February 15th, 2019

Re: Revisions of manuscript:

Rataud et al. Evaluating functional dispersal and its eco-epidemiological implications in a nest ectoparasite

Dear Editor,

Please find below our reply to reviewer comments on our manuscript "Evaluating functional dispersal and its eco-epidemiological implications in a nest ectoparasite". We have carefully taken into consideration all remarks and have either modified the text accordingly, or have provided a complete rebuttal as to why changes were not made. We thank both reviewers for taking the time to provide us with this feedback, which we feel has improved the overall quality of the manuscript.

Please note that reviewer comments are in black and our replies in blue.

Sincerely,

Karen D. McCoy

On behalf of all authors

Reviewer 1

First, there have been other studies on hard ticks using mark-recapture studies that have not been cited or discussed.

We were unaware of other studies that used CMR analyses to examine tick survival and dispersal in natural populations and would have appreciated receiving references for these articles from the reviewer. However, given this remark, we searched the literature again and found that we had missed some important articles in our initial searches. Three articles use CMR methods to make demographic estimations, but only one of these actually focuses on dispersal(Carroll et al. 1991; Daniels et al. 2000; Eads and Smith, 1983). These references have now been added and cited in the text (Introduction, second paragraph and Discussion, second paragraph). We would also like to note that there are other articles that mark ticks to examine dispersal distance, but these studies do not estimate movement using CMR analyses.

Second, a major concern is the duration of the mark-recapture study in relation to the lifespan of soft ticks (or ticks in general). Some species of soft ticks have been documented to live multiple months to even years between blood meals. Thus, even on failed breading season might not be long enough to induce dispersal. This should be discussed more directly as a limitation of this study.

We fully agree with the reviewer that dispersal may occur over longer time periods and point this out in the discussion (Discussion, paragraph 5). However, to better highlight this idea, we have mentioned it again in the discussion in relation to dispersal propensity (Discussion paragraph 7). As an anecdote, we actually found a couple of marked adult ticks from 2017 in 2018 in the same nest areas where they were marked, suggesting limited between-year dispersal.

Third, the survival probability seems to be limited. Only three dead ticks were found. This could have only be a random occurrence, even though this was noted to be different between successful failed nests. This needs to be clarified.

We are not sure what the reviewer would like clarified. Tick survival probability for each treatment was based on the recapture histories of each tick and took into account observed mortality (i.e., the three dead ticks), but also unobserved mortality and dispersal probability. Indeed, the three dead ticks were observed in successful nests, but the survival estimate is higher for this tick group.

Fourth, the authors cite unpublished data to support a few points in the discussion. These seems to some points of moderate importance, but should be used only as secondary support.

We agree that it is not optimal to cite unpublished work, but as we are in the initial stages of our monitoring program, and almost nothing has been previously done on this tick system, we are obliged to ask the reader to trust us. However, to limit the use of 'unpublished data', we now cite the master's thesis (in french) that presents analyses from the 2018 season and double checks some of the potential weaknesses outlined in the discussion (transient effects, etc).

Fifth, the author discuss that there might be a lack of gene flow, but this might have been missed due to the duration of the study and could create a disconnect between actual dispersion and measured dispersion. It is mentioned that genetic studies are necessary, but this should be more clear.

We are unsure how to make this point more clear. As we outline in the text and mention in relation to this reviewer's second point, we fully agree that gene flow might occur and notably via inter-seasonal movements of ticks within the colony (Discussion, paragraph 8). We are currently planning to test this hypothesis, but require the appropriate genetic markers to do so.

<u>Reviewer 2</u>

This paper describes a study to quantify the probability of functional dispersal of a tick within a colony of nesting gulls. The study constitutes one of the few attempts to undertake mark-recapture study on tick vectors and provides novel results of this aspect of the demography of this species. The experimental design and statistical analysis of the study are both robust. I believe the study makes a worthy contribution for PCI ecology and will be of interest to many readers and researchers. I do however have several reservations and comments that need to be addressed before I can recommend this study.

Major comments

1. It is not clear whether ticks are able to disperse between nests independently of hosts or only via host movement. Indeed in the discussion you actually contradict yourself in this respect: you first write “Dispersal of O. maritimus via host movement is of course possible, but was considered unlikely because of the short duration of the blood meal and the limited movements of yellow-legged gulls within the colony during the breeding period”, but then subsequently write “As this tick seems to depend entirely on passive movements via the host for dispersal…”

a. This is obviously a critical point for the interpretation of the findings of this paper and should clarified from the outset.

b. For example, if the ticks are dispersed by their hosts, and nest failure triggers the host to abandon the nest (see comment below under DISCUSSION), then lower dispersal in failed nests would be expected.

