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Peer Review Information

Journal: Nature Ecology & Evolution
Manuscript Title: Patrick Kennedy
Corresponding author name(s): Diminishing returns drive altruists to help extended family

Reviewer Comments & Decisions:

Decision Letter, initial version:

3rd August 2020

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

Dear Patrick,

Your manuscript entitled "Diminishing returns drive altruists to help extended family" has now been seen by three reviewers, whose comments are attached. The reviewers have raised a number of concerns which will need to be addressed before we can offer publication in Nature Ecology & Evolution. We will therefore need to see your responses to the criticisms raised and to some editorial concerns, along with a revised manuscript, before we can reach a final decision regarding publication.

You will see that reviewers would like you to broaden the discussion and Reviewer #1 in particular has detailed comments about that. We encourage you to follow their suggestions and note that we have a 3500 word limit for our Articles, which gives you the opportunity to expand the text.

We therefore invite you to revise your manuscript taking into account all reviewer and editor comments. Please highlight all changes in the manuscript text file in Microsoft Word format.

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

When revising your manuscript:

* Include a “Response to reviewers” document detailing, point-by-point, how you addressed each reviewer comment. If no action was taken to address a point, you must provide a compelling

argument. This response will be sent back to the reviewers along with the revised manuscript.

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

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

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

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Note: This URL links to your confidential home page and associated information about manuscripts you may have submitted, or that you are reviewing for us. If you wish to forward this email to co-authors, please delete the link to your homepage.

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

Nature Ecology & Evolution is committed to improving transparency in authorship. As part of our efforts in this direction, we are now requesting that all authors identified as ‘corresponding author’ on published papers create and link their Open Researcher and Contributor Identifier (ORCID) with their account on the Manuscript Tracking System (MTS), prior to acceptance. ORCID helps the scientific community achieve unambiguous attribution of all scholarly contributions. You can create and link your ORCID from the home page of the MTS by clicking on ‘Modify my Springer Nature account’. For more information please visit please visit www.springernature.com/orcid.

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

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

Yours sincerely,

[REDACTED]

Reviewer expertise:

Reviewer #1: social evolution, empirical approach

Reviewer #2: social evolution theory, including wasps

Reviewer #3: social evolution theory and experiments, including wasps

Reviewers' comments:

Reviewer #1 (Remarks to the Author):

I must first apologize to the authors for the two-week delay in reviewing this paper, which was due to a serious medical emergency in my family. I am glad that the editors allowed me the time to review it, though, because I really enjoyed reading this interesting and well-conceived paper. It elegantly tests three hypotheses to explain “drifting” behavior in workers in a Neotropical paper wasp. As outlined in the introduction, the paradox of drifting is that individual workers occasionally help at multiple nests simultaneously or at nests to which they are not closely related, even when nests of higher relatedness are available. The paper first presents mathematical arguments to show that two possible hypotheses – bet-hedging and indirect reciprocity – probably do not explain drifting behavior, whereas the third – diminishing returns on cooperative behavior with worker number – can. Empirical evidence from Polistes canadensis colonies in Panama then shows that colonies do indeed experience diminishing returns on worker investment with increasing worker number, consistent with the hypothesis. The third section of the paper claims to show that the spatial arrangements of local colonies can realistically promote drifting; although I don’t doubt the findings, this section is so brief, and the methods so abbreviated, that I confess I did not get much out of it. Overall, although I am an empiricist rather than a theoretician, I found the paper easy to follow, nicely grounded in biology, and quite convincing.

Given my lack of expertise in mathematical modeling, my comments have more to do with the biological context of the paper rather than the methods. First, the paper is very short (<2200 words); while admirably concise, there were many places that I thought needed some additional explanation. Basic information on the natural history of this species and on spatial kin structure among neighboring colonies would be particularly helpful.

