

Reply to recommender

First, I would like to apologize for how long it took me to make the decision – it was difficult to get reviewers in the summer. After considering two reviews and my own reading of the manuscript I ask you to revise the manuscript. Both the reviewers and I think that it would be a valuable contribution if you address the comments. I especially appreciate the temporal scale of the data and the strength of the evidence which comes with it. Currently the manuscript is narrowly focused on temperature effect on the parasites. In addition to reviewer comments, I would like you to explicitly consider aspects of host-parasite dynamics in the manuscript in addition to temperature. Could you test if there is evidence for dependence of the parasite population on performance or population size of the host in previous year, or in some other way relate parasitoid dynamics to host dynamics?

Thanks for your constructive comments on our manuscript. We have tried to address all of the referees' comments and hope both you and them will find our answers clarifying.

Regarding your request to add host dynamics to the picture: we agree that this was an aspect that we should have explicitly mentioned, and we have now found a way to test for a relation between host and parasite dynamics in our study system. Because these parasites have a broad host range, and because we only monitor those blue tits that breed in our nestboxes, we can unfortunately not have an accurate measure of either host or parasite population size.

Instead, we used two measures that can be used as workable proxies for host 'performance' in our case, namely brood size (number of nestlings, i.e. number of hosts for blowfly parasitic larvae) and chick mass close to fledging (taken here to represent the 'quality' of the hosts available to blowflies, as heavier chicks will contain more blood than lighter ones).

We re-ran our analysis of interannual variation in blowfly intensity, now including these two variables in the initial set of explanatory variables. Neither of the two variables was retained after model selection (AIC-based), and the final model remained the same as in the previous version of the manuscript. We have detailed this in the methods, results and discussion of our manuscript, and hope that this it is now more complete. We thank the editor for this suggestion which has helped improve our manuscript.

Reply to Reviewer 1

Summary: This study describes how local temperature affect blowfly abundance in blue tits nesting in a Mediterranean habitat based on a survey over 18 years. Authors convincingly show that environmental temperature is a potent mediator of parasite abundance, both within breeding seasons across years, and between different years.

General comments: I congratulate the authors on a fine contribution that will interest a range of ornithology and ecology scholars. The ms is well-written and clear for the most part, data were appropriately collected and analyzed, and conclusions follow. All in all, I found this neat paper, and have relatively few further recommendations offer. I have made note of some more itemized issues that you may wish to address. I hope you will find these useful.

Minor comments: 1. Line 20: Please italicize species names.

=> *Done (L22-23)*

1. Lines 23-24: I think it would be easier to understand this effect should you express it as temperature differentials, e.g. what is a high “previous summer temperature”.
2. Lines 26-28: Sure, but blowflies are hardly range restricted as is?
3. Lines 29-32: This should be revised for clarity.

=> *We have now rephrased the abstract.*

4. Line 54: What is the rate of activity? Movements per hour?

=> *We referred to activity levels and not rates. This has been corrected (L60).*

5. Line 87: You need to be more specific at this point – “physiological performance” is both vague and subjective.

=> *We used the term physiological performance in the same sense as in the paper by Thomas et al. (2007) – i.e. referring to aerobic capacity. We have now rephrased and clarified this (L90-92).*

6. Line 119: Which other breeding attempts would there be in the net boxes?

=> *We see that this sentence was unclear. This part has now been rephrased (L123).*

7. Line 120: It would suffice to say you visited boxes to determine start of breeding. References to Julian day are superfluous.

=> *OK – removed (L123).*

8. Lines 123-125: It would be prudent to state dimensions here.

=> *Done (L127).*

9. Line 130: By “wing plumage color” you mean that you checked for a molt limit between the primary coverts + alula and the greater coverts?

