170 ***approximate the differences in thermoregulatory expense. That said, our ground-***  
1171 ***truthed physiological measurements also agree with the conclusions drawn from***  
1172 ***the model. Our previous work, also cited in the paragraphs concerned <sup>1</sup>, illustrates***  
1173 ***the expected heart rate decrease while in a warmer environment. The formulated***

34



1174 ***NicheMapR model is consistent with these previously observed relationships and***  
1175 ***tries to give them an approximate magnitude and convert them into kilojoules. Even***  
1176 ***if the general assumptions are somewhat off, the large magnitude of the differences***  
1177 ***suggests that the energetic benefits of the migratory phenotype are likely***  
1178 ***qualitatively valid. In other words, our observations of heart rate, body temperature,***  
1179 ***and ambient temperature by themselves (without the model) strongly imply an***  
1180 ***energy ‘surplus’ for migrants arising from reduced thermoregulatory burden. The***  
1181 ***NicheMapR model is consistent with this expectation and is robust to temperature***  
1182 ***deviations of several degrees (see Extended Data Fig. 4). In the revised manuscript,***  
1183 ***we have amended sections dealing with model assumptions and results***  
1184 ***interpretation to reflect these considerations more accurately, ensuring our***  
1185 ***conclusions remain conservative and supported by our data, the model’s***  
1186 ***theoretical framework***<sup>5,6</sup>***, and previous studies***<sup>1,7</sup>***. All to say, we have made a more***  
1187 ***explicit acknowledgement that physiological, morphological, or behavioural***  
1188 ***differences among the strategies could influence the model estimates, but we note***  
1189 ***that these differences would need to be quite substantial to account for the***  
1190 ***magnitude of energy differential our findings suggest.***

1191

1192

1193 Just to be clear, heart rate data were not converted to metabolic rates? It might be worth adding  
1194 a sentence or two explaining why not, since this has often been done in previous studies.

1195

1196 ***Thank you for your question. Initially, we tried to calibrate the HRT rate measures,***  
1197 ***performing cliometrics measurements for each recaptured bird in a metabolic***  
1198 ***chamber as soon as we got hold of them. However, due to the difficult recapture***  
1199 ***procedure, spread out return dates and the nature of seasonal differences in heart***  
1200 ***rate and body temperature (see***<sup>1</sup> ***and previous comment), we couldn’t correctly***  
1201 ***calibrate the physiological measurements to metabolic rates. Since this would***  
1202 ***technically be just a conversion to another currency without adding any extra***  
1203 ***information regarding a comparison of migratory phenotypes, it was omitted during***  
1204 ***the process. Critically, our heart rate data suggest equivalent overall energy***  
1205 ***expenditure thus conversion to units of energy is not needed to compare***  
1206 ***components of this budget because the terms would cancel. The hidden expenses***  
1207 ***can also be seen just in the physiological data alone. We added such a disclaimer***  
1208 ***and explanation in the revised version (lines 59, 81, 95, 227-232, 248-254)***



1209

1210 Clarification is needed on the combined mass of the Star Oddi loggers and backpack-mounted  
1211 transmitters. In line 445, the mass of each logger is given as 3.3 g, and in line 449 the mass of  
1212 the backpack transmitters as  $\leq 2.6$  g. This is a combined mass of 5.9 g, equivalent to 6.6 % of the  
1213 blackbirds' 90-g body mass, not 4.9 g and 5.4 % as currently stated in line 452. The generally  
1214 accepted upper limit for attached devices on birds is 5 % of body mass, and I think the authors  
1215 need to carefully consider whether their data and variables like migration speed or duration may  
1216 have been influenced?

1217

1218 ***Thank you for pointing out this discrepancy in our calculations. You are correct that***  
1219 ***the combined weight of the logger (3.3g) and radio tag (2.6g) should total 5.9g, which***  
1220 ***equates to 6.56% of a 90g bird. The weight of the transmitter varied from around 1.8g***  
1221 ***to 2.6g, and we ensured that the heavier birds got the heavier tags of any batch,***  
1222 ***which may mitigate the relative burden. We also acknowledge that besides the***  
1223 ***mass, the aerodynamic effects of external tags may play an important factor in a***  
1224 ***bird's flight performance. By their location within the body, the implanted loggers***  
1225 ***likely have reduced aerodynamic influence, potentially contributing to lesser***  
1226 ***negative impacts on the birds. This factor has been crucial in our comparison of***  
1227 ***return rates between blackbirds with only transmitters and those with additional***  
1228 ***internal loggers. Recapture, and migratory return rates were not lower for birds with***  
1229 ***implanted loggers compared to only radiotagged birds from previous years. Return***  
1230 ***rates for birds with implanted loggers were 90%, compared to 43% for the control***  
1231 ***group, and recapture rates were 80% versus 23%, respectively. The experimental***  
1232 ***setup may have influenced these findings, which required extensive recapturing***  
1233 ***efforts to retrieve the loggers and continuous monitoring, making direct***  
1234 ***comparisons challenging. We added this information in our revised manuscript***  
1235 ***(lines 592-609).***

1236

1237 The title overstates the significance of the study to the point of being misleading. The study  
1238 involved one species of European partial migrant in which some individuals migrate 800 km, but  
1239 the title makes it sound like you have shown a lack of an energetic cost for a migratory lifestyle  
1240 among migratory passerines in general, some of which fly many thousands of kilometers.