Second, I occasionally got the feeling that the authors were using overly complicated techniques (or at least, overly complicated language) to explain rather simple concepts. This is especially true of the empirical section. Even the central message of the paper – that diminishing fitness returns to the colony can favor helping at less closely related colonies – boils down to a very simple demonstration of Hamilton’s Rule. This is made very clear by eq. 4.12 in the supplementary information (line 738), but never stated in the main text. To me, this is important because it implies that (somewhat contrary to the opening claims of the abstract and introduction), genetic relatedness between worker and colony is still crucial in maintaining drifting, and that relatedness between worker and colony must be non-zero (i.e. the diminishing returns hypothesis cannot explain drifting by workers if they are entirely unrelated to the colonies that they help). This doesn’t make the paper any less interesting, but I think it’s important to acknowledge that the findings lie solidly in the realm of traditional kin selection theory. Similarly, spatial kin structuring between neighboring colonies would seem essential to the last section of the paper, but is not adequately treated. That section instead invokes competition between neighboring colonies/workers, but there is no biological context in the paper for understanding what such competitive effects would look like (what are they competing over?).

Finally, the brevity of the paper also short-changes references to the literature. There is almost no discussion of similar phenomena in other social species (i.e. diminishing returns with group size) and little discussion of how widely this might be applicable in other social insects. Again, biological context is largely missing. I think that these pieces can be easily filled in, and that this paper will make a valuable and thoughtful addition to the literature on cooperation and helping behavior in social animals.

Line-by-line comments:

19: the abstract would be immeasurably stronger if it included a brief description of exactly which returns are diminishing, and why. Lines 52-54 provide a much clearer statement of the main findings; this should be in the abstract as well.
59-76: I am not sure whether the mathematical evidence is the same, but there are several papers in the ornithological literature that make a similar argument: that bet-hedging cannot explain patterns of brood parasitism in birds (i.e., that it is not adaptive to spread risk by parasitizing multiple nests). The argument that I have seen is that selection on a trait depends on the average fitness for all individuals carrying that trait. So the average fitness of a drifter that helps at just one nest should be equal to the average fitness of a drifter that helps at multiple nests, which eliminates any possible advantage of risk-spreading (see Bulmer 1984, Hopper et al. 2003). Your finding that this whole argument depends on (likely rare) fluctuations in the entire population's average reproductive success (w) seems entirely consistent with this.
77-79: I agree with the authors that there seems to be no a priori reason to expect that only colonies that produce drifters should accept them. However, it would be interesting to know whether, empirically, colonies ever *reject* drifters, and whether such behavior is linked to the incidence of non-cooperative behaviors like (for example) parasitism.
86-103: Although I am not a modeler, this seems to me consistent with the general outlines of Hamilton's rule: if the benefits of helping (to the recipient colony) decrease with the number of workers helping, then a lower coefficient of relatedness between worker and colony can still be evolutionarily stable. Crucially, though, this should not extend to entirely unrelated colonies (r ~0), unless some sort of direct fitness benefit is also possible.
122-124: Basic information on the breeding biology of this species is needed here. What is colony size? Single foundress or multiple? What do workers actually do – how do they help raise the brood? Are direct fitness benefits like parasitism or nest inheritance possible?
137: Fig 2. I understand the rationale behind the Markov model, but it's not clear to me why transitions to death are equivalent to transitions back to the egg stage.
144-162: The basic idea here – that the value of a worker to the brood diminishes as the number of workers increases – is straightforward enough, and the slopes of Fig 3d show the diminishing returns. But it is not clear how the empirical observations contributed to the simulations. I think lines 125-134, rather than emphasizing the large sample sizes of observations, should state more clearly that the aim was to use empirical data to correlate the rate of development in a brood (from egg to adult) to the size of the brood and the number of workers. I find the left panels in Fig 3 very hard to interpret; the right panels are much more illustrative, but the y axis labels could be more clearly explained (for example, the y axis "Payoff" in Fig. 3F – is this from the inclusive fitness perspective of the colony being helped? The individual worker who is added to the colony?)
171-177: Does this result come about because of kin structuring among nearby colonies? It would seem that the diminishing returns argument depends on some non-zero level of relatedness, such that correlations between mean colony-drifter relatedness and spatial distance would be very important.

Reviewer #2 (Remarks to the Author):

See attached file.

Up front, this paper deserves to be published in Nature Ecology & Evolution but not in its current state.

