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Gadfly petrels use knowledge of the windscape, not memorized foraging patches, to optimize foraging trips on ocean-wide scales

Francesco Ventura, José Pedro Granadeiro, Oliver Padget and Paulo Catry

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Original submission:	30 July 2019
1st revised submission:	28 October 2019
2nd revised submission:	11 December 2019
Final acceptance:	12 December 2019

Note: Reports are unedited and appear as submitted by the referee. The review history appears in chronological order.

Review History

RSPB-2019-1775.R0 (Original submission)

Review form: Reviewer 1

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
Yes

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

Is it accessible?
Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
In their manuscript, "Gadfly petrels use knowledge of the windscape, not memorised foraging patches, to optimise foraging trips on ocean-wide scales", Ventura et al. explore the role of wind in shaping the foraging behaviour of Desertas petrel. The study is conducted during the breeding season when individuals are constrained to return to the breeding colony regularly. Despite this constraint, individuals tracked using miniaturised GPS devices travelled large distances (on average 8000 km) to target foraging patches far from the colony. The authors argue it is the use of known wind conditions that allow individuals to travel large distances at relatively low energetic cost and target ephemeral prey patches.

The manuscript is novel and interesting, but I have a number of comments both major and minor.

Firstly, the author's assert that individuals travel large distance to increase the probability of encountering ephemeral prey. However, Figure 1a suggests that tracked individuals visit a known seabird biodiversity hotspot in the Northwest Atlantic. This region, between the Grand Banks and Mid-Atlantic Ridge has a high abundance and diversity of pelagic seabirds and is thought to be important for other wide-ranging marine predators including cetaceans. This area is also a fisheries hotspot, and has recently been proposed for protection as an MPA, more information can be seen in the OSPAR MPA nomination:
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Given the location of the colony in relation to this area, individuals could use the prevailing wind conditions, the north east trade winds to soar west, and westerlies to return east. This would also explain the clockwise direction of foraging trips. An alternative hypothesis, therefore, is that individuals use knowledge of prevailing wind conditions to minimise transport costs to a known foraging hotspot.

Secondly, the authors use hidden Markov models to explore the foraging behaviour of individuals while at sea. Given that individuals may travel faster when they have a strong tail wind, the authors include tail wind as a covariate that acts on the state distributions of the hidden Markov model. As I understand it, this provides some flexibility to the model and allows the mean of the step length and turning angle distributions to vary with wind conditions. I think this needs to be described better to the reader in the manuscript, rather than be referred to in the supplementary materials. Furthermore, I am concerned that this introduces some circularity to the analysis. After allowing a component of local wind conditions to change what is defined as foraging and transiting by the HMM, the authors then perform a post-hoc GAMM to explore the links between wind and flight behaviour. Given the flexibility of HMMs to analyse animal movement data I am left wondering whether it would be possible to do all of this in a single HMM that would avoid this circularity. For example, why not have the different wind components acting on both the state transitions and state distributions? Wind conditions are a key component to the movement of Gadfly petrels, and I think they could be better explored in the HMM analysis than the current set of undefined covariates. The HMM would also intrinsically addresses the temporal autocorrelation in telemetry data that the post-hoc GAMM ignores.

Specific comments (this is more difficult as there are no line numbers):

Abstract:
Opening sentence: Are seabird targeting ephemeral resources? Or are they patchy but predictable at large scales? See: Weimerskirch 2007 Deep Sea Res II

Sentence 4: I disagree. There's evidence here that they are targeting a known hotspot.

Introduction:
Paragraph 2 sentence 4: Switch from "dynamic soaring" to "shear-soaring" with no explanation. This is confusing.

Paragraph 2 final sentence: switch to past tense. Reword: "The ground speed attained during flight is affected by…

Paragraph 3 sentence 2: Rephrase: "Gadfly petrels are highly mobile, …"

Paragraph 5: Final sentence: It appears from Figure 1a (and the kernels in supplementary materials) that individuals target a specific area.

Hypothesis 3: I would argue that the pelagic domain is predictable: wide-ranging individuals gain knowledge through life, including the location of seasonally productive regions and persistent wind regimes. In this study, it appears all birds forage in a known NW Atlantic seabird hotspot. Individuals could simply use available wind conditions to minimise transport costs to a known foraging area?

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2.1 The data:
Paragraph 1: Can you infer foraging behaviour at a 2 hour temporal resolution? How long does a foraging bout typically last? Perhaps 'transit' and 'searching' are more appropriate terms?

Paragraph 2: The "physiographic, oceanographic, biological, distance-related and temporal explanatory variables" need to be introduced and justified here in turn. Why was each covariate included? What is the a priori link to changes in movement?

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Paragraph 1: Perhaps a little pedantic, but the model doesn't predict behavioural states. The HMM estimates the step length and turning angle distributions for the two states, and the Viterbi algorithm estimates the most likely sequence of states to have generated the observations based on the fitted model. This is mentioned in the ESM but should be described here.

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Paragraph 2: How did you calculate the UDs? What was the smoothing parameter, this will impact the size of the kernel and so impact the measure of overlap.

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It would be better to write the equation rather than the model formula to describe this process. As I understand this formulation, the individual random effect allows for different intercepts for each individual (eg different mean step lengths for each individual). It doesn't address the serial autocorrelation between successive locations from the same individual. That would require and AR1 process.

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Final paragraph: I'm unsure what the benefit of the energy model is to the paper.

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3.1 Spatial analysis: It's interesting that despite their proximity to the Canary current upwelling, few individuals visited this region. Why do you think this is, could it be displacement due to competition?

What was the a priori expected link between the covariates and transition probabilities? What do the plots of the covariate effects look like?

3.2 Wind use analysis: What were the overall wind conditions like? All movements are clockwise, does this mean the individuals are following the prevailing clockwise winds in the north Atlantic? It would be interesting to see a plot of the wind field overlaid on an animal track e.g Figure 5 in McClintock & Michelot 2018 MEE:
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Discussion:
Paragraph 1: Does it challenge optimal foraging theory? These animals use predictable ocean basin scale wind regimes to target a known foraging hotspot.

Are these waters oligotrophic? This region sees the confluence of the warm gulf stream with the cold waters of the Labrador current. It is a marine vertebrate and fisheries hotspot.

Hypothesis 3: Is there limited overlap between individuals? This doesn't seem to be the case based on Figure 1.

I would also argue based on Weimerskirch 2007 Deep Sea Res (Ref 44 in the manuscript) that the predictability of prey patches is high at large and mesoscales, and not 'unpredictable' as quoted in the manuscript.

Do you have repeat tracks for multiple individuals? Would it be possible to test for consistency in foraging behaviour?

Hypothesis 4: Paragraph 1. Last sentence. This is great, exactly what I think is going on. However, I would argue they know where they are going and so using these winds to target a known foraging hotspot.

Paragraph 2 last sentence. However, wind is also a driver of the state distributions. Could it be that the tail winds on the return leg of the trip influence the behavioural state in someway? It would be useful to include a plot of state distributions and the link to winds from the HMM.

Conclusion: At the risk of sounding like a stuck record, I disagree that the marine domain is unproductive and unpredictable.

ESM: Heart rate is not a good measure of energy expenditure.

Figure 1 – Why only show 5 example tracks and not either all of them, or the UD summary from the ESM? This figure is also in a WGS projection, which distorts at large spatial scale. This can be seen in the shape of Newfoundland in the three panels. These should all be projected to an equal area projection centred on the centre of the study region (i.e. the Azores). You may see the overlap metric change once you are using an equal area projection.

Figure 2b – Is wind intensity included in the GAMM as a factor or a continuous variable? Is it just presented in the figure as two levels to make interpretation easier? If so what is the justification for 16 km/h and 36 km/h – how do these fit with the wind speeds experienced by individuals?

Review form: Reviewer 2

Recommendation
Major revision is needed (please make suggestions in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Excellent

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
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Should the paper be seen by a specialist statistical reviewer?
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Is it clear?
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Is it adequate?
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Do you have any ethical concerns with this paper?
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Comments to the Author
The authors analyse GPS tracking data from Desertas petrels in the Atlantic Ocean to demonstrate how their extremely long foraging trips take advantage of predictable winds at ocean-basin scales. Using a novel methodology, which includes simulations, the authors demonstrate that foraging trips are optimised according to prevailing winds. This study adds to growing evidence that wind may be more important than prey availability at driving the foraging distributions of gadfly petrels.

I thoroughly enjoyed reading this paper, and congratulate the authors for their efforts. The paper is well-written and structured to explicitly address its hypotheses. The authors conducted a sophisticated set of analyses, which are, for the most part, appropriate for the identified aims. However, I have raised a few important issues (see below) that I believe need to be addressed before the paper can be considered for publication.

Major comments:

I appreciate the defined hypotheses that are followed through into the discussion, however a several analyses have been conducted and it's not always clear how they relate to hypotheses in methods and results. Specifically:

1) It's not immediately clear what the main aims of the hidden Markov model analysis are – it seems from your hypotheses (Hp1) that you want to separate "foraging" and "travelling" states, but then you also model covariate effects on state-switching probabilities and then the effect of

tailwind component on the step length distribution. This second comparison seems very similar to the GAMMs later conducted looking at effect of wind speed and direction of step lengths. Could you be clearer (in spatial analysis section of methods) as to why you conduct all of these separate analyses, and what results do you expect? If the aim is to look at whether habitat or wind covariates better explain state-changes, would it not make more sense to construct competing models, one with just habitat covariates, one with just wind, a null model and then a full model, and compare these? The purpose of these tests could be better weaved into methods and results.

2) I think both the labelling of states ("foraging" and "travelling") and investigation of state-changes is problematic with such coarse data (every 2 hours). As you mention in the introduction, gadfly petrels can forage when conducting movement behaviour characteristic of area-restricted search and directed flight ("commuting"), and in discussion you mention birds "rely on a foraging strategy based on covering large distances to increase the probability of encountering unpredictable prey patches along the route". If foraging behaviour can occur en route, then perhaps the "foraging" state would be best labelled "area-restricted search" or something similar. Moreover, gadfly petrels are highly manoeuvrable and I would imagine state-changes likely occur over much smaller scales than every 2 hours. Indeed, how long did the average behavioural bout from HMMs last? It would be good to have a sentence or two in the discussion explicitly dealing with these points, including the limitations of inferring switches in behaviour at this time-scale.