1241

1242 ***We agree that the previous title might have been overemphasising the implications.***  
1243 ***We changed the title to "Migratory lifestyle carries no overall energy cost in a partial***

36



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1244 **migratory songbird” to be more specific and to further clarify and avoid any**  
1245 **confusion for the reader (line 1).**

1246

1247 1. Abstract: please remove adjectives like “solid” and “critical”... this is not good scientific  
1248 writing style.

1249

1250 **Thank you for your comment. In the revised version, we have removed those**  
1251 **adjectives for the sake of clarity and to be more specific from the start on (lines 13-**  
1252 **27)**

1253

1254 2. Lines 40-45: Is there any information available on how the proportion of blackbirds  
1255 migrating has changed in recent decades with factors like urbanisation and climate  
1256 warming? If there is, please add a sentence or two here.

1257

1258 **Thank you for your question. Indeed, studies have investigated the influence of**  
1259 **climate change and urbanisation on blackbirds<sup>8,9</sup>. Current data shows that with**  
1260 **increasing urbanisation, blackbirds might become more resident, likely as a result**  
1261 **of the different microclimates that exist in cities with ambient conditions being less**  
1262 **harsh and additional feeding keeping a constant supply of food availability for birds**  
1263 **in these areas. We have added this information in the revised paragraph (line 50).**

1264

1265

## Response Letter References

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## Decision Letter, first revision:

Our ref: NATECOLEVOL-23123033A

23rd July 2024

Dear Dr. Linek,

Thank you for your patience as we've prepared the guidelines for final submission of your Nature Ecology & Evolution manuscript, "Migratory lifestyle carries no overall energy cost in a partial migratory songbird" (NATECOLEVOL-23123033A). Please carefully follow the step-by-step instructions provided in the attached file, and add a response in each row of the table to indicate the changes that you have made. Please also check and comment on any additional marked-up edits we have proposed within the text. Ensuring that each point is addressed will help to ensure that your revised manuscript can be swiftly handed over to our production team.

**\*\*We would like to start working on your revised paper, with all of the requested files and forms, as soon as possible (preferably within two weeks). Please get in contact with us immediately if you anticipate it taking more than two weeks to submit these revised files.\*\***

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In recognition of the time and expertise our reviewers provide to Nature Ecology & Evolution's editorial process, we would like to formally acknowledge their contribution to the external peer review of your manuscript entitled "Migratory lifestyle carries no overall energy cost in a partial migratory songbird". For those reviewers who give their assent, we will be publishing their names alongside the published article.

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If you have any further questions, please feel free to contact me.

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Reviewer #2:

Remarks to the Author:

Thank you for your thoughtful responses to our questions and for making the appropriate changes to the manuscript. Our only suggestion is that the title still suggests there is no cost of migrating and and so perhaps changing it to Migratory lifestyle carries no ADDED overall energy cost in a partial migratory songbird is appropriate





Reviewer #3:

Remarks to the Author:

In my opinion, the authors did an excellent job in revising this manuscript and the concerns I raised last time were well addressed. I only have some minor editorial suggestions are listed below for the authors to consider:

1. Title: Echoing other reviewers' comments, I was indeed thinking if the title matches with the actual findings of this study. Although the authors have changed the title, I still think that the current title is still simplistic and probably does not accurately convey the gist of the study. However, because the exciting and important findings of this study are pretty nuanced, I find it very difficult to make a title that is succinct and catchy at the same time. So, while I think it would be better to change the title again, I have no idea what to suggest to the authors. My apologies.

2. Lines 25-26: I would suggest slightly rephrasing the sentence to "Moreover ... insights suggesting that the maintenance of migration is associated with..."

3. Lines 38-39 "whereas others may require different life history strategies to overcome energy deficits": semantically unclear, probably better to rephrase.

4. Lines 54-56: It's not clear without reading the figure legend, perhaps slightly rephrasing it would help. For example, "... experience on average  $\sim 5.7$  °C warmer ambient temperatures ( $T_a$ ) over 39 years ..."