In this study the authors explore the conditions under which *drifting* of workers between haplodiploid colonies can evolve. According to their analytical modelling of three hypotheses, only diminishing returns can provide a selective environment where drifting can arise and back this qualitative result with experimental data. Being a theoretician, I refuse to comment on the validity of the experimental setup and its analysis. Paradoxically, the paragraph on lines 144-162 instantly convinced me of the value of this manuscript. This is a welcomed step away from the per-capita approach earlier studies have made and this is *the paper* I wish was published a few years ago when writing about diminishing returns in helping.

However, the paper is not ready to be published because of the way the models are explained and notated. I focused on the diminishing returns model but could not follow it through. The equations have either typos, pure mistakes, or are lacking explanations of what is being done. All in all, the paper felt very unpolished.

My main concern is whether the analysis considers if the size of the workforce is at a stable equilibrium before drifting evolves. It would benefit the reader if this were discussed and explained along with the requirement of variation in worker numbers for drifting to be beneficial in the main text.

I am confused about some of the variables and their definitions. While it is reasonable to have overlaps in notation, especially when so many are needed, I feel that some used variables should retain their unique definitions while some are needlessly relabelled between treatments. At least the symbols used in the main text should retain their uniqueness.

Rest of the comments are in no particular order and the numbers refer to lines.

66, 67, 89, 303, 511 A sentence should not start with a symbol.

It would benefit the reader if the values used for the example on lines 98-103 were the same as in one of the points in Fig. 1f. I also do not see why 3.5 should be considered as *mild* value for T.

Avoid using superscripts (lines 634-635) as they can be confused with exponents, especially if they are left as italics.

523 *multiplying -> dividing*

Overbars, for example on line 485, should just be over the variable and not extend over the indexes.

Table S3 states that $w_{x,j}$ is the absolute fitness of individual j **if** it develops as a female/male. However, the probability of developing as either female or male is embedded in the $w_{x,j}$ terms (S2.2 and S2.4), and the remaining part ($(1-x)K_j$ for the female for example) is the absolute fitness of individual j if it develops as a female.

Symbol $\mathbb{C}$ is reserved for complex numbers and should not be used for covariance.

Similarly, symbol π is reserved for pi and Π for a sequence product and should not be used for anything else.

Symbol ϕ is defined in Table S3 as relative group size of the colony and on line 462 as relative worker number. Later, ϕ is used for transitions (line 589) and N as workforce size. Could these be somehow unified for clarity?

Some indexes should be upright instead of italics. For example, H and L used in equation 1.6 as they present words High and Low.

Variable X_1 is the average level of altruistic sterility in the focal nest (line 475) and X_2 in the partner nest. Should Equation 3.1 have X_1 instead of $\bar{x}$ and Equation 3.2 have X_2 instead of $\bar{x}$ (like Equation S2.2 suggests)?

Should Equations 3.3 and 3.4 use z instead of $\bar{z}$ like in Equations 3.1 and 3.2?

Variable m is the focal individual's acceptance of drifters (Table S3). Should Equation 3.4 have $\bar{m}$ instead of m?

Treatment of colony types versus individuals should be clearer. For example, in the Supplementary lines 42-46 j is said to represent both colony type and individual.

In the Supplementary line 62 variable g is said to denote trait value, should this be genic value and then assume 1:1 genotype-phenotype mapping?

Indexing and term usage for *focal*, *donor*, *recipient*, *partner*, and *home* should be unified and only one pair used throughout the manuscript if possible.

757 Should the uppercase H be lowercase?

Use SetDirectory[NotebookDirectory[]]; instead of SetDirectory["/Users/patri/Desktop/rJAGS Output - 19-09-2019"]; in the submitted Mathematica code.

Suggestions for the authors that can be ignored.

8 *apparently -> seemingly*

33, 36, 40, 202, 207 To me *primitively eusocial* is a more familiar term than *simple eusociality*. However, there has been debate on this terminology and I am happy with either as long as you have made a conscious choice.

Signed,

Petri Rautiala

Reviewer #3 (Remarks to the Author):

This is a well written and well executed ms presenting a theoretical exploration of the conditions that can favour ‘drifting’ or helping at multiple nests. The paper presents three theoretical analyses which suggest that diminishing returns provides the most plausible explanation for drifting. This is accompanied by a detailed analysis of one Polistes species in which drifiting is very common. The empirical results show that the efficiency of nests in raising offspring to adulthood increases with group size at a decelerating rates. Thus the case study shows diminishing returns. Finally there is an exploration of spatial structure, showing that selection for drifting is stronger when helpers help at a smaller scale than the scale of at which competition occurs.