3) I do not believe the "energy model" contributes to the paper and should be removed as there is potential to mislead readers. Given that morphology, wind use, energetics and flight behaviour vary between gadfly and large albatrosses (Spear and Ainley 1997, Shaffer 2001), I am not sure it is accurate to extrapolate between species. Also, the relationship heart rate and energy expenditure does not scale proportionally and is species-dependent. See Green 2011 for a detailed review – "It is certainly essential to avoid the obvious pitfall of assuming that a % change in heart rate equates to exactly the same % change in metabolic rate". Ultimately, as the results of the energy model match that of the trip duration model (which is expected as you have assumed a linear relationship), it's easier to just remove it and say in your discussion that in other species birds expend less energy using tailwinds (Weimerskirch et al. 2000), so the observed trips likely have reduced energy expenditure to randomized trips (due to greater tailwind use).

Minor comments:

In future, I suggest use of line numbers to make it easier for reviewers to comment.

Abstract

Line 12: could you briefly provide a description of "pseudo-random" trips, as the other types of randomized trips are fairly self-explanatory.

Line 14: efficient for time or energy, or both?

Introduction

2nd para, line 13: low energetic cost?

3rd para, line 8: remove "rather".

4th para, line 10: while hidden Markov models are a form of state-space models, given that they are fairly established in movement ecology, it would be clearer, here and throughout the paper, to just refer to them as HMMs.

5th para, lines 1-5: what exactly do you mean by "as their internal state changes" – is it a change in motivation, such as from wanting to forage as opposed to search for another prey patch? Also I'm not sure I understand the main message of the next sentence "The constraints on optimisation…." – perhaps you could rephrase to make clearer?

6th para, line 13: is this overlap of flight routes and foraging areas between individuals (rather than within individuals) – if so, could you explicitly state this?

8th para, line 5-7: I find hypotheses 3 and 4 quite general compared to the first two. Perhaps you could state how these hypothesis links directly to your test/results. E.g. for H1 = if birds rely on wind rather than targeting specific foraging grounds, then commuting areas would overlap more than foraging areas; for H2 = if birds both follow predictable regional winds and adjust tracks to local conditions en route, routes taken would be more efficient than tracks randomized spatially and temporally, respectively.

Methods

2nd para, lines 1-3 – It's not immediately clear why you want to consider these variables – perhaps you could include a sentence or two saying what these variables represent. For example, which represent foraging vs. commuting habitats?

3rd para – as mentioned previously, could you provide a bit more information in the main text about why you are modelling both transition probabilities and step lengths in relation to covariates?

4th para – I am under the impression that the bootstrapping is just to increase the sample size, however, I am not sure doing this creates a robust "population map" as you are still limited in assuming that the individuals tracked are representative of the wider population. Please rephrase the text to make this point clearer.

Results

2nd para – perhaps in supplementary section we could have some plots of probability of transitioning from one state to another with important covariates?

5th para – does the increased speed observed tracks compensate for their more circuitous route, i.e. what was the difference in duration of return portions of observed trips vs. beeline trips?

Figure 3 – how did you define whether variation in trip durations of simulated trips was significantly different from the observed as many of the boxplots go below zero (showing overlap with observed trips)? This should be detailed more clearly in the methods section. Also the plot might be better represented with trip durations on the y axis and a box for observed trips as well (currently the horizontal black line represents the mean?). Also, I suggest labelling the y-axis to include numbers < 0.

Discussion

1st para, lines 1-2 - which theoretical predictions of optimal foraging theory (there are many)?

2nd para, lines 14-15 - what do you mean by "causes"?

Figure 1 or Appendix – it would be good to have a few examples of trips annotated with foraging and travelling states to see how often birds switch between the two, and how long these states last for. This would help determine if it's appropriate to connect travelling segments by a straight line in simulation analyses.

Appendix

State-space modelling section, 2nd para – does this mean wind speed and relative direction were modelled on state transition probabilities or just step lengths? This could be made slightly clearer from the start (and in the main text).

State-space modelling section, 2nd para – change "stepwise down model selection" to "backwards selection".

Figure S1 – it would be good also to have a map indicating how individual foraging and travelling areas overlap - perhaps kernels for each individual overlaid with some level of transparency.

References

Green JA (2011) The heart rate method for estimating metabolic rate: Review and recommendations. Comp Biochem Physiol A Mol Integr Physiol 158:287–304.

Shaffer SA (2011) A review of seabird energetics using the doubly labeled water method. Comp Biochem Physiol A Mol Integr Physiol 158:315–322.

Spear LB, Ainley DG (1997) Flight behaviour of seabirds in relation to wind direction and wing morphology. Ibis 139:221–233.

Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. Proc Biol Sci 267:1869–74.

Decision letter (RSPB-2019-1775.R0)

23-Sep-2019

Dear Dr Ventura,

Your manuscript has now been peer reviewed and the reviews have been assessed by an Associate Editor. The reviewers' comments (not including confidential comments to the Editor) and the comments from the Associate Editor are included at the end of this email for your reference. As you will see, the reviewers and the Editors have raised some concerns with your manuscript and we would like to invite you to revise your manuscript to address them.

We do not allow multiple rounds of revision so we urge you to make every effort to fully address all of the comments at this stage. If deemed necessary by the Associate Editor, your manuscript will be sent back to one or more of the original reviewers for assessment. If the original reviewers are not available we may invite new reviewers. Please note that we cannot guarantee eventual acceptance of your manuscript at this stage.

To submit your revision please log into http://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions", click on "Create a Revision". Your manuscript number has been appended to denote a revision.

When submitting your revision please upload a file under "Response to Referees" - in the "File Upload" section. This should document, point by point, how you have responded to the reviewers' and Editors' comments, and the adjustments you have made to the manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Your main manuscript should be submitted as a text file (doc, txt, rtf or tex), not a PDF. Your figures should be submitted as separate files and not included within the main manuscript file.

When revising your manuscript you should also ensure that it adheres to our editorial policies (https://royalsociety.org/journals/ethics-policies/). You should pay particular attention to the following:

Research ethics:
If your study contains research on humans please ensure that you detail in the methods section whether you obtained ethical approval from your local research ethics committee and gained informed consent to participate from each of the participants.

Use of animals and field studies:
If your study uses animals please include details in the methods section of any approval and licences given to carry out the study and include full details of how animal welfare standards were ensured. Field studies should be conducted in accordance with local legislation; please include details of the appropriate permission and licences that you obtained to carry out the field work.

Data accessibility and data citation:
It is a condition of publication that you make available the data and research materials supporting the results in the article. Datasets should be deposited in an appropriate publicly available repository and details of the associated accession number, link or DOI to the datasets must be included in the Data Accessibility section of the article (https://royalsociety.org/journals/ethics-policies/data-sharing-mining/). Reference(s) to datasets should also be included in the reference list of the article with DOIs (where available).

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should also be fully cited and listed in the references.

If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link http://datadryad.org/submit?journalID=RSPB&manu=(Document not available), which will take you to your unique entry in the Dryad repository.

If you have already submitted your data to dryad you can make any necessary revisions to your dataset by following the above link.

For more information please see our open data policy http://royalsocietypublishing.org/data-sharing.

Electronic supplementary material:
All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI. Please try to submit all supplementary material as a single file.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

Please submit a copy of your revised paper within three weeks. If we do not hear from you within this time your manuscript will be rejected. If you are unable to meet this deadline please let us know as soon as possible, as we may be able to grant a short extension.

Thank you for submitting your manuscript to Proceedings B; we look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Best wishes,
Professor Loeske Kruuk
mailto: proceedingsb@royalsociety.org

Associate Editor
Board Member: 1
Comments to Author:
I have enjoyed reading this manuscript and find the data and story compelling. However, the referees do share two concerns. First, regarding the categorization of behaviour with a 2hr resolution. And second, on whether overlapping models could be more effectively compared/combined to address your hypotheses. With regards the latter, referee 2 also queries the empirical basis of the energy model. In addition, referee 1 points out that while tracks converge on a known foraging hotspot, the manuscript tends to present wind use and hotspot use as mutually exclusive strategies. The referees' specific and useful comments on these and other minor issues should be addressed in a revision.

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
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I would also argue based on Weimerskirch 2007 Deep Sea Res (Ref 44 in the manuscript) that the predictability of prey patches is high at large and mesoscales, and not 'unpredictable' as quoted in the manuscript.

Do you have repeat tracks for multiple individuals? Would it be possible to test for consistency in foraging behaviour?

Hypothesis 4: Paragraph 1. Last sentence. This is great, exactly what I think is going on. However, I would argue they know where they are going and so using these winds to target a known foraging hotspot.

Paragraph 2 last sentence. However, wind is also a driver of the state distributions. Could it be that the tail winds on the return leg of the trip influence the behavioural state in someway? It would be useful to include a plot of state distributions and the link to winds from the HMM.

Conclusion: At the risk of sounding like a stuck record, I disagree that the marine domain is unproductive and unpredictable.

ESM: Heart rate is not a good measure of energy expenditure.

Figure 1 – Why only show 5 example tracks and not either all of them, or the UD summary from the ESM? This figure is also in a WGS projection, which distorts at large spatial scale. This can be seen in the shape of Newfoundland in the three panels. These should all be projected to an equal area projection centred on the centre of the study region (i.e. the Azores). You may see the overlap metric change once you are using an equal area projection.

Figure 2b – Is wind intensity included in the GAMM as a factor or a continuous variable? Is it just presented in the figure as two levels to make interpretation easier? If so what is the justification for 16 km/h and 36 km/h – how do these fit with the wind speeds experienced by individuals?