5. Tense: Through out the paper, there are many places where I think the authors should have used past tense. I have to admit that tense is not my strong suit, but I nevertheless list those places for the authors to check:

- a. Line 59: examined
- b. Line 60: investigated
- c. Line 61: quantified
- d. Line 124: occurred
- e. Line 129: which we "did" not
- f. Line 133: all birds "were"
- g. Line 152: were
- h. Line 153: migrated
- i. Line 154: travelled
- j. Line 159: migrants' nocturnal Tb "was"
- k. Line 191: this difference "was"
- l. Line 194: did not allow

6. Line 61: I suggest adding "(i.e., migrants versus residents)" after "among phenotypes"

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7. Line 63 “negatively colinear with Ta”: not sure if this is a correct way to say it. Would “negatively correlated with Ta” or “covaries with Ta negatively” work here?

8. Line 65: add “thus”, i.e., “We thus predicted...”

9. Line 68 “incur”: how about “bear”?

10. Line 68 “from”: due to?

11. Lines 85-86: This sentence has a long clause “the fact that...” without a follower verb. Perhaps change it to “Moreover, migratory blackbirds exhibited a slightly...”?

12. Line 97 “does”: This word is superfluous. Delete it.

13. Line 98 “various overwintering stages”: What does it mean?

14. Line 147: clearer if saying “an even greater 36.4% increase”

15. Line 168: clearer if adding “that” after “we observed”

16. Line 175: delete “the initial”, not necessary here

17. Line 178 “can already be seen”: could be seen already

18. Line 185 “lead-up to spring migration”: not sure what it meant, perhaps delete “to”?

19. Line 230” delete “is”, i.e., “as implied by”

20. Lines 594-595 “the heavier birds received the heavier tags”: I think the two articles “the” are not necessary here.

21. Line 595 “mass”: weight?

22. Lines 600-602: You conducted a pilot study in 2015 and then what?

23. Lines 604-606: Thank you for providing the information. This is super intriguing as both the return rates and recapture rates were so much higher in tagged birds than in control birds. Perhaps it was due to the huge effort you paid, but would it be a sign of inadvertent biases?



24.Line 746: I suggest slightly rephrasing it as “This assigned each single measurement of a resident a “stage of migration” ...”

Reviewer #4:

Remarks to the Author:

Thanks for your thoughtful responses to the concerns I raised. This is a very exciting study and a substantial contribution to our understanding of avian energetics. Congratulations!

**Author Rebuttal, first revision:**

## Reviewer #2:

Thank you for your thoughtful responses to our questions and for making the appropriate changes to the manuscript. Our only suggestion is that the title still suggests there is no cost of migrating so perhaps changing it to Migratory lifestyle carries no ADDED overall energy cost in a partial migratory songbird is appropriate

***Thank you for all your effort and help in improving our manuscript. We agree and adapted your suggested change of the title.***

## Reviewer #3:

In my opinion, the authors did an excellent job in revising this manuscript and the concerns I raised last time were well addressed. I only have some minor editorial suggestions are listed below for the authors to consider:

***Thank you for your immense input, and we are happy that all your concerns could have been solved. Thank you also for those last suggestions to further refine our manuscript's clarity and correct grammatical issues.***

1. Title: Echoing other reviewers' comments, I was indeed thinking if the title matches with the actual findings of this study. Although the authors have changed the title, I still think that the current title is still simplistic and probably does not accurately convey the gist of the study. However, because the exciting and important findings of this study are pretty nuanced, I find it very difficult to make a title that is succinct and catchy at the



same time. So, while I think it would be better to change the title again, I have no idea what to suggest to the authors. My apologies.

***We agree that this is a difficult one but think that now with the suggestion of reviewer 2 we found a good solution. The revised title is now “Migratory lifestyle carries no added overall energy cost in a partial migratory songbird”.***

2. Lines 25-26: I would suggest slightly rephrasing the sentence to “Moreover ... insights suggesting that the maintenance of migration is associated with...”

***Thank you very much for this comment. We changed it according to your suggestions (lines 25-27).***

3. Lines 38-39 “whereas others may require different life history strategies to overcome energy deficits”: semantically unclear, probably better to rephrase.

***Thank you very much for this comment. We changed it according to your suggestions (lines 37-39).***

4. Lines 54-56: It’s not clear without reading the figure legend, perhaps slightly rephrasing it would help. For example, “... experience on average ~5.7 °C warmer ambient temperatures (Ta) over 39 years ...”