Each component of the ms is interesting and technically accomplished, and I feel that this is useful in helping to understand the conditions that favour drifting. However, the ms is slightly frustrating at present. The authors seems to me to oversell the drifting phenomenon at the outset, and then restrict their discussion to single underwhelming paragraph. I think the paper would be much stronger if a few things were tightened up.

1. The generality of the phenomenon.
1.1 Line 32 onward seems like you want to imply that the idea that social insect colonies are fortresses is wrong in some way. Yet nearly all of your examples of drifting appear to be references to Polistes species, except one reference to a paper on unicolonial ants. But the unicolonial ant case doesn’t seem to fit the assumptions of the systems that the authors are trying to model – at least in the Helantera et al paper where it is argued that indiscriminate helping may be due to perceived high relatedness at foreign and home nests (the conditions that favour bet hedging in model 1).

1.2 Moreover, the introduction glosses over the observation that many (most) Polistes don’t show drifting – group members are highly aggressive to intruders from neighbouring groups. Presumably you might predict on the basis of your model that these species (e.g. P. dominula) don’t show diminishing returns? That would offer up a nice strong falsifying test, to go with your confirmatory one, wouldn’t it? Or would you be wary of making this prediction? Note these other Polistes also nest in clusters as per your spatial model.

Obviously a much stronger test would be to include two or more systems, with and one without drifting, but I understand that this isn't data that you can just magic up from somewhere. However it would be good to point the way to a stronger test in your paper.

1.3. I think you should point out that diminishing returns are extremely common in social insects – where it even has a name, the reproductivity effect. So why isn’t drifting more common?

A stronger ms would be more transparent about the extent of this phenomenon, whether and why it is certain Polistes only that offer good systems for this modelling exercise. Just some better attempt to give biological context and perspective on this problem. It would not weaken the manuscript to be up front and honest about the frequency (or rarity) of drifting, and to provide some commentary as to why it is restricted to certain systems.

2. The broader importance of diminishing returns in models of social evolution. It might be nice to try to reach across to other areas in behavioural ecology where diminishing returns have been highlighted as important, e.g.reproductive skew theory (Cant & Johnstone 1999 Behav Ecol Costly young) and cooperation theory (Foster 2004 JEB Diminishign returns in social evolution). In both cases diminishing returns result in 'sharing' of benefits. The authors obviously have much theoretical strength – can you pull out the overarching principle at work here and comment on its generality in social evolution. In general I felt the last para was a bit short and rushed – maybe due to word limits– but the paper has a lot of ideas that are modelled, and could use more space to interpret the broader implications and place the results in context with what is known about the diversity of helping systems in social insects and other taxa.

********************END********************

Author Rebuttal to Initial comments

Response to Reviewers

Diminishing returns drive altruists to help extended family

Thank you to the three reviewers for their positive and constructive comments, which have improved the manuscript. We provide our responses in bold beneath each comment, with line numbers referring to the revised MS, where changes are highlighted in blue.

Reviewer 1:

I must first apologize to the authors for the two-week delay in reviewing this paper, which was due to a serious medical emergency in my family. I am glad that the editors allowed me the time to review it, though, because I really enjoyed reading this interesting and well-conceived paper. It elegantly tests three hypotheses to explain "drifting" behavior in workers in a Neotropical paper wasp. As outlined in the introduction, the paradox of drifting is that individual workers occasionally help at multiple nests simultaneously or at nests to which they are not closely related, even when nests of higher relatedness are available. The paper first presents mathematical arguments to show that two possible hypotheses – bet-hedging and indirect reciprocity – probably do not explain drifting behavior, whereas the third – diminishing returns on cooperative behavior with worker number – can. Empirical evidence from *Polistes canadensis* colonies in Panama then shows that colonies do indeed experience diminishing returns on worker investment with increasing worker number, consistent with the hypothesis. The third section of the paper claims to show that the spatial arrangements of local colonies can realistically promote drifting; although I don't doubt the findings, this section is so brief, and the methods so abbreviated, that I confess I did not get much out of it. Overall, although I am an empiricist rather than a theoretician, I found the paper easy to follow, nicely grounded in biology, and quite convincing.