=> *Yes, we do. This has now been rephrased (L132-135).*

10. Line 133: Because these females could not be caught?

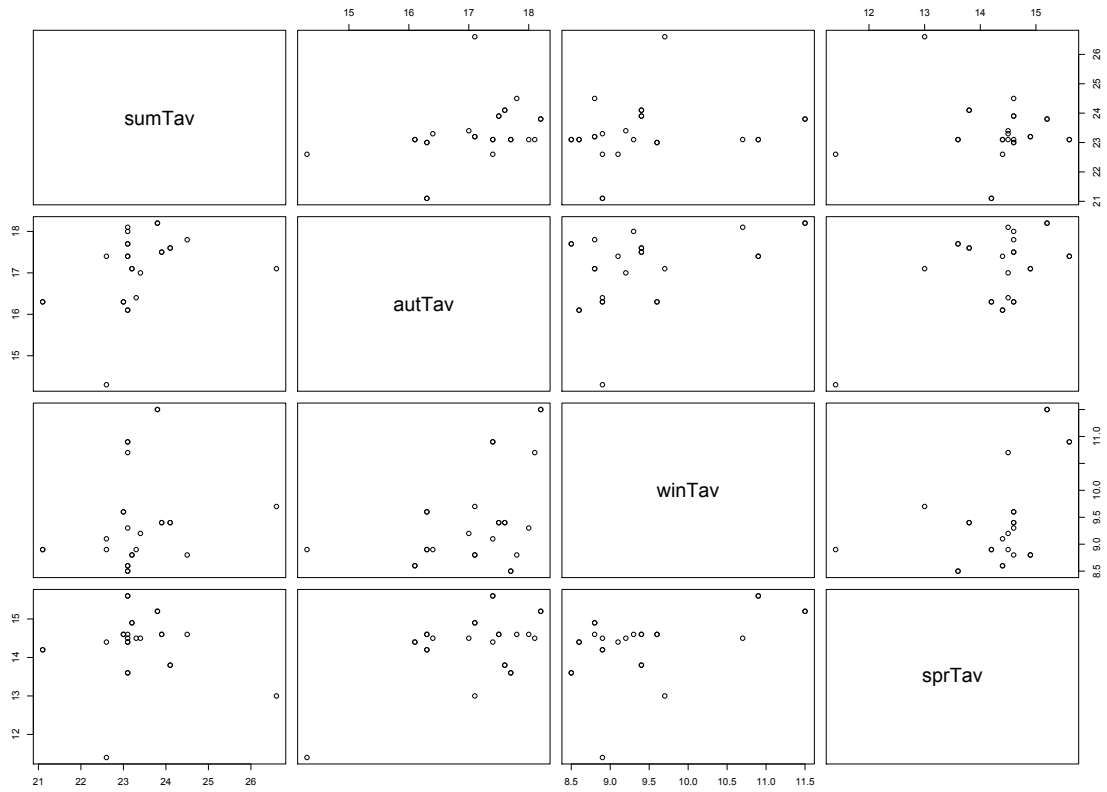
=> *Indeed. This has now been rephrased (L137-138).*