***Thank you very much for this comment. We changed it according to your suggestions (line 54).***

5. Tense: Through out the paper, there are many places where I think the authors should have used past tense. I have to admit that tense is not my strong suit, but I nevertheless list those places for the authors to check:

- a. Line 59: examined
- b. Line 60: investigated
- c. Line 61: quantified
- d. Line 124: occurred
- e. Line 129: which we “did” not
- f. Line 133: all birds “were”
- g. Line 152: were
- h. Line 153: migrated
- i. Line 154: travelled



- j. Line 159: migrants' nocturnal Tb "was"
- k. Line 191: this difference "was"
- l. Line 194: did not allow

***Thank you for spotting these imprecisions in the use of tense. We changed it according to your suggestions (lines 59, 60, 62, 126, 131, 139, 155, 156, 161, 193, 196).***

- 6. Line 61: I suggest adding "(i.e., migrants versus residents)" after "among phenotypes"

***Thank you for your suggestion. We agreed and changed it (line 61).***

- 7. Line 63 "negatively colinear with Ta": not sure if this is a correct way to say it. Would "negatively correlated with Ta" or "covaries with Ta negatively" work here?

***Thank you for your question. Yes, your suggested phrase works as well. We have changed it based on your suggestion, even though the original phrase was also correct (lines 63 and 64).***

- 8. Line 65: add "thus", i.e., "We thus predicted..."

***Thank you for this comment. We changed it (lines 65 and 66).***

- 9. Line 68 "incur": how about "bear"?

***We have adopted the proposed change (line 68).***

- 10. Line 68 "from": due to?

***Thank you for this comment. We changed it (line 69).***

- 11. Lines 85-86: This sentence has a long clause "the fact that..." without a follower verb. Perhaps change it to "Moreover, migratory blackbirds exhibited a slightly..."?

***We completely agree that it was a hard-to-read sentence and revised it according to your suggestion (line 86-87).***



12.Line 97 “does”: This word is superfluous. Delete it.

***You are right. We deleted it (line 98).***

13.Line 98 “various overwintering stages”: What does it mean?

***Thank you for this comment. We rewrote the sentence and added explanatory examples (lines 99-100).***

14.Line 147: clearer if saying “an even greater 36.4% increase”

***We added the proposed specification of the direction of change (line 149).***

15.Line 168: clearer if adding “that” after “we observed”

***Thank you for this comment. We agreed and added the word “that” (line 171).***

16.Line 175: delete “the initial”, not necessary here

***That is right. We deleted the phrase (line 174).***

17.Line 178 “can already be seen”: could be seen already

***We changed it to ‘could be seen already’ as your proposed (lines 180-181).***

18.Line 185 “lead-up to spring migration”: not sure what it meant, perhaps delete “to”?

***Thank you for this comment. We hope it became clearer now with the revised version we deleted the word ‘to’ (line 187).***



19.Line 230” delete “is”, i.e., “as implied by”

***We changed the sentence according to your suggestion (line 232).***

20.Lines 594-595 “the heavier birds received the heavier tags”: I think the two articles “the” are not necessary here.

***Thank you for this comment. We deleted the first article but kept the second one because we think it enhances the flow of reading (lines 329-330).***

21.Line 595 “mass”: weight?

***The word ‘weight’ could have been used too. However, we keep ‘mass’ as we want to be certain here, and weight can be different with active flight acceleration and similar behavioural changes.***

22.Lines 600-602: You conducted a pilot study in 2015 and then what?

***Thank you for your question. We rewrote the paragraph to clearly state the outcomes of the pilot study. And separated the sentence in two (lines 335-337).***

23.Lines 604-606: Thank you for providing the information. This is super intriguing as both the return rates and recapture rates were so much higher in tagged birds than in control birds. Perhaps it was due to the huge effort you paid, but would it be a sign of inadvertent biases?

***Thank you for this important comment! However, it wasn’t higher in the tagged ones but in the implanted ones. You are correct about the mentioned bias, and one could argue that this is likely inherent in every type of fieldwork with wild animals. The main purpose of the comparison, however, is to serve ethical considerations and highlight that recapture and survival rates are for sure not lower for our experimental birds with implants.***

24.Line 746: I suggest slightly rephrasing it as “This assigned each single measurement of a resident a “stage of migration”...”



***Thank you for your suggestion. We agree and changed the sentence according to your proposed way (line 481).***

## **Reviewer #4:**

Thanks for your thoughtful responses to the concerns I raised. This is a very exciting study and a substantial contribution to our understanding of avian energetics. Congratulations!

***Thank you very much for your previous valuable input and acknowledgement of our work.***

### **Final Decision Letter:**

Dear Dr Linek,

We are pleased to inform you that your Article entitled "Migratory lifestyle carries no added overall energy cost in a partial migratory songbird", has now been accepted for publication in Nature Ecology & Evolution.

Over the next few weeks, your paper will be copyedited to ensure that it conforms to Nature Ecology and Evolution style. Once your paper is typeset, you will receive an email with a link to choose the appropriate publishing options for your paper and our Author Services team will be in touch regarding any additional information that may be required

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