Referee: 2

Comments to the Author(s)
The authors analyse GPS tracking data from Desertas petrels in the Atlantic Ocean to demonstrate how their extremely long foraging trips take advantage of predictable winds at ocean-basin scales. Using a novel methodology, which includes simulations, the authors demonstrate that foraging trips are optimised according to prevailing winds. This study adds to growing evidence that wind may be more important than prey availability at driving the foraging distributions of gadfly petrels.

I thoroughly enjoyed reading this paper, and congratulate the authors for their efforts. The paper is well-written and structured to explicitly address its hypotheses. The authors conducted a sophisticated set of analyses, which are, for the most part, appropriate for the identified aims. However, I have raised a few important issues (see below) that I believe need to be addressed before the paper can be considered for publication.

Major comments:

I appreciate the defined hypotheses that are followed through into the discussion, however a several analyses have been conducted and it’s not always clear how they relate to hypotheses in methods and results. Specifically:

1) It’s not immediately clear what the main aims of the hidden Markov model analysis are – it seems from your hypotheses (Hp1) that you want to separate “foraging” and “travelling” states, but then you also model covariate effects on state-switching probabilities and then the effect of tailwind component on the step length distribution. This second comparison seems very similar to the GAMMs later conducted looking at effect of wind speed and direction of step lengths. Could you be clearer (in spatial analysis section of methods) as to why you conduct all of these separate analyses, and what results do you expect? If the aim is to look at whether habitat or wind covariates better explain state-changes, would it not make more sense to construct competing models, one with just habitat covariates, one with just wind, a null model and then a full model, and compare these? The purpose of these tests could be better weaved into methods and results.

2) I think both the labelling of states (“foraging” and “travelling”) and investigation of state-changes is problematic with such coarse data (every 2 hours). As you mention in the introduction, gadfly petrels can forage when conducting movement behaviour characteristic of area-restricted search and directed flight (“commuting”), and in discussion you mention birds “rely on a foraging strategy based on covering large distances to increase the probability of encountering unpredictable prey patches along the route”. If foraging behaviour can occur en route, then perhaps the “foraging” state would be best labelled “area-restricted search” or something similar. Moreover, gadfly petrels are highly manoeuvrable and I would imagine state-changes likely occur over much smaller scales than every 2 hours. Indeed, how long did the average behavioural bout from HMMs last? It would be good to have a sentence or two in the discussion explicitly dealing with these points, including the limitations of inferring switches in behaviour at this time-scale.

3) I do not believe the “energy model” contributes to the paper and should be removed as there is

potential to mislead readers. Given that morphology, wind use, energetics and flight behaviour vary between gadfly and large albatrosses (Spear and Ainley 1997, Shaffer 2001), I am not sure it is accurate to extrapolate between species. Also, the relationship heart rate and energy expenditure does not scale proportionally and is species-dependent. See Green 2011 for a detailed review – "It is certainly essential to avoid the obvious pitfall of assuming that a % change in heart rate equates to exactly the same % change in metabolic rate". Ultimately, as the results of the energy model match that of the trip duration model (which is expected as you have assumed a linear relationship), it's easier to just remove it and say in your discussion that in other species birds expend less energy using tailwinds (Weimerskirch et al. 2000), so the observed trips likely have reduced energy expenditure to randomized trips (due to greater tailwind use).

Minor comments:

In future, I suggest use of line numbers to make it easier for reviewers to comment.

Abstract

Line 12: could you briefly provide a description of "pseudo-random" trips, as the other types of randomized trips are fairly self-explanatory.

Line 14: efficient for time or energy, or both?

Introduction

2nd para, line 13: low energetic cost?

3rd para, line 8: remove "rather".

4th para, line 10: while hidden Markov models are a form of state-space models, given that they are fairly established in movement ecology, it would be clearer, here and throughout the paper, to just refer to them as HMMs.

5th para, lines 1-5: what exactly do you mean by "as their internal state changes" – is it a change in motivation, such as from wanting to forage as opposed to search for another prey patch? Also I'm not sure I understand the main message of the next sentence "The constraints on optimisation…." – perhaps you could rephrase to make clearer?

6th para, line 13: is this overlap of flight routes and foraging areas between individuals (rather than within individuals) – if so, could you explicitly state this?

8th para, line 5-7: I find hypotheses 3 and 4 quite general compared to the first two. Perhaps you could state how these hypothesis links directly to your test/results. E.g. for H1 = if birds rely on wind rather than targeting specific foraging grounds, then commuting areas would overlap more than foraging areas; for H2 = if birds both follow predictable regional winds and adjust tracks to local conditions en route, routes taken would be more efficient than tracks randomized spatially and temporally, respectively.

Methods

2nd para, lines 1-3 – It's not immediately clear why you want to consider these variables – perhaps you could include a sentence or two saying what these variables represent. For example, which represent foraging vs. commuting habitats?

3rd para – as mentioned previously, could you provide a bit more information in the main text about why you are modelling both transition probabilities and step lengths in relation to covariates?

4th para – I am under the impression that the bootstrapping is just to increase the sample size, however, I am not sure doing this creates a robust "population map" as you are still limited in assuming that the individuals tracked are representative of the wider population. Please rephrase the text to make this point clearer.

Results

2nd para – perhaps in supplementary section we could have some plots of probability of transitioning from one state to another with important covariates?

5th para – does the increased speed observed tracks compensate for their more circuitous route, i.e. what was the difference in duration of return portions of observed trips vs. beeline trips?

Figure 3 – how did you define whether variation in trip durations of simulated trips was significantly different from the observed as many of the boxplots go below zero (showing overlap with observed trips)? This should be detailed more clearly in the methods section. Also the plot might be better represented with trip durations on the y axis and a box for observed trips as well (currently the horizontal black line represents the mean?). Also, I suggest labelling the y-axis to include numbers < 0.

Discussion

1st para, lines 1-2 - which theoretical predictions of optimal foraging theory (there are many)?

2nd para, lines 14-15 - what do you mean by "causes"?

Figure 1 or Appendix – it would be good to have a few examples of trips annotated with foraging and travelling states to see how often birds switch between the two, and how long these states last for. This would help determine if it's appropriate to connect travelling segments by a straight line in simulation analyses.

Appendix

State-space modelling section, 2nd para – does this mean wind speed and relative direction were modelled on state transition probabilities or just step lengths? This could be made slightly clearer from the start (and in the main text).

State-space modelling section, 2nd para – change "stepwise down model selection" to "backwards selection".

Figure S1 – it would be good also to have a map indicating how individual foraging and travelling areas overlap - perhaps kernels for each individual overlaid with some level of transparency.

References

Green JA (2011) The heart rate method for estimating metabolic rate: Review and recommendations. Comp Biochem Physiol A Mol Integr Physiol 158:287–304.

Shaffer SA (2011) A review of seabird energetics using the doubly labeled water method. Comp Biochem Physiol A Mol Integr Physiol 158:315–322.

Spear LB, Ainley DG (1997) Flight behaviour of seabirds in relation to wind direction and wing morphology. Ibis 139:221–233.

Weimerskirch H, Guionnet T, Martin J, Shaffer SA, Costa DP (2000) Fast and fuel efficient? Optimal use of wind by flying albatrosses. Proc Biol Sci 267:1869–74.

Author's Response to Decision Letter for (RSPB-2019-1775.R0)

See Appendix A.

RSPB-2019-1775.R1 (Revision)

Review form: Reviewer 1

Recommendation
Accept with minor revision (please list in comments)

Scientific importance: Is the manuscript an original and important contribution to its field?
Good

General interest: Is the paper of sufficient general interest?
Good

Quality of the paper: Is the overall quality of the paper suitable?
Good

Is the length of the paper justified?
Yes

Should the paper be seen by a specialist statistical reviewer?
No

Do you have any concerns about statistical analyses in this paper? If so, please specify them explicitly in your report.
No

It is a condition of publication that authors make their supporting data, code and materials available - either as supplementary material or hosted in an external repository. Please rate, if applicable, the supporting data on the following criteria.

> **Is it accessible?**
> Yes

Is it clear?
Yes

Is it adequate?
Yes

Do you have any ethical concerns with this paper?
No

Comments to the Author
The authors have done an excellent job of addressing my previous concerns. I have only a couple of minor comments to add to this version of the manuscript:
Line 44: ‘However, how’ perhaps rephrase to something like ‘Nevertheless, how’
Line 67: “seabird”
Line 84: “datasets”
Line 204: the model estimates the distributions, it doesn’t predict them
Line 235: the equation is missing the AR1 and individual-level random intercept terms
Line 299: I’m still unsure of how useful this stage is. The environmental covariates aren’t well explained, and have a minimal impact on the state classification. The interesting figures of the transition probabilities are in the appendix, which is a shame but I understand the space constraints.
Line 314: The test statistic value is linked to the sample size. Does this suggest that all animal locations have been considered as independent samples? Is there a way to address this?
Line 336: remove “what”
Line 344: “The Gadfly petrels’ impressive motility…”

Decision letter (RSPB-2019-1775.R1)

09-Dec-2019

Dear Dr Ventura

I am pleased to inform you that your manuscript RSPB-2019-1775.R1 entitled "Gadfly petrels use knowledge of the windscape, not memorised foraging patches, to optimise foraging trips on ocean-wide scales" has been accepted for publication in Proceedings B.

The referee and Associate Editor have recommended publication, but also suggest some minor revisions to your manuscript. Therefore, I invite you to respond to the referee's comments and revise your manuscript. Because the schedule for publication is very tight, it is a condition of publication that you submit the revised version of your manuscript within 7 days. If you do not think you will be able to meet this date please let us know.

To revise your manuscript, log into https://mc.manuscriptcentral.com/prsb and enter your Author Centre, where you will find your manuscript title listed under "Manuscripts with Decisions." Under "Actions," click on "Create a Revision." Your manuscript number has been appended to denote a revision. You will be unable to make your revisions on the originally submitted version of the manuscript. Instead, revise your manuscript and upload a new version through your Author Centre.

When submitting your revised manuscript, you will be able to respond to the comments made by the referee(s) and upload a file "Response to Referees". You can use this to document any changes you make to the original manuscript. We require a copy of the manuscript with revisions made since the previous version marked as 'tracked changes' to be included in the 'response to referees' document.