11. Line 166: “Statistical analyses”

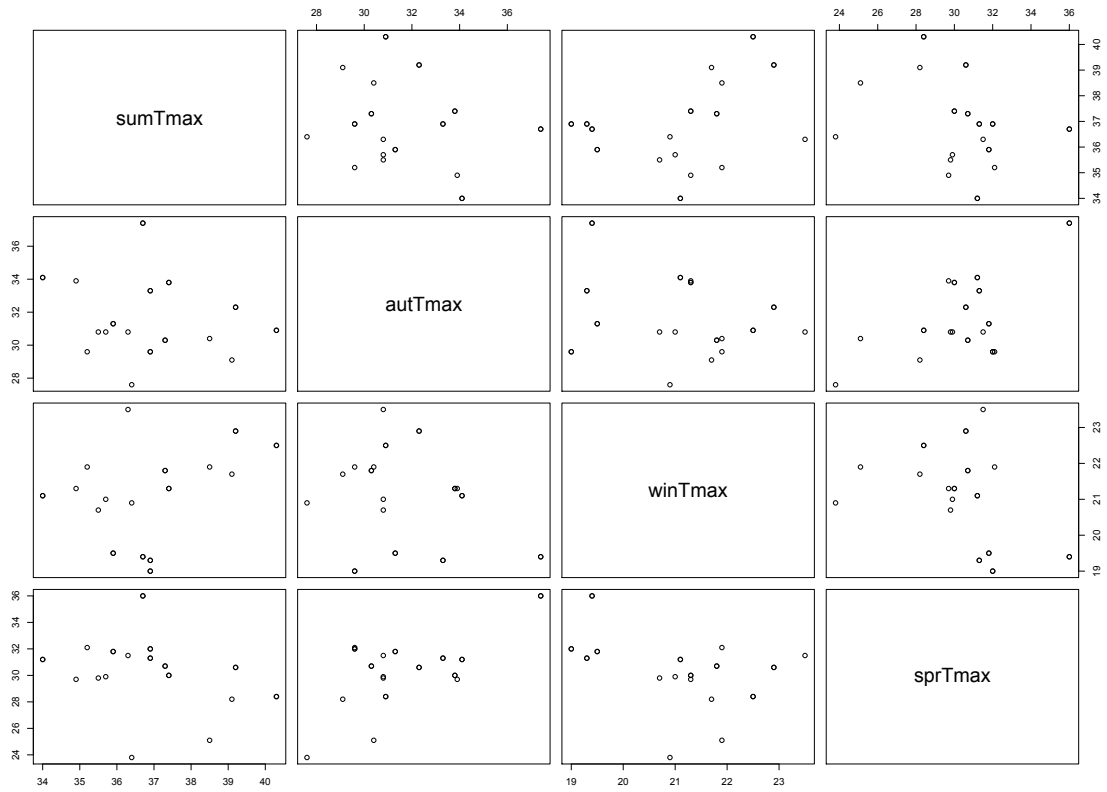
=> *Corrected (L175).*

12. Lines 196-197: Were temperature indices for the different 3-month periods correlated?

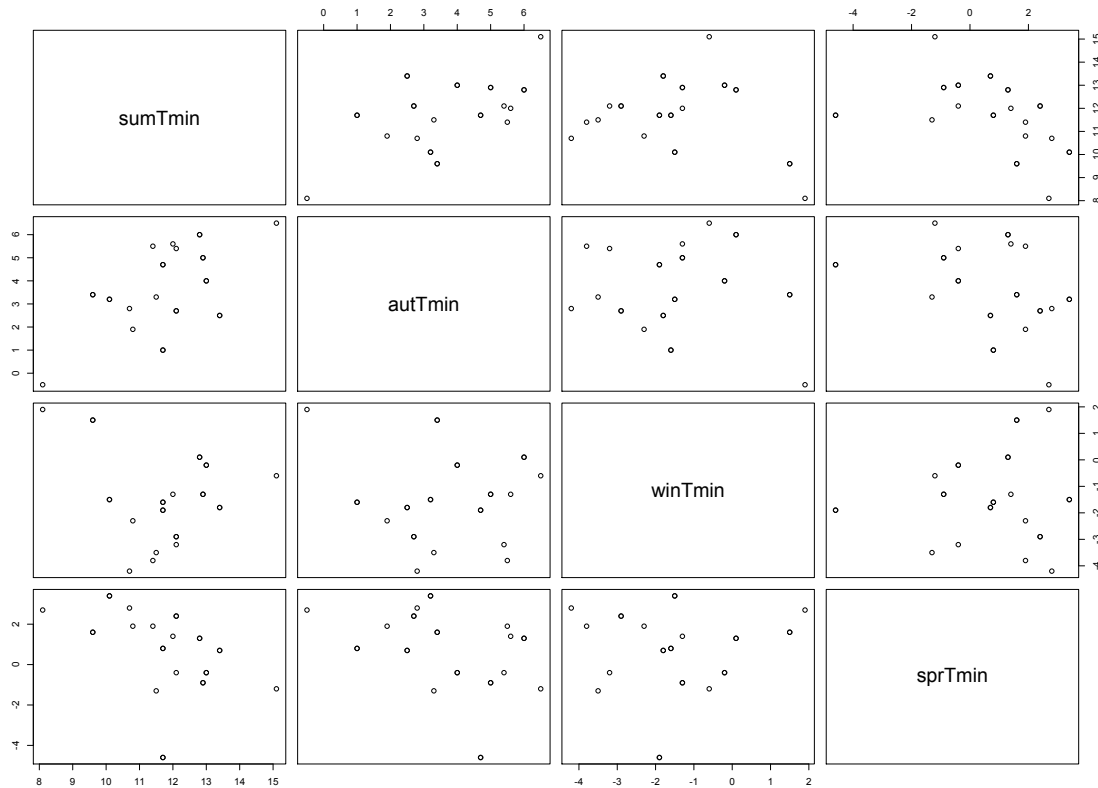
=> *We checked this both graphically and statistically. Two types of correlations stood out: positive correlations in average temperatures between periods following each other (autumn-winter, winter-spring, spring-summer) as well as a positive correlation between summer and autumn minimal temperatures (see scatterplot matrices below). The explanatory variables retained after forward model selection (average temperature during nesting stage, minimal spring temperature and average temperature in previous summer) are not correlated. We have added this in the manuscript (L210-211).*



Scatterplot matrix for average temperatures. $sumTav$ = average summer temperature; $autTav$ = average autumn temperature; $winTav$ = winter average temperature; $sprTav$ = spring average temperature.