We agree that this is an important point and understand that confusion arises because both types of dispersal are possible in this system and depend on spatial scale (e.g.,, only host-associated dispersal is possible between colonies). In general, we do not yet have a good idea on the relative importance of active (where the tick walks to a new location) versus passive (carried by its host) dispersal at small scales in ticks in general. We know for some species ticks can walk (even run) to find a new host (eg. *Hyalomma* ticks on horses or camels, *Ornithodoros savignyi* that comes out of hiding to bite sleeping camels when the opportunity arises), but such examples are often for exophilic ticks that are easily observed. Information on more discrete nidicolous ticks such as *O. maritimus* are rare and the question of what motivates ticks to move is open. In order to clarify the dispersal options for this tick, we have have outlined our assumptions earlier in the revised version (Material and Methods, paragraph 1).

2. A key component of this study (and quite a lengthy component of the discussion) centres on inferring epidemiological consequences of tick dispersal in this colony. You write in the discussion: “In contrast to predictions based on the distribution of infectious agents within the colony (Dupraz et al. 2017), overall inter-nest dispersal rates of O. maritimus were very low”. I’m not sure I follow the logic here, as the distribution of pathogens within ticks would also depend on the distribution of pathogens within the host, which it seems has not been sampled, and is not known. Moreover, if any of these pathogens can be transmitted by a non-vectored route (e.g. vertical transmission from mother to offspring) then this offers a route for pathogen transmission to be less strongly coupled to tick movements.

First, we fully agree that the distribution of infectious agents in ticks depends on the distribution of these agents in the host birds and that this is unknown in our system. However, we have assumed (but clearly not explicitly enough) that birds are limited to the area of their nest site during the breeding season and that philopatry should be high (ie, a return to the same breeding location within the colony the next season, Coulson 2016). We have also implicitly assumed that ticks are only active during the breeding season when hosts are readily available. Given these assumptions, and if active tick dispersal is limited or absent, endophilous ticks within a nest should all be exposed to the same bird family and therefore receive the same infectious agents from these birds, regardless of whether these agents are vertically transmitted or not. We have attempted to make these assumptions more explicit in the introduction (Introduction, paragraph 4).

a. Given that much of the disease dynamics and vector biology remain unknown in this system, I suggest the authors temper their inferences regarding the epidemiological consequences of their findings, acknowledge the numerous areas that remain unknown about disease dynamics in this system, and substantially reduce this section in the discussion.

We feel that we have already been quite explicit about the fact that we know little about the dynamics in infectious agents in this system. However, as requested, we have attempted to reduce some of the discussion on this aspect (Discussion, paragraph 8)

b. Please change the quoted sentence above to read "In contrast to predictions based on the distribution of infectious agents IN TICKS within the colony (Dupraz et al. 2017), overall inter-nest dispersal rates of O. maritimus were very low". And elsewhere in the manuscript.

Done.

Minor comments

1. Could you please replace the word "circulation" throughout with "transmission" as this is the correct epidemiological term.

We argue that these terms are not synonymous. Transmission refers to the exchange of an infectious agent from one host to another, whereas circulation includes both transmission and the movement of the infectious agent with the host. As in the case of our system, we are particularly interested in how movements at different scales alter the dynamics of tick-borne pathogens, the word circulation is more appropriate.

2. METHODS

a. Could you add information on the lifespan of an adult tick (and other life stages if this is known) as this would help in the interpretation of results and study design.

This is completely unknown. We could add anecdotal information from other species kept in laboratory conditions for years, but in the interest of space, we have not done this. We do now state that these ticks may live for several years (Discussion, paragraphs 5 and 7).

b. Page 3/top of second column = I assume that when you say "feeding rapidly" – this means that they spend less total time on their hosts compared with hard ticks? Please state this if that is what is meant.

We have changed this to be more explicit (Material and Methods, paragraph 1).

c. GPS – should be capitalised.

Done.

d. Only 30 adult and nymphal ticks from each nest were marked. Could you comment on why you limited the number of marked ticks to this many, and not simply mark all the ticks in a nest? Could you also state what proportion of the ticks in a nest this constituted (on average)? This is also relevant in terms of the effect on tick density of adding 30 ticks from nearby nests. Could increasing the density in this way have affected survival of these ticks (competition for blood meals, etc)?