Before uploading your revised files please make sure that you have:

1) A text file of the manuscript (doc, txt, rtf or tex), including the references, tables (including captions) and figure captions. Please remove any tracked changes from the text before submission. PDF files are not an accepted format for the "Main Document".

2) A separate electronic file of each figure (tiff, EPS or print-quality PDF preferred). The format should be produced directly from original creation package, or original software format. PowerPoint files are not accepted.

3) Electronic supplementary material: this should be contained in a separate file and where possible, all ESM should be combined into a single file. All supplementary materials accompanying an accepted article will be treated as in their final form. They will be published alongside the paper on the journal website and posted on the online figshare repository. Files on figshare will be made available approximately one week before the accompanying article so that the supplementary material can be attributed a unique DOI.

Online supplementary material will also carry the title and description provided during submission, so please ensure these are accurate and informative. Note that the Royal Society will not edit or typeset supplementary material and it will be hosted as provided. Please ensure that the supplementary material includes the paper details (authors, title, journal name, article DOI). Your article DOI will be 10.1098/rspb.[paper ID in form xxxx.xxxx e.g. 10.1098/rspb.2016.0049].

4) A media summary: a short non-technical summary (up to 100 words) of the key findings/importance of your manuscript.

5) Data accessibility section and data citation
It is a condition of publication that data supporting your paper are made available either in the electronic supplementary material or through an appropriate repository.

In order to ensure effective and robust dissemination and appropriate credit to authors the dataset(s) used should be fully cited. To ensure archived data are available to readers, authors should include a 'data accessibility' section immediately after the acknowledgements section. This should list the database and accession number for all data from the article that has been made publicly available, for instance:
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• Phylogenetic data: TreeBASE accession number S9123
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• Climate data and MaxEnt input files: Dryad doi:10.5521/dryad.12311
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If you wish to submit your data to Dryad (http://datadryad.org/) and have not already done so you can submit your data via this link
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6) For more information on our Licence to Publish, Open Access, Cover images and Media summaries, please visit https://royalsociety.org/journals/authors/author-guidelines/.

Once again, thank you for submitting your manuscript to Proceedings B and I look forward to receiving your revision. If you have any questions at all, please do not hesitate to get in touch.

Sincerely,

Professor Loeske Kruuk
Editor, Proceedings B
mailto:proceedingsb@royalsociety.org

Reviewer(s)' Comments to Author:

Referee: 1

Comments to the Author(s)
The authors have done an excellent job of addressing my previous concerns. I have only a couple of minor comments to add to this version of the manuscript:

Line 44: 'However, how' perhaps rephrase to something like 'Nevertheless, how'

Line 67: "seabird"

Line 84: "datasets"

Line 204: the model estimates the distributions, it doesn't predict them

Line 235: the equation is missing the AR1 and individual-level random intercept terms

Line 299: I'm still unsure of how useful this stage is. The environmental covariates aren't well explained, and have a minimal impact on the state classification. The interesting figures of the transition probabilities are in the appendix, which is a shame but I understand the space constraints.

Line 314: The test statistic value is linked to the sample size. Does this suggest that all animal locations have been considered as independent samples? Is there a way to address this?

Line 336: remove "what"

Line 344: "The Gadfly petrels' impressive motility…"

Author's Response to Decision Letter for (RSPB-2019-1775.R1)

See Appendix B.

Decision letter (RSPB-2019-1775.R2)

12-Dec-2019

Dear Dr Ventura

I am pleased to inform you that your manuscript entitled "Gadfly petrels use knowledge of the windscape, not memorised foraging patches, to optimise foraging trips on ocean-wide scales" has been accepted for publication in Proceedings B.

You can expect to receive a proof of your article from our Production office in due course, please check your spam filter if you do not receive it. PLEASE NOTE: you will be given the exact page length of your paper which may be different from the estimation from Editorial and you may be asked to reduce your paper if it goes over the 10 page limit.

If you are likely to be away from e-mail contact please let us know. Due to rapid publication and an extremely tight schedule, if comments are not received, we may publish the paper as it stands.

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Thank you for your fine contribution. On behalf of the Editors of the Proceedings B, we look forward to your continued contributions to the Journal.

Sincerely,

Editor, Proceedings B
mailto: proceedingsb@royalsociety.org

Appendix A

Dear Editor,

Thank you for your positive response to our manuscript. We are grateful to you and the reviewers for the careful review and for suggesting very insightful changes to our original manuscript. We have addressed each comment below and incorporated them into a revised version of our article.

Francesco Ventura, José Pedro Granadeiro, Oliver Padget and Paulo Catry

Responses to comments by editor

I have enjoyed reading this manuscript and find the data and story compelling.

** Thank you.

However, the referees do share two concerns. First, regarding the categorization of behaviour with a 2hr resolution.

** We acknowledge this useful comment by the referees regarding the 2hr temporal resolution of our dataset and the limitations that this causes to the behavioural classification. To address this thoroughly, we added a section to the revised Discussion and explained why the results of our analysis are only minimally affected by the data coarse temporal resolution and clarified how, at most, we may have missed short search episodes that would not change our main results and conclusions (line 418-429). This section reads: "Due to the petrels' high manoeuvrability, state-changes may occur over smaller scales than the temporal resolution of our data. However, on the one hand, during transiting, birds travelled at a ground speed of 33 km/h (sd = 8 km/h, see Appendix for details) suggesting a fast, direct movement, which we expect the HMM to detect with a low rate of false positives. Importantly, as the ground speed calculation does not account for the sinuosity of the dynamic soaring flight within the 2-hour movement steps, the speed values are likely to be underestimated. On the other hand, while searching, the animals' ground speed was 14 km/h (sd = 8 km/h), excluding – at least for most of the movement step – the occurrence of transit behaviour. Thus, while acknowledging the limitation of inferring behavioural modes at 2-hour resolution, we argue that the results of our analysis are robust and only minimally affected by the data coarse temporal resolution".

And ***second****, on whether overlapping models could be more effectively compared/combined to address your hypotheses.*

** We believe that the HMM analytical step and, in more in general, the link between the hypotheses and the methods, required some restructuring and clarification. While we appreciate the suggestion, the aim of HMM was to obtain a behavioural classification output – and not to test hypotheses linked to the role of wind/habitat in determining the probability of engaging in a given behavioural state. The reasons why we allowed (i) habitat covariates to affect the state-switching probabilities and (ii) tail wind component to affect the mean parameter of the step length distribution of both states was, ultimately, to enhance the model biological realism (and capture the processes shaping the tracked animals movement behaviour), thus yielding a better classification output. We address the reviewers' comments and describe and discuss this in the revised section 2.2 Spatial Analysis (beginning at line 212).

With regards the latter, referee 2 also queries the empirical basis of the energy model.

** The energy model was included in the original manuscript in order to present a quantitative – but coarse and extrapolated – measure of how heart rate is affected by wind. We followed the referee suggestion and removed the energy model from the paper to make it more focused. As suggested, we now make a "qualitative" comparison with other species, discussing how less energy expenditure was associated to tail and favourable cross-winds in albatrosses (line 435-437).

In addition, referee 1 points out that while tracks converge on a known foraging hotspot, the manuscript tends to present wind use and hotspot use as mutually exclusive strategies.

** We appreciate this comment by referee 1 and addressed it carefully in our manuscript. First, we discuss how the petrels seem indeed to use more intensely the waters of the North-Atlantic Current and mid-Atlantic Subpolar frontal system, characterised by enhanced productivity at the large scale (line 492-502). We therefore conclude that "[...] along their long and efficiently-designed routes, Desertas petrels did target a broad area of enhanced productivity, but at a large oceanic scale (> 1000 km^2), continuously searching for food and maximising the probability of prey encounter by covering more ground within this region and also while travelling to and from this region" (line 498-502). Second, we updated figure 1a, which previously represented only a limited part of the vast area covered by Desertas petrels and now show all the "looping" tracks performed by our study animals. The new figure and the quantitative results presented below in this document suggest a limited overlap between the petrels' space use and the OSPAR proposed marine protected area mentioned by referee 1. Moreover, we further discuss why our results – particularly the results regarding the homebound sections of the track – do not support the hypothesis of minimum transport to reach a known localised foraging hotspot, but they rather support a "looping" type movement strategy, with the animals continuously looking for food along the route (see the revised Hp3 and Hp4 sections beginning at line 471). Finally, consistently throughout the text, whenever we discuss the marine resources predictability, we specify the scale considered to improve the clarity of the revised manuscript.

** Together with the edits made to the manuscript to thoroughly address the referees' feedback, we realised that our manuscript needed an addition regarding the tracking data processing – an oversight that we are really sorry about. The raw data comprised both "long" and "short" trips. As we now discuss in the revised manuscript (line 183-190) and in the ESM, the short trips, performed by the animals after long trips, were extremely limited in terms of both temporal duration and spatial extent and represented less than 14% of the total time spent at-sea by the study animals. Crucially, the role of these short tracks (also documented in other pelagic seabirds) is uncertain and it is perhaps not linked to foraging (or involves a different, complementary, foraging strategy). We therefore adopted an analytical framework (k-mean clustering based on distance from colony and trip duration) to quantitatively distinguish between long and short tracks, and only considered the long tracks for our analysis of wind use and foraging behaviour. We clarify this at lines 183-190 and further describe it in the ESM, where we also present a map comprising both long and short trips (fig.1a in the ESM). We would like to clearly flag and apologise for this omission – which was a genuine oversight – and believe that the readers will recognise the validity of our approach. Although these short trips were not retained in this research, we are in the process of submitting all GPS data concerning them to the BirdLife Seabird Tracking Database.