Scatterplot matrix for maximal temperatures. sumTmax = maximal summer temperature; autTmax = maximal autumn temperature; winTmax = maximal winter temperature; sprTmax = maximal spring temperature.



Scatterplot matrix for minimal temperatures. *sumTmin* = minimal summer temperature; *autTmin* = minimal autumn temperature; *winTmin* = minimal winter temperature; *sprTmin* = minimal spring temperature.

13. Lines 210-215: How influential was the one very warm Fango summer for these results?

=> *We understand that looking at Figure 3 one might wonder whether this year (2003) is driving the relation between average summer temperature on parasite load. To test this, we performed again both the model selection and the analysis, after removing this year from our sample. Model selection resulted in the same set of variables for the final model, which means that even when removing the year with the warmest (but real) summer, average summer temperature still improves the fit of the model. We have added this result to the manuscript (L232-233). The effect falls short of being significant though ($P = 0.12$), but given the rather limited sample size this might correspond to a real trend and, in this case, deserves to be reported. Note that we could go on, eliminating the data point for the second warmest summer also pretty much situated in the bottom right corner – but these years were real and thus cannot quite be ignored.*

14. Lines 223-226: You could downplay this effect I think. It was prudent testing for it, but it is not essential for the Discussion to keep it in. Also, out of

interest, if the loss argument holds where would the nest parasites otherwise have disappeared, and why?

=> This has now been removed from the first paragraph of the discussion. To answer the referee's question: as these nestboxes have a front opening, these bags were designed in the 1990s to make sure that the (tiny) first-stage larvae would not accidentally fall out when the nestboxes were opened soon after hatching. We agree that this is not a spectacular result; in addition this has been known since 1996 (cf Hurtrez-Boussès et al. 1999).

15. Line 227: Thermal dependence is an awkward term, please swap for something less ambiguous.

=> We have now rephrased this sentence (L248-249).

16. Line 232: Why would you expect it to be?

=> We would not. This sentence was unclear and has been rephrased (L250-252).

17. Line 239: I agree insofar that thermal limits to development are as likely in blowflies as in other insects. However, given the vast distributional range of the Calliphoridae, I would be careful with drawing broad conclusions about taxon-wide temperature tolerance.

=> We agree, and have removed the sentence referring to other Calliphoridae species.

18. Line 241: Summer heat, or warmer summer temperatures? This is an important distinction.

=> Corrected – here we meant warmer summer temperatures (L263).

19. Line 247: “High” is rather subjective a term in this context.

=> This part has now been removed from the manuscript.

20. Lines 241-250: This reasoning is in analogy with a recent study that manipulated nest temperature in blue tits (Andreasson et al. J Avian Biol 2018) found that nestlings in heated nests had higher body condition and suggested this could have been a result of increased parasite mortality at high environmental temperature.

=> Thanks for the tip! This study, though, does not show higher nestling body condition in heated nests (but rather that neither condition at fledging nor fledging success was significantly reduced by heat stress, and that recruitment even seems

higher for heat-exposed nestlings). It is anyway relevant here and we have now referred to it (L257-260). We have also referred to another study published this year in J. Avian Biol., showing decreased blowfly intensities in experimentally heated nests (Castaño-Vazquez et. al 2018).

21. Lines 271-277: This gets a bit repetitive.

=> Here we assume that Reviewer 1 meant that parts of this were also detailed in the introduction. We have accordingly rephrased the introduction (L90-100), and removed some of these considerations from the discussion. We hope the text flows better now.

22. Lines 281-285: You should have the data to test this?

=> Yes, it is the next logical step. We have added one sentence at the end of the paragraph to clarify this (L306-315).

23. Line 296: There are evidence for similar effects also in homeotherms, which you might consider acknowledging here.

=> Done (L326-327).

24. Lines 291-307: I am not convinced by this reasoning, as there are already blowflies at latitudes considerably colder than at your study sites. I am not sure how much this adds to the ms.

=> We agree that our results do not allow predictions concerning range shift, and have removed this part from our reasoning. Yet even if blowflies are present at higher latitudes, they are so in much lower prevalence and intensities. Given both the clear relations that we found between temperature and blowfly abundance and the current climate projections, the question of whether this will result in increasing blowfly intensities in sites where they have historically been moderately abundant deserves (in our opinion) to remain in the manuscript. We have rephrased this part to make it clearer and a little more 'humble' (L338-348).