We limited the number of ticks marked and remarked to reduce the overall time in the colony and minimize the disturbance associated with our work. For each focal nest, there were a total of 60 marked ticks to be followed (30 from the focal and 30 extra from peripheral nests). A removal study that we carried out in 2016 found that nests could easily contain over a 100 ticks, suggesting that adding 30 extra ticks to a nest would correspond to a moderate to high natural infestation level (Dupraz et al. 2017).

e. Could you include a table (or summary in the text) of distances among nests in a group vs between nests from different groups

This information has now been added to the text (Material and Methods, Experimental procedures, paragraph 1).

f. What was the average clutch size in this colony? Did this vary greatly among the "successful" nests?

Gulls have clutches of 2 to 3 eggs. In 2017, average clutch size was 2.6 at hatching. This information has been added to the methods (Material and Methods, Experimental procedures, paragraph 1).

g. Could you verify that nests that were left to be successful (ie where the eggs were not removed), did actually go on to be successful nests (i.e. they produced young).

Yes, the status of the nest was followed at each visit. One successful nest failed early in egg incubation and one failed nest relaid. Otherwise, all successful nests produced young. This detail has been added to the text ((Material and Methods, Experimental procedures, paragraph 1).)

3. RESULTS

a. The results for the transition parameters estimated as 1.00 with no Cis available indicate problems with estimation of the parameters at the boundaries. It seems to me that there were too few data (observed transitions) to obtain meaningful estimates for these parameters, and that thus you should not try and obtain inferences from them.

The confidence interval was computed (with the Wald method) based on the asymptotic property of the maximum likelihood estimator. This property does not remain true when a parameter is estimated at a boundary thus no CI is available for parameters estimated at one. We used a non-parametric bootstrap method with 100 draws to compute the confidence interval on the boundary. Results show that the transition estimate is always estimated at 1 for each sampling of the data. Considering that this method is quite robust and conservative, we are quite confident about our estimate and our conclusions on tick movement

b. In the table legends for the CMR results could you add – "Only the top five models of xxx that were included in the candidate set are presented".

Done.

c. In figure 2 → Could you add another example of colour coding for a tick that was captured in those same nests but in trip 2 and 4 – i.e. for capture history 12020. This would make it clearer how the colours for visits and nests align/differentiate.

As requested, we have added a second example of colour coding to demonstrate our marking scheme.

4. DISCUSSION

a. Page 9/2nd column, 2nd paragraph → nymphs constituted only 24% of your "captured" ticks (not "recaptured" as you write). The recapture rates for nymphs and adults were approximately equal as indicated by the model results (only 1 of the top 5 models included an effect of life stage on recapture rates) and the raw numbers themselves. So I don't believe there is very strong evidence for different recapture rates of the two life stages. Yet you go on to discuss this at length.

We agree that we have only very weak evidence of a difference in recapture rates between adult and nymphal ticks. However, the point we wanted to make here is to state that the lower sample size of nymphs may have reduced our power to detect this difference. We have modified this aspect of the discussion accordingly (Discussion, paragraph 4).

i. Do you know anything about the demographic structure of this tick population? Are nymphal stages less abundant than adult stages? Why? Do the gulls remove ticks somehow?

We have no observational data on the selective removal of ticks in the nest by gulls, but our initial study on tick life stage dynamics suggested that adult ticks appear first during incubation period followed by nymphal ticks (Dupraz et al. 2017). At least during the early part of the season, adult ticks appear to be in higher abundance in the nest.

b. The behaviour of gulls at failed nests almost certainly differs from their behaviour at successful nests yet this is never discussed. Do the adults at failed nests remain and try and nest again? Or do they leave immediately?

We did not follow the behaviour of the gulls in detail because we only made weekly visits to the colony and adult birds are not colour-marked. However, if yellow-legged gulls behave like other Laridae, we would expect them to leave the nest site and start to prospect after failure (e.g ., Boulinier et al. 2008). In 2017, one gull pair laid a second clutch so some gull pairs do stay at the nest site at least initially after failure.

i. This information is needed to help interpret tick survival at/dispersal from failed nests, and could also explain why the detection probability of soft ticks was higher in failed nests (i.e. if the configuration/maintenance of failed nests differed due to different host behaviour associated with nest failure and success, which led to more ticks being detected?).

We agree that this information would be useful to help interpret results in relation to tick survival. However, we assume that ticks focus their activity at the nest area and likely feed off adults during incubation and chicks during early chick rearing. After failure, it may be that adult birds continue to defend the territory, but are likely indifferent to the nest per se, unless they attempt to relay. To avoid speculation, we have not added these details.

References cited:

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