Responses to referees

Referee: 1

In their manuscript, "Gadfly petrels use knowledge of the windscape, not memorised foraging patches, to optimise foraging trips on ocean-wide scales", Ventura et al. explore the role of wind in shaping the foraging behaviour of Desertas petrel. The study is conducted during the breeding season when individuals are constrained to return to the breeding colony regularly. Despite this constraint, individuals tracked using miniaturised GPS devices travelled large distances (on average 8000 km) to target foraging patches far from the colony. The authors argue it is the use of known wind conditions that allow individuals to travel large distances at relatively low energetic cost and target ephemeral prey patches. The manuscript is novel and interesting, but I have a number of comments both major and minor.

Firstly, the author's assert that individuals travel large distance to increase the probability of encountering ephemeral prey. However, Figure 1a suggests that tracked individuals visit a known seabird biodiversity hotspot in the Northwest Atlantic. This region, between the Grand Banks and Mid-Atlantic Ridge has a high abundance and diversity of pelagic seabirds and is thought to be important for other wide-ranging marine predators including cetaceans. This area is also a fisheries hotspot, and has recently been proposed for protection as an MPA, more information can be seen in the OSPAR MPA nomination: https://www.ospar.org/site/ass

****** We realise that the previous Figure 1a was somehow misleading, as our selection of example trips represented only a limited part of the vast area covered by Desertas petrels, and that could mislead the reader. We therefore updated figure 1a, showing the tracks performed by our study animals. While it is true that part of the animals' space use falls within the OSPAR MPA, the areas most intensively used by the animals are to the South of the proposed MPA and the South-East, off the coasts of the Azores, as showed by **fig. I a** below. Of all the GPS fixes, only 7.7% fall within the OSPAR boundary. When considering only the "searching" portions of the tracks (depicted as red dots in fig. I a), only 11% of them fall within the proposed MPA.

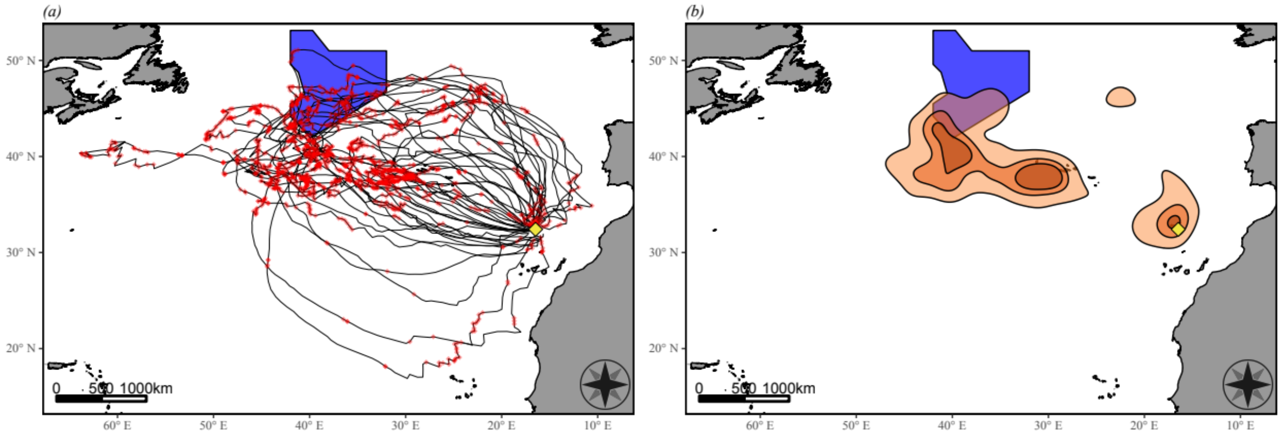

Figure I – a) Desertas petrels' tracks. The red dots represent the spatial locations classified as searching by the Viterbi algorithm based on the HMM model output; the yellow rhombus is the colony in Bugio Island; the blue polygon depicts the proposed OSPAR MPA. b) The 10%, 25% and 50% kernel Utilization Distributions are showed in red, orange and light orange, respectively.

Furthermore, in figure I b, we show the 10%, 25% and 50% kernel utilisation distributions (UDs) generated using a bandwidth equal to 120 km, i.e. the maximum step length travelled by the tracked animals in 2 hours (the resolution of our tracks). The spatial overlap of the 10%, 25% and 50% UDs with the OSPAR area is equal to 0.45%, 4.9% and 10%, respectively. In other words, out of the total area of the 10%UD (equal to 218,760 km^2), only 0.45% (976 km^2) falls within the OSPAR MPA. Hence, our data do not seem to suggest that the Desertas petrels target that region. Nevertheless, we agree with the referee's suggestions regarding both the scale of the predictability of the marine resources and the higher productivity of the North-West Atlantic, at the large scale (please refer to the comment below). We therefore modified our original manuscript to better discuss the topic (line 492-502). Moreover, consistently throughout our manuscript, whenever we mention marine resources predictability, we now explicitly state the scale at which this is considered.

Given the location of the colony in relation to this area, individuals could use the prevailing wind conditions, the north east trade winds to soar west, and westerlies to return east. This would also explain the clockwise direction of foraging trips. An alternative hypothesis, therefore, is that individuals use knowledge of prevailing wind conditions to minimise transport costs to a known foraging hotspot.

** We acknowledge that our manuscript required clarification regarding the predictability of prey distribution. In fact, we argue that individuals use the prevailing wind conditions to maximise the distance covered flying over waters that are, *at the large scale* (> 1000 km^2, following the same nomenclature as *Weimerskirch 2007, Deep Sea Res II*), predictably more productive (the West-North West Atlantic). We incorporated this suggestion in our manuscript and, in particular, we discussed how the animals' space use is more intense in the waters of the North-Atlantic Current and mid-Atlantic Subpolar frontal system (line 492-502). However, the results of our analysis do not support the hypothesis of a "commuting type" movement (as described in *Weimerskirch 2007, Deep Sea Res II)*, with individuals targeting a meso- (100-1000 km^2) or coarse-scale (1-100 km^2) foraging hotspot and minimising the commuting time to reach it. Together with the limited overlap with the OSPAR proposed MPA discussed in the comment above, the results presented in our manuscript strongly suggest that when returning to their colony, Desertas petrels keep maximising the distance covered, rather than flying homeward following a beeline (which we show would be a faster route than the long loop the birds opt to do). Additionally, the percentage of "search" behaviour in the return section of the tracks is similar to the one calculated for the outbound portion. Consistently with *Weimerskirch (2007, Deep Sea Res II)*, we argue that these key results do not support the hypothesis of minimum transport to reach a known localised foraging hotspot. Rather, the animals show a "looping" type movement strategy, with several foraging bouts all along their way, suggesting that they are continuously looking for food (*Weimerskirch 2007, Deep Sea Res II)*. We have expanded and further discussed this in the revised version of our manuscript (refer to the revised Hp3 and Hp4 sections beginning at line 471).

Secondly, the authors use hidden Markov models to explore the foraging behaviour of individuals while at sea. Given that individuals may travel faster when they have a strong tail wind, the authors include tail wind as a covariate that acts on the state distributions of the hidden Markov model. As I understand it, this provides some flexibility to the model and allows the mean of the step length and turning angle distributions to vary with wind conditions. I think this needs to be described better to the reader in the manuscript, rather than be referred to in the supplementary materials.

** We acknowledge that our manuscript was not sufficiently clear about this analytical step. We have clarified and further described the modelling details in the revised section "2.2 Spatial Analysis" (beginning at line 212) and further described our methodological framework in the Appendix.

Furthermore, I am concerned that this introduces some circularity to the analysis. After allowing a component of local wind conditions to change what is defined as foraging and transiting by the

HMM, the authors then perform a post-hoc GAMM to explore the links between wind and flight behaviour.

** In the HMM model, we included a set of environmental variables as explanatory variables for the state switching probabilities. However, the HMM may fail to detect the effects of the environmental variables on the state switching probabilities due to the effect of tail wind component on the step length. Therefore, while modelling the effects of the environmental variables on the probability of switching between "transiting" and "searching", we simultaneously accounted for the effect of tail wind component on the mean parameter of the step length distribution, ensuring more biological credibility to our model. Ultimately, the inclusion of tail wind component in the HMM model changes the final results only marginally (see below). We acknowledge that our manuscript needed some explanations on this part of the analysis, and hope that the edits that we made to the text now clarify why we consider our analysis not circular, but rather sequential. The tail wind component is allowed to affect the mean parameter of the state-specific step length distributions of both states, whereas simultaneously the state switching probabilities are modelled as a function of the selected set of environmental variables. We did that in order to ensure more biological realism to our model, in order to ultimately yield a better classification output. Then, once obtained the best possible classification, we fit the GAMM to the locations classified as "transit" by the HMM, aiming to examine in more detail the relationship between step lengths and wind direction and intensity. Thus, in the HMM step wind is used to enable the model to best select among two alternative states. In the following step, we examined the points identified as transit and investigated the extent to which wind affects the birds' ground speed. Ultimately, we argue that our classification methodology does not affect the results and conclusion on the wind use. After reanalysing the dataset adopting a HMM framework that does not contain tail wind component in its design matrix formulation, less than 6% of the tracking points changed classification. The GAMM results obtained on the tracks decoded using this new HMM did not change, further highlighting that the HMM formulation does not affect the wind model results. We clarified and discussed this in the revised section "2.2 Spatial Analysis" and presented the results of the HMM without wind in its design matrix in the ESM.

Given the flexibility of HMMs to analyse animal movement data I am left wondering whether it would be possible to do all of this in a single HMM that would avoid this circularity. For example, why not have the different wind components acting on both the state transitions and state distributions? Wind conditions are a key component to the movement of Gadfly petrels, and I think they could be better explored in the HMM analysis than the current set of undefined covariates. The HMM would also intrinsically addresses the temporal autocorrelation in telemetry data that the post-hoc GAMM ignores.

** We acknowledge that we did not justify our statistical approach sufficiently well in our original manuscript and have revised our explanation on the methodology in order to address this useful comment by the referee and clarify why tail wind component was included in the HMM design matrix (line 221-235). The HMM framework is based on the assumption that the knowledge that behaviours are clustered temporally can improve the ability of the model to distinguish periods in time where the emission values are ambiguous with respect to behavioural state. In this sense, the HMM itself does not account for autocorrelation in a classical sense. Following the useful suggestion by the referee, we reformulated our GAMM, which now implements a residual AR-1 auto-correlation structure applied to each individual track, while still retaining individual ID as random effect (line 260-264). The results obtained based on this new model formulation are only minimally different and the conclusions remain therefore unaltered.