Reply to Reviewer 2

Dear Editor, I found this MS very interesting and mostly well analysed and written. I have some, mostly minor queries intended as constructive with the aim to improve the paper. As detailed to authors, I think that one of my queries, that concerning making explicit the percent variance explained by two interesting factors, should be addressed 'mandatorily' as its dissection and eventual discussion may throw light on the role of two additional factors -genetic (bird host) and environmental (nest identity)- in this host-parasite system. I hope this review may be useful for the editorial team to reach a recommendation. Best regards.

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- Title: this may be a matter of different personal taste but, in my view, only one of the two adjectives (wild, passerine) should remain in the title.

=> *We have removed 'passerine' from the title.*

- L. 49. 'relevant': to me, this adjective is dubious in this context and raises the question what 'irrelevant host-parasite systems' would be to the authors. My advice is to change wording here.

=> *We have rephrased and hope to have clarified the sentence (L51-52).*

- L.51-61. in my opinion, the stated rationale falls short of being complete in a host-parasite framework by only dealing with the (ecto) parasite life histories part and ignoring any, theoretical at least, dynamic response (e.g. immune responses, behavioural changes) on the part of hosts. That, is, what I am asking for here is some background on host (bird) dynamics in relation to the purported responses of parasites to climate change.

=> *We have now mentioned host-parasite dynamics in the introduction (L47-48 & 53-54), included two measures of host performance in the set of variables for model selection (L207-209 – note that none of them was retained in the final model), and provided a potential explanation why in the discussion (L241-244).*

- L.77. I am familiarised with a relatively old paper by Bennett and Whitworth (Bennett, G. F., & Whitworth, T. L. (1991). Studies on the life history of some species of Protocalliphora (Diptera: Calliphoridae). Canadian Journal of Zoology, 69(8), 2048-2058) but I am unaware of a paper of (seemingly) the same authors cited as 'in press' but not included in the reference list.

=> *Thanks for pointing this out! This was clearly an error in our reference manager that has now been corrected.*

- L.131. It would be better give a citation here or explaining the rationale for considering female age and no other female traits in relation to nest

sanitation. Readers have to wait to find the citation/explanation later, in l. 182-184.

=> *The explanation has now been moved up (L135-137).*

- L.154. If I understand well, here 'replaced' seems to indicate that nestlings had not yet fledged by the time researchers removed the nests as replacement of nests with mosses would not be necessary if chicks had fledged. For the sake of clarity, authors should be more explicit when describing the procedure.

=> *We have now added more information (L163-164).*

- L.169-170. While I can understand removing predated nests from the analyses, it is plausible that nests heavily infested by blowflies are in turn more exposed to predation, due to increased begging by nestlings due to worsened nestling condition and/or a larger number of feeding visits by parents attracting predators to the nests. Hence, I think that, if possible – i.e. if blowflies could still be sampled after predation, as the number of (depredated) chicks surely is known - , some test should ideally be presented to demonstrate that the omission of those nests does not affect the results of this study; or to demonstrate that what I have just written is wrong and therefore, heavily parasitized nests do not attract predators differentially. Independently of whether these ideas/tests are included or not, I think that the identity of predators (woodpeckers, colubrid, mustelids, etc.? should be mentioned explicitly.

*=> This is an interesting question, but unfortunately we do not have the data to address it. The reason why we collected nests before fledging was because blowflies pupate quickly after the chicks have left the nest (either due to fledging or predation), and are then much more difficult to extract and count (pupae are tightly rolled in lining materials and with the usually high abundances that we have in Corsican blue tit nests this means that the nest becomes a compact mass of materials difficult to tear apart). In addition, to obtain accurate measures of parasite load per individual chick we needed to scale the number of blowfly larvae in a nest to the number of nestlings alive in the nest at the time of sampling – which is obviously impossible to do after fledging. For these reasons blowflies were rarely sampled from nests that had been predated. The main predator of nestlings in these sites is by far the green whip snake (*Hierophus viridiflavus*) – an excellent climber and very efficient at spotting active nests. We have added more information in the manuscript (L179-180).*

- L.177. Authors include both biotic and abiotic factors, so 'or' should be 'and'.

=> *Corrected (L187).*

- L.182-184. Ok, but this should be better placed before (see above re: L.131).