We thank the reviewer for the supportive comments. In response to the point that the third section of the paper (the spatial simulation section) was too abbreviated, we have expanded the main text to describe more fully the simulated population (lines 201–216), the six treatments we consider (lines 217–223), and the biological implications (lines 223–227).

Given my lack of expertise in mathematical modeling, my comments have more to do with the biological context of the paper rather than the methods.

First, the paper is very short (<2200 words); while admirably concise, there were many places that I thought needed some additional explanation. Basic information on the natural history of this species and on spatial kin structure among neighboring colonies would be particularly helpful.

We have added a description of the natural history of *Polistes canadensis* (lines 145–151), describing the monogynous dominance hierarchies (lines 145–148), the types of tasks workers perform (lines 148-150), and typical colony sizes (lines 146-147). The most relevant reference for spatial kin structure among neighbouring colonies is Sumner et al. (2007), who found $r = 0.56 \pm 0.14$ of drifters towards eggs on their natal nest and $r = 0.19 \pm 0.05$ towards eggs on nests in their 'drifter group' (line 144). The extent of female and male philopatry in *P. canadensis* awaits genetic analyses; we have tried to remain agnostic (e.g., considering both global and local nest-founding in the simulation model, lines 199-229). In the Discussion, we have also added more natural history, especially in comparing tropical versus temperate *Polistes* wasps (lines 293–304), and we cite Parsons et al. (2019) (line 304) in describing spatial kin structure in the related temperate species *P. dominula*; a similarly fine-scale genetic analysis of spatial kin structure is still needed in *P. canadensis*.

Second, I occasionally got the feeling that the authors were using overly complicated techniques (or at least, overly complicated language) to explain rather simple concepts. This is especially true of the empirical section. Even the central message of the paper – that diminishing fitness returns to the colony can favor helping at less closely related colonies – boils down to a very simple demonstration of Hamilton's Rule. This is made very clear by eq. 4.12 in the supplementary information (line 738), but never stated in the main text. To me, this is important because it implies that (somewhat contrary to the opening claims of the abstract and introduction), genetic relatedness between worker and colony is still crucial in maintaining drifting, and that relatedness between worker and colony must be non-zero (i.e. the diminishing returns hypothesis cannot explain drifting by workers if they are entirely unrelated to the colonies that they help). This doesn't make the paper any less interesting, but I think it's important to acknowledge that the findings lie solidly in the realm of traditional kin selection theory.

We have been through the manuscript carefully scrutinising for cases of overly complicated language, and simplified where possible. For instance, we have expanded on the meaning of *"payoff"* (lines 185–186), describing how it can be seen as *"an empirical estimate of the benefit b in Hamilton's rule"* (line 186). We have also simplified *"predicted marginal change in colony productivity"* to *"predicted payoff"* (line 189). To make the purpose of the longitudinal model clearer, we have added *"We aimed to assess how a colony's success at producing new adults is associated with the numbers of worker and brood on the colony"* (lines 152–153).

We agree that diminishing returns offers a simple and intuitive explanation for cooperative drifting as predicted by Hamilton's rule, and relatedness is crucial. To make this clearer, we have added *"as potential to help home recipients declines, diversion of altruism towards more-distantly-related recipients can satisfy Hamilton's rule (increase in benefit b more than compensates for the decrease in relatedness r)"* (lines 90–92). To highlight that relatedness is still important, we have added *"to the (nonzero) proportions…"* (line 100). The Discussion emphasises that nonzero relatedness is required: "*Under positive kinship, spatial kin clustering, and diminishing returns…*" (lines 266–267).

Similarly, spatial kin structuring between neighboring colonies would seem essential to the last section of the paper, but is not adequately treated. That section instead invokes competition between neighboring colonies/workers, but there is no biological context in the paper for understanding what such competitive effects would look like (what are they competing over?).