Specific comments (this is more difficult as there are no line numbers):

** Apologies for this oversight.

Abstract:
Opening sentence: Are seabird targeting ephemeral resources? Or are they patchy but predictable at large scales? See: Weimerskirch 2007 Deep Sea Res II

** We agree with the referee, our statement was incomplete, as we did not specify the scale at which prey predictability is considered. We therefore changed the sentence to: "[...] exploit heterogeneously distributed oceanic resources" (line 15).

Sentence 4: I disagree. There's evidence here that they are targeting a known hotspot.

** Please refer to the comments above.

Introduction:
Paragraph 2 sentence 4: Switch from "dynamic soaring" to "shear-soaring" with no explanation. This is confusing.

** We changed "shear-soaring" to dynamic soaring, as suggested (line 56-57).

Paragraph 2 final sentence: switch to past tense. Reword: "The ground speed attained during flight is affected by…

** We rephrased it as suggested (line 62-63).

Paragraph 3 sentence 2: Rephrase: "Gadfly petrels are highly mobile, …"

** We rephrased the sentence (line 73).

Paragraph 5: Final sentence: It appears from Figure 1a (and the kernels in supplementary materials) that individuals target a specific area.

** We acknowledge that Figure 1a was not appropriate to represent the full extent of the tracked animals space use and updated it. Regarding the UDs, please refer to the comment above in which we show the limited overlap with the OSPAR proposed MPA. We nonetheless specified the scale of the process and the line now reads "These predictions should hold true particularly if the animals' foraging strategy does not rely on targeting stable meso- (100-1000 km²) and coarse-scale (1-100 km²) features of the seascape, i.e. if they are unconstrained in their route planning" (line 111-114).

Hypothesis 3: I would argue that the pelagic domain is predictable: wide-ranging individuals gain knowledge through life, including the location of seasonally productive regions and persistent wind regimes. In this study, it appears all birds forage in a known NW Atlantic seabird hotspot. Individuals could simply use available wind conditions to minimise transport costs to a known foraging area?

** We agree with the reviewer and reformulated the hypothesis to explicitly state the scale of the predictability. The line now reads: "In the pelagic domain used by gadfly petrels, characterised by patchy and unpredictable resources distribution at the coarse- to meso-scale, their foraging strategy relies upon covering large areas at low cost in search of prey along the route, rather than targeting specific foraging grounds" (line 153-156). However, please refer to the comments above regarding the commuting type movement. The results of our analysis do not support this hypothesis.

Methods:

2.1 The data:

Paragraph 1: Can you infer foraging behaviour at a 2 hour temporal resolution? How long does a foraging bout typically last? Perhaps 'transit' and 'searching' are more appropriate terms?

** We agree with the referee regarding this issue. The median duration of a "searching" bout is 9 hours (interquartile range = 4 – 16 hours) – we added it to the text (line 337-339). We agree that considering the temporal resolution of our tracks, "foraging" is not the right term. We therefore updated the terms to "transit" and "searching" throughout the text. While we cannot infer foraging behaviour, we can assume that shorter step lengths and higher variability in turning angles are proxies for the searching behavioural mode. The transiting behaviour instead – characterised by higher speed, more ground covered and more movement directionality – is less subject to false-positive errors. In the revised discussion, we state the limitations of classifying movement behaviour at the time-scale considered, and discuss why our results are only minimally affected by the data limitation (line 418-429).

Paragraph 2: The "physiographic, oceanographic, biological, distance-related and temporal explanatory variables" need to be introduced and justified here in turn. Why was each covariate included? What is the a priori link to changes in movement?

** We agree that the covariates included should be justified more thoroughly. Due to page limit and since the focus of our paper is wind use, the reasons for the inclusion of each covariate to the HMM were added to the ESM (Table I).

2.2 Spatial Analysis:

Paragraph 1: Perhaps a little pedantic, but the model doesn't predict behavioural states. The HMM estimates the step length and turning angle distributions for the two states, and the Viterbi algorithm estimates the most likely sequence of states to have generated the observations based on the fitted model. This is mentioned in the ESM but should be described here.

** We acknowledge that our manuscript needed some clarification. We restructured section "2.2 Spatial Analysis" and clarified the points raised by the reviewer.

While I like the idea. The intrinsic effect of tail wind component on step length needs to be better explained. Is the effect going to be different between the two states? How does including TWC at this stage in the analysis impact your inclusion of wind in the GAMM of travelling and foraging behaviour? It would also be informative to include a plot of step and turn distributions for the two behavioural states, and how these are modified by TWC.

** The restructured section "2.2 Spatial Analysis" clarifies and better explains this part of the analysis and addresses the questions raised by the referee (line 224-235). The plot suggested by the referee was added to the ESM (figure 3).

Paragraph 2: How did you calculate the UDs? What was the smoothing parameter, this will impact the size of the kernel and so impact the measure of overlap.

** We used the adehabitatHR package in R and set the smooting parameter as the longest step length recorded in our temporal resolution of 2 hours (120 km). We clarified it in the text (line 242-244).

2.3 Wind use analysis

Given that wind is included in the HMM to estimate the behavioural states, is it not circular to estimate the influence of wind on the behavioural states using a GAMM?

** Please refer to the comment above regarding circularity. Tail Wind Component (TWC) was included in the HMM in order to account for the – biologically realistic – intrinsic effect of tail wind on the animals' step length, and it does not explicitly affect the probability of switching between states. Furthermore, while we argue that the inclusion of wind improves the realism of our model – and the final classification output – we explicitly state in the manuscript (line 224-235) and discuss in the ESM that the inclusion of wind in the HMM design matrix changes the final results only marginally.

It would be better to write the equation rather than the model formula to describe this process. As I understand this formulation, the individual random effect allows for different intercepts for each individual (eg different mean step lengths for each individual). It doesn't address the serial autocorrelation between successive locations from the same individual. That would require and AR1 process.

** As suggested by the referee, we restructured the section describing the GAMM formulation, stated the model formula and clarified on the implementation of residual AR-1 auto-correlation structure applied to each individual track and on the inclusion of individual birds as random effects to the intercept (line 257-266).

2.4 Track simulation
I'm unsure why this step was taken. The opening paragraph needs an introductory paragraph, or a link to the hypothesis. At the moment it jumps into description of trip metrics. In general, the hypotheses needs to link better to the methods, and results.

** We agree with comment, which is consistent with the comment by referee2. We added a paragraph to the hypotheses statements (line 161-176), in which we make an explicit link between hypotheses, methods and results. We agree with both reviewers that this greatly improves the logical flow of our manuscript.

It is possible to simulate tracks from an HMM model by sampling the distribution of step lengths and turning angles: eg. Michelot et al. 2017 Ecology
https://esajournals.onlinelibr

** When designing the simulation protocol, we discussed this possibility. The reason why we did not simulate tracks using the momentuHMM built-in functions is because they generate simulated tracks dependent on the parameters estimated by the model. While this could be a useful tool in a series of other research question (or "qualitative" model diagnostics checks), we decided to adopt "conservative" simulation protocols, where the simulated trips were geometrically equivalent (or even identical, in the case of the time-lag trips) to the real ones.

Final paragraph: I'm unsure what the benefit of the energy model is to the paper.

** We included the energy model to have a coarse idea of the energy expenditure along the track. However, we acknowledge that it was perhaps too coarse and extrapolated from other species. Moreover, as pointed out by the referee in the comment below, heart rate is not a good measure of energy expenditure. Therefore, we agree with the referee and removed the energy model from the revised manuscript.

Results:

3.1 Spatial analysis: It's interesting that despite their proximity to the Canary current upwelling, few individuals visited this region. Why do you think this is, could it be displacement due to competition?

** Yes, it may be due to displacement due to competion or to kleptoparasitism, we added a short sentence to our text (line 413-414).

What was the a priori expected link between the covariates and transition probabilities? What do the plots of the covariate effects look like?

** Please refer to the comments above. The biological reasons for the selected covariates inclusion in the model was outlined in the ESM, where we also present the significant covariates' effects on the transition probabilities (Table I and fig. 4).

3.2 Wind use analysis: What were the overall wind conditions like? All movements are clockwise, does this mean the individuals are following the prevailing clockwise winds in the north Atlantic? It would be interesting to see a plot of the wind field overlaid on an animal track e.g Figure 5 in McClintock & Michelot 2018 MEE:
https://besjournals.onlinelibr

** To address this comment by the referee, we added a 2-panel plot to the ESM (fig. 2) in which we show the real-time wind conditions experienced along an example tracks (fig. 2a), and the "overall" wind conditions, i.e. the wind direction and intensity averaged across the duration of the track (fig. 2b). This plot is visually effective in showing that birds follow the prevailing clockwise winds and adjust their track to the real-time conditions, as described in the text.

Discussion:
Paragraph 1: Does it challenge optimal foraging theory? These animals use predictable ocean basin scale wind regimes to target a known foraging hotspot.

** Consistently with what suggested by referee2, we rephrased the sentence, which now reads: "The impressive Gadfly petrels' motility challenges our intuitive understanding of the central tenet of the optimal foraging theory, which predicts that animals should minimise foraging costs (in time and energy) and maximise energy intake" (line 408-411). Please refer to the comments above regarding the commuting to a known foraging hotspot.

Are these waters oligotrophic? This region sees the confluence of the warm gulf stream with the cold waters of the Labrador current. It is a marine vertebrate and fisheries hotspot.

** At the large scale, the waters of the North-Atlantic Current and mid-Atlantic Subpolar frontal system are not oligotrophic (as discussed in the text, line 492-502). We therefore deleted "oligotrophic" from the sentence (line 416).

Hypothesis 3: Is there limited overlap between individuals? This doesn't seem to be the case based on Figure 1.