=> *This has now been moved further up (L135-137).*

- L.185. Authors show differences among valleys in blow fly prevalence as 'differ markedly in a range of factors' (L.190). Therefore, it would be very interesting to know whether other environmental - or even (host) genetic) - factors apart from valley affect blow fly prevalence. The statistical analyses include, as stated, female and nest box identities, in addition to year, as random factors. In my opinion, the article would improve significantly if authors 'dissect' a bit more their results and give (and discuss) the amount of variance explained by female ring and nest box location as random factors. As authors likely know, these stats can be extracted within the R stat environment, e.g. by following routines in Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4(2), 133-142, freely available here <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.2041-210x.2012.00261.x>.

=> *We are very grateful to referee 2 for pointing this out. This does improve our paper significantly and opens for more discussion! We have now included information on variance partitioning among random effects in our results (L221-224 & Table 2), and rewrote parts of the discussion accordingly (L244-247 & L309-320).*

- L.195. Are laying date means corrected for female age? As the age distribution in the population may vary among years and young birds lay much later than older birds, I think it would be advisable to do so, in similar vein to your inclusion of female age in the GLMM in the former section (lines 182-184). I note that authors use a similar approximation for parasite load, when they correct for ambient temperature during nesting (legend to Fig. 3).

=> *In our dataset laying date varies across years (Anova, $F_{17,501} = 22.47$, $p < 10^{-4}$), but there is no significant effect of female age ($F_{1,501} = 1.86$, $p = 0.17$), and no significant interaction with year either ($F_{15,501} = 1.24$, $p = 0.24$). Note, by the way, that in Figure 3 we plot residual parasite load (after accounting for the effect of average temperature during nesting, already shown in Figure 2) for the sake of clarity in the figure only (i.e. to better focus on the effect of temperature in previous summer) – but we do not “correct” for it in the analysis.*

- L. 207. I wonder whether the nest cleaning behaviour of females is disrupted or modified by the cotton bags 'enveloping' the nest and this could affect the differences in abundance. Maybe the cotton enclosure impedes females to manipulate mosses, etc. 'correctly' to find and remove larvae and puparia? Do authors have data (e.g. videofilming) on female cleaning behaviour in those nests?

=> *If we understand correctly, referee 2 assumes that females remove blowfly larvae from the nest, and that cotton nests impede them – which might explain the higher abundance in nests surrounded by cotton bags. The answer is that the referee's assumption seems to be wrong: field studies using video monitoring of female behaviour within the nest cavity revealed that females did not remove (or eat) blowfly larvae from the nests (see L296-297). Instead, they dig their head in the nest materials and “shake” them – which we think might help make the larvae that were on their way up to suck the blood of nestlings fall at the bottom of the nest again. The amount of time spent by the female performing this behaviour increases with parasite infestation (cf Hurtrez-Boussès et al. 2000, J. Avian Biol.). Another explanation why parasite loads are affected by cotton bags is provided in our response to referee 1.*

- L.241 forward. I hate to say this but...could the research itself affect blow fly mortality? Larvae and puparia are collected from nests by researchers and hence, adult flies do not emerge from the nests. I realize that the invasive technique employed is maybe unavoidable to study this system but, if all nests are 'cleaned' from blow fly propagulae, it is not hard to infer this may affect the demography of the fly population. Maybe this may be solved by stating that blow flies parasitize nests of other bird species in the area, if this is the case, that are not emptied from its parasitic contents? (I am assuming here that there no many natural holes where tits and other hole-nesters may breed and be parasitized by blow flies, but I do not know for sure).

=> *We do not think this could be an issue here, for several reasons:*

- *if this was the case, we would expect lower blowfly abundances in years following larger studies that required many nests to be deparasitised, for example in the Fango valley in years 2000 (after field experiments conducted by S. Hurtrez-Boussès) and 2006 (after field experiments conducted by A. Mennerat). We find no indication that this might have occurred (see Table 1).*
 - *Protocalliphora blowflies have a very wide range of host species and are found in other nests in the area – not only blue tit nests in nestboxes*
 - *the prevalence in blue tits is very close to 100% and in most years and at most study sites only a subsample of blue tit nests were collected, while ectoparasites in other nests were left undisturbed. In addition, none of the great tit nests (also using nestboxes) were collected.*
- L.259-260. 'shortly after post-winter emergence'. When is it? Post-winter seems too loose a term having in mind that the fly will not search for bird nests to parasitize until there are hatched fledglings, as stated earlier in the MS (L.80). Please mention concrete dates if available from your study or from the bibliography.

=> *We have now rephrased and hopefully improved this part (L278-280).*