We have expanded this section and now describe the sources of competition in the simulation: lottery competition among males for mating (line 209) and lottery competition among eligible reproductive females to colonise recently available nest sites (lines 206–209). In the model, a new opportunity for nesting arises, and competitors who have produced more females are more likely to have one of their daughters be the successful coloniser. Although this is naturally framed in terms of nest-site saturation where only one nest is able to be built, it could be seen as many nests being founded locally, but only one ultimately surviving in that spatial 'cell' of simulated landscape to produce offspring. Female 'eligibility' to colonise the new nest site depends on the presence or absence of natal philopatry (lines 206–209), which is crucial for the build-up of spatial kin structure (lines 223–227). In the simulation results shown in Fig. 4, global female dispersal (Fig. 4c,f) does not allow kin structuring, and drifting consequently fails to invade. To highlight this, we have expanded Figure 4 accordingly, showing the six treatments in the simulation.

Finally, the brevity of the paper also short-changes references to the literature. There is almost no discussion of similar phenomena in other social species (i.e. diminishing returns with group size) and little discussion of how widely this might be applicable in other social insects. Again, biological context is largely missing. I think that these pieces can be easily filled in, and that this paper will make a valuable and thoughtful addition to the literature on cooperation and helping behavior in social animals.

We agree that the original submission did not provide enough biological context (and a similar comment was also made by Reviewer 3). We have added extensively to the Discussion, highlighting Michener's paradox and findings in other species on diminishing returns with group size (lines 285–292), suggesting potential reasons why there may be interspecific variation in the levels of drifting among primitively social insects (lines 296–305), discussing ant supercolonies (lines 306–319), and citing other effects of diminishing returns to cooperation in biology more broadly (lines 329–331).

Line-by-line comments:

19: the abstract would be immeasurably stronger if it included a brief description of exactly which returns are diminishing, and why. Lines 52-54 provide a much clearer statement of the main findings; this should be in the abstract as well.

We have added (a slightly reworded version of) the original lines 52–54 to the Abstract (lines 14–17): *"As the worker-to-brood ratio rises on a worker's home colony, the predicted marginal benefit of a worker for expected colony productivity diminishes. Helping on related colonies can allow effort to focus upon related brood that are more in need of care."*

59-76: I am not sure whether the mathematical evidence is the same, but there are several papers in the ornithological literature that make a similar argument: that bet-hedging cannot explain patterns of brood parasitism in birds (i.e., that it is not adaptive to spread risk by parasitizing multiple nests). The argument that I have seen is that selection on a trait depends on the average fitness for all individuals carrying that trait. So the average fitness of a drifter that helps at just one nest should be equal to the average fitness of a drifter that helps at multiple nests, which eliminates any possible advantage of risk-spreading (see Bulmer 1984, Hopper et al. 2003). Your finding that this whole argument depends on (likely rare) fluctuations in the entire population's average reproductive success (w) seems entirely consistent with this.

Thank you for suggesting that we point to the parallel examples, which are very relevant. We have added "*The same logic underpins why bet-hedging against randomly occurring clutch failure is an unlikely explanation for birds distributing eggs over multiple nests or parasitoids distributing eggs over multiple hosts*" (lines 72–75), citing Bulmer (1984) for birds and Hopper et al. (2003) for parasitoids.

77-79: I agree with the authors that there seems to be no a priori reason to expect that only colonies that produce drifters should accept them. However, it would be interesting to know whether, empirically, colonies ever *reject* drifters, and whether such behavior is linked to the incidence of non-cooperative behaviors like (for example) parasitism.

This is a fascinating question, and something that we have begun to address in a separate manuscript on the closely related species *P. satan*. Colonies are broadly accepting, but do reject some incoming drifters. However, the extent to which colonies in these species make tactical decisions over whether to accept drifters who may be voluntarily cooperative remains unresolved. We have added this point to the Discussion as a focus for the future: "*…investigating how discriminating workers are in evaluating incoming drifters, and whether workers adjust acceptance thresholds (m) adaptively when the colony is in greater need*" (lines 321–323).

86-103: Although I am not a modeler, this seems to me consistent with the general outlines of

Hamilton's rule: if the benefits of helping (to the recipient colony) decrease with the number of workers helping, then a lower coefficient of relatedness between worker and colony can still be evolutionarily stable. Crucially, though, this should not extend to entirely unrelated colonies (r ~0), unless some sort of direct fitness benefit is also