** We believe that the updated Figure 1a in the manuscript is more informative and depicts more effectively the results on the limited foraging overlap between individuals.

I would also argue based on Weimerskirch 2007 Deep Sea Res (Ref 44 in the manuscript) that the predictability of prey patches is high at large and mesoscales, and not 'unpredictable' as quoted in *the manuscript.*

** We now explicitly specify the considered scale at which prey distribution is unpredictable (line 477-478).

Do you have repeat tracks for multiple individuals? Would it be possible to test for consistency in foraging behaviour?

** Unfortunately, we only have 2 individuals tracked multiple times across consecutive foraging trips and it is therefore not possible to quantitatively test for foraging behaviour consistency within individuals. We can nonetheless describe and discuss the repeated tracks and the respective 25%UD in our dataset (depicted in fig. II). Both individuals undertake "looping" trips (as described in *Weimerskirch 2007*, *Deep Sea Res II*), suggesting a continuous search for foraging opportunities along the route rather than a targeted commuting type movement. The individual in fig. II a shows an impressively limited consistency both in the UD and in the routes' configuration. Moreover, the animal shows a striking variability in the angle of departure from the colony, from South-West to North-West. This further suggests unpredictability in the coarse-scale locations of foraging grounds (*Weimerskirch 2007*, *Deep Sea Res II*). The individual in fig. II b shows a degree of consistency both in trip configuration and 25%UD. However, even within the overlapping 25%UD, most locations from different tracks are separated by hundreds of kilometres and would not be classified as "consistent" following the methodology described in Weimerskirch (2007, *Deep Sea Res II*). In conclusion, we argue that at the large scale, animals' space use is more intense in regions that are on average "better" (such as the waters to the West-NorthWest of the Azores), but, because of the large scale considered and given the evidence described here and in the text, this does not suggest that individuals consistently target predictably good patches at the coarse-scale.

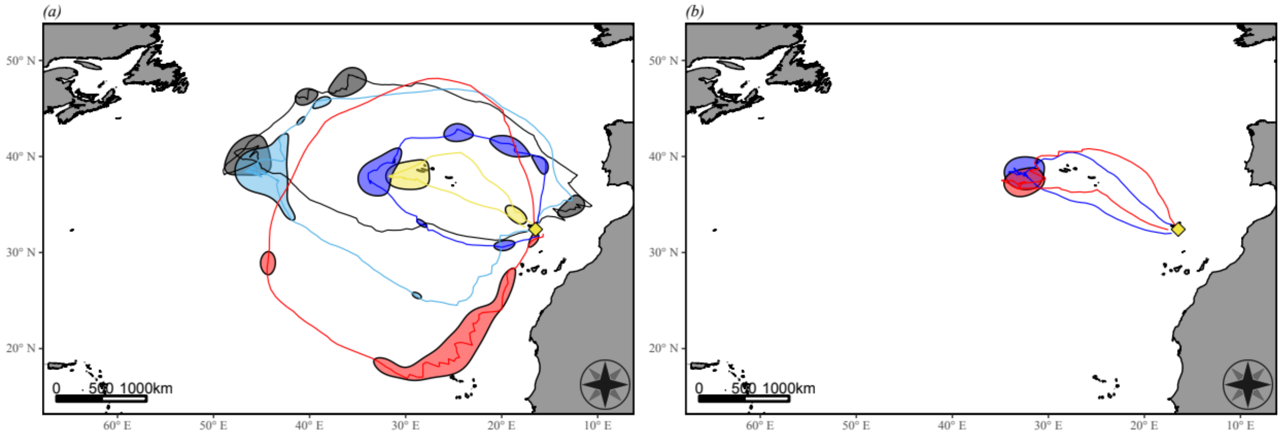

Figure II – The repeated tracks from two individuals in our dataset. The tracks and the respective 25%UD are represented using the same colours.

Hypothesis 4:
Paragraph 1. Last sentence. This is great, exactly what I think is going on. However, I would argue they know where they are going and so using these winds to target a known foraging hotspot.

** Please refer to the previous comments.

Paragraph 2 last sentence. However, wind is also a driver of the state distributions. Could it be that *the tail winds on the return leg of the trip influence the behavioural state in someway? It would be useful to include a plot of state distributions and the link to winds from the HMM.*

** We agree with the referee's suggestion and added the plot to the ESM (fig. 3). The inclusion of tail wind in the design matrix of the HMM model allows for accounting for the effect of tail wind on the mean of the step length distributions for both states, while the HMM simultaneously models the state switching probabilities as a function of the specified environmental variables. While we believe that the inclusion of wind in the design matrix of the HMM enriches the model formulation with more biological realism, ultimately it results in a very marginal change in the classification output (6% of the locations, please refer to the comment above). The results on the homebound section of the trips described in our manuscript – with the animals maximising their speed to cover more ground and deviating from the beeline trajectory – suggest that they continue their search for food (and hence engaging in the "searching" state) also on the way back.

Conclusion: At the risk of sounding like a stuck record, I disagree that the marine domain is unproductive and unpredictable.

** Please refer to the comments above.

ESM: Heart rate is not a good measure of energy expenditure.

** We removed the energy model from the manuscript.

Figure 1 – Why only show 5 example tracks and not either all of them, or the UD summary from the ESM? This figure is also in a WGS projection, which distorts at large spatial scale. This can be seen in the shape of Newfoundland in the three panels. These should all be projected to an equal area projection centred on the centre of the study region (i.e. the Azores). You may see the overlap metric change once you are using an equal area projection.

** The updated figure 1a now shows all the tracks, as suggested by the referee. All the figures' projection is now the Lambert equal-area azimuthal centred on the centre of the study area. Reprojecting the UDs does not affect the metrics of overlap.

Figure 2b – Is wind intensity included in the GAMM as a factor or a continuous variable? Is it just presented in the figure as two levels to make interpretation easier? If so what is the justification for 16 km/h and 36 km/h – how do these fit with the wind speeds experienced by individuals?

** Yes, wind is included in the GAMM as a continuous variable and we chose those values to visualise the model results. To be more rigorous, we updated the plots with two new thresholds for low and high wind intensity: 17 km/h and 31 km/h, which are the 25% and 75% quantile, and described it in the plot legend of figure 2.

Referee: 2

The authors analyse GPS tracking data from Desertas petrels in the Atlantic Ocean to demonstrate how their extremely long foraging trips take advantage of predictable winds at ocean-basin scales. Using a novel methodology, which includes simulations, the authors demonstrate that foraging trips are optimised according to prevailing winds. This study adds to growing evidence that wind may be more important than prey availability at driving the foraging distributions of gadfly petrels. I thoroughly enjoyed reading this paper, and congratulate the authors for their efforts.

** We thank the referee for that.

The paper is well-written and structured to explicitly address its hypotheses. The authors conducted a sophisticated set of analyses, which are, for the most part, appropriate for the identified aims. However, I have raised a few important issues (see below) that I believe need to be addressed before the paper can be considered for publication.

Major comments:

I appreciate the defined hypotheses that are followed through into the discussion, however a several analyses have been conducted and it's not always clear how they relate to hypotheses in methods and results.

** We restructured the paragraph in which we present our hypothesis in order to better link them to methods and results (line 161-176). We further address this in the comments below.

Specifically:

1) It's not immediately clear what the main aims of the hidden Markov model analysis are – it seems from your hypotheses (Hp1) that you want to separate "foraging" and "travelling" states, but then you also model covariate effects on state-switching probabilities and then the effect of tailwind component on the step length distribution. This second comparison seems very similar to the GAMMs later conducted looking at effect of wind speed and direction of step lengths. Could you be clearer (in spatial analysis section of methods) as to why you conduct all of these separate analyses, and what results do you expect?

** We acknowledge that the HMM analytical step was not well introduced and motivated in our original manuscript. Following this comment by the referee, we restructured the paragraph "2.2 Spatial analysis" to improve clarity (please refer to our answers to the specific comments below).

If the aim is to look at whether habitat or wind covariates better explain state-changes, would it not make more sense to construct competing models, one with just habitat covariates, one with just wind, a null model and then a full model, and compare these? The purpose of these tests could be better weaved into methods and results.

** While we appreciate this idea by the referee, the aim of HMM was, overall, to classify the movement behaviour along the track. As we now better described in the revised text, we included habitat (to model the state-switching probabilities) and wind (in the model's design matrix, to account for the effect of tail wind on the mean of the step length distributions for both states) in order to improve the biological realism of our HMM model and obtain the best possible classification output. Ultimately, to determine how much habitat and wind affect the final classification, we generated a covariates-free and design-matrix-free model, respectively, and estimated that both the inclusion of habitat and tail wind cause only marginal changes (2% and 6%, respectively) in the final classification output. Please see the answers below for further details.

2) I think both the labelling of states ("foraging" and "travelling") and investigation of state-changes is problematic with such coarse data (every 2 hours). As you mention in the introduction, gadfly petrels can forage when conducting movement behaviour characteristic of area-restricted search and directed flight ("commuting"), and in discussion you mention birds "rely on a foraging strategy based on covering large distances to increase the probability of encountering unpredictable prey patches along the route". If foraging behaviour can occur en route, then perhaps the "foraging" state would be best labelled "area-restricted search" or something similar.

** We appreciate this comment by the referee, which is consistent with the comment above by referee1. Therefore, we changed the categories to "searching" and "transit", which better describe the movement behavioural states that can be inferred using 2 hour-resolution tracks.

Moreover, gadfly petrels are highly manoeuvrable and I would imagine state-changes likely occur over much smaller scales than every 2 hours. Indeed, how long did the average behavioural bout from HMMs last? It would be good to have a sentence or two in the discussion explicitly dealing with these points, including the limitations of inferring switches in behaviour at this time-scale.

** We thank the referee for this useful suggestion. In the spatial analysis results section (3.1 Spatial analysis) we quantify the median (and inter quartile range) of transit/searching bouts. Moreover, in the discussion, we state the limitations of classifying movement behaviour at this time-scale and we discuss why we argue that our results are only minimally affected by the data coarse temporal resolution. We also clarify that the calculation of distance travelled and speed are underestimated due to sinuosity in the birds' path (line 418-429).

3) I do not believe the "energy model" contributes to the paper and should be removed as there is potential to mislead readers. Given that morphology, wind use, energetics and flight behaviour vary between gadfly and large albatrosses (Spear and Ainley 1997, Shaffer 2001), I am not sure it is accurate to extrapolate between species. Also, the relationship heart rate and energy expenditure does not scale proportionally and is species-dependent. See Green 2011 for a detailed review – "It is certainly essential to avoid the obvious pitfall of assuming that a % change in heart rate equates to exactly the same % change in metabolic rate". Ultimately, as the results of the energy model match that of the trip duration model (which is expected as you have assumed a linear relationship), it's easier to just remove it and say in your discussion that in other species birds expend less energy using tailwinds (Weimerskirch et al. 2000), so the observed trips likely have reduced energy expenditure to randomized trips (due to greater tailwind use).

** We followed this advice by the referee (consistent with a previous comment by referee1) and removed the energy model from the manuscript. As suggested, we make a "qualitative" comparison with other species showing less energy expenditure using tail and favourable cross-winds (line 435-437).

Minor comments:

In future, I suggest use of line numbers to make it easier for reviewers to comment.

** We apologise for the confusion.

Abstract

Line 12: could you briefly provide a description of "pseudo-random" trips, as the other types of randomized trips are fairly self-explanatory.

** Due to the word limit, rather than a description we changed randomized trips' name from "pseudo-random" to "reshuffled-random", which better relates to the simulation protocol used (line 26).

Line 14: efficient for time or energy, or both?

** Time efficient. We therefore rephrased the sentence: "[...] we show that this resulted in trajectories that were close to the fastest possible, given the location and time" (line 27-28).

Introduction

2nd para, line 13: low energetic cost?

** Yes, thank you for the correction and apologies for the typo.

3rd para, line 8: remove "rather".

** We removed it, as suggested (line 75).

4th para, line 10: while hidden Markov models are a form of state-space models, given that they are fairly established in movement ecology, it would be clearer, here and throughout the paper, to just refer to them as HMMs.

** We appreciate this suggestion by the referee, which improves the logical flow of our text, and consistently used HMMs throughout the manuscript.

5th para, lines 1-5: what exactly do you mean by "as their internal state changes" – is it a change in motivation, such as from wanting to forage as opposed to search for another prey patch? Also I'm not sure I understand the main message of the next sentence "The constraints on optimisation…." – perhaps you could rephrase to make clearer?

** Yes, we referred to the change in motivation. We restructured the sentences to clarify (line 101-108).

6th para, line 13: is this overlap of flight routes and foraging areas between individuals (rather than within individuals) – if so, could you explicitly state this?

** We rephrased the sentences to explicitly state that we are considering overlap between individuals (line 125 and 132-133).

8th para, line 5-7: I find hypotheses 3 and 4 quite general compared to the first two. Perhaps you could state how these hypothesis links directly to your test/results. E.g. for H1 = if birds rely on wind rather than targeting specific foraging grounds, then commuting areas would overlap more than foraging areas; for H2 = if birds both follow predictable regional winds and adjust tracks to local conditions en route, routes taken would be more efficient than tracks randomized spatially and temporally, respectively.

** We are grateful to the reviewer for this useful advice. To improve the logical flow, we restructured the paragraph and added a section that links each hypothesis to the methods and the predicted results (line 153-176).

Methods

2nd para, lines 1-3 – It's not immediately clear why you want to consider these variables – perhaps you could include a sentence or two saying what these variables represent. For example, which represent foraging vs. commuting habitats?

** In the revised text, we specified that the variables were extracted to be included in the HMM model in the subsequent analytical step (line 199-201). We then describe in the ESM the hypotheses explaining why each environmental covariate may affect the probability of switching between states and engaging in a transiting/searching behaviour (Table I in the ESM).

3rd para – as mentioned previously, could you provide a bit more information in the main text about why you are modelling both transition probabilities and step lengths in relation to covariates?

** In the revised manuscript, we restructured the section "2.2 Spatial analysis" in order to clarify: what is the aim of the HMM analysis (i.e. the final classification); why we include environmental covariates to model the state transition probabilities; and why we allow TWC to affect the mean parameter of the step length distributions for both states (i.e. in order to have a biologically realistic model and thus obtaining the best possible classification).

4th para – I am under the impression that the bootstrapping is just to increase the sample size, however, I am not sure doing this creates a robust "population map" as you are still limited in assuming that the individuals tracked are representative of the wider population. Please rephrase the text to make this point clearer.

** We agree with the point raised by the referee regarding the adequacy of our terminology. We therefore deleted "population" (and refer to the ESM for the description of the bootstrapping protocol) (line 241).

Results

2nd para – perhaps in supplementary section we could have some plots of probability of transitioning from one state to another with important covariates?

** Consistently with the useful suggestions by both referees, we added the plots depicting the HMM output to the ESM (figure 3 and 4).

5th para – does the increased speed observed tracks compensate for their more circuitous route, i.e. what was the difference in duration of return portions of observed trips vs. beeline trips?

** The higher speed does not compensate for the longer route and the difference in duration between real vs beeline trips is 27.3 hours. We specify it at line 368.

Figure 3 – how did you define whether variation in trip durations of simulated trips was significantly different from the observed as many of the boxplots go below zero (showing overlap with observed trips)? This should be detailed more clearly in the methods section. Also the plot might be better represented with trip durations on the y axis and a box for observed trips as well (currently the horizontal black line represents the mean?). Also, I suggest labelling the y-axis to include numbers < 0.

** We realise that the boxplot presented in our original manuscript needed some restructuring to improve clarity. We therefore followed the suggestions by the referee and updated figure 3, which now better links to the results description. The significance tests used (paired t-tests) are stated in the results section (line 353-364).

Discussion

1st para, lines 1-2 - which theoretical predictions of optimal foraging theory (there are many)?

** We clarified and rephrased the sentence, which now reads: "The impressive Gadfly petrels' motility challenges our intuitive understanding of the central tenet of the optimal foraging theory, which predicts that animals should minimise foraging costs (in time and energy) and maximise energy intake" (line 408-411).

2nd para, lines 14-15 - what do you mean by "causes"?

** We rephrased to "[...] could be driven by a series of factors" (line 448).

Figure 1 or Appendix – it would be good to have a few examples of trips annotated with foraging and travelling states to see how often birds switch between the two, and how long these states last for. This would help determine if it's appropriate to connect travelling segments by a straight line in simulation analyses.

** We agree with the referee and incorporated both suggested changes in our revised manuscript. We updated figure 1a in the main text, annotating the searching bouts along the tracks, and we stated the median (and inter-quartile range) of searching/transiting bouts (line 337-338).

Appendix

State-space modelling section, 2nd para – does this mean wind speed and relative direction were modelled on state transition probabilities or just step lengths? This could be made slightly clearer from the start (and in the main text).

** Tail wind component was included in the design-matrix of the HMM to account for the effect of tail wind on the animals' step length, and was not used to model state-switching probabilities. We specified it in the revised text (section 2.2 Spatial analysis) and in the ESM (section 2.1 Hidden Markov model).

State-space modelling section, 2nd para – change "stepwise down model selection" to "backwards selection".

** We reworded it as suggested

Figure S1 – it would be good also to have a map indicating how individual foraging and travelling areas overlap - perhaps kernels for each individual overlaid with some level of transparency.

** While addressing referee1 comment regarding the within-individual consistency in foraging hotspots, we had to split the two individuals' repeated tracks in two different panels because the plot was not easy to understand. Generating and visualising kernels for the 25 tracks would be difficult to interpret on a single map. To have a visual overview of the individuals' transit and searching areas we updated figure 1a in the manuscript, showing all the tracks and highlighting the searching bouts.

Appendix B

Dear Editor,

We are very pleased to have received your response accepting our manuscript for publication. We hereby address the comments raised by the reviewer and incorporate these minor revisions into the final version of our paper.

Francesco Ventura, José Pedro Granadeiro, Oliver Padget and Paulo Catry

Responses to comments by referee 1

*** Line 44: 'However, how' perhaps rephrase to something like "Nevertheless, how"*
We changed the text as suggested.

*** Line 204: the model estimates the distributions, it doesn't predict them*
We agree with the reviewer and edited the text accordingly.

*** Line 235: the equation is missing the AR1 and individual-level random intercept terms*
We changed the text at lines 239-248 to more formally describe the inclusion of the autoregressive AR1 term accounting for the temporal autocorrelation and for the dependency between observations collected on the same birds.

*** Line 299: I'm still unsure of how useful this stage is. The environmental covariates aren't well explained, and have a minimal impact on the state classification. The interesting figures of the transition probabilities are in the appendix, which is a shame but I understand the space constraints.*
We appreciate the referee's understanding of the space limits. It's true that the environmental covariates affect the final classification only marginally. We argue that this finding is an important element backing up our conclusions regarding Desertas petrels' foraging behaviour. Stable features of the seascape minimally affect the transitions between travelling and searching behaviour: this further supports our hypotheses of "unconstrained route planning" during the transit state (line 102-105), and of a foraging strategy that relies upon maximising distance covered rather than targeting predictable foraging grounds.

*** Line 314: The test statistic value is linked to the sample size. Does this suggest that all animal locations have been considered as independent samples? Is there a way to address this?*
As correctly stated by the referee, all animal locations were considered in the Mann-Whitney-Wilcoxon non parametric test adopted. To address the point raised by the referee, we fitted a linear mixed effect model with formula
delta angle ~ states, random=~1|ID,
accounting for individual ID as random effect. The inclusion of the categorical variable "states" (searching/transiting) was highly significant ($p < 0.001$); the model estimated the transiting state to reduce delta angle by an average of 4.3 degrees. We presented these results at line 316-320 of the revised manuscript.

** *Line 336: remove "what"*
We changed the text accordingly.

** *Line 344: "The Gadfly petrels' impressive motility"*
We reworded the sentence as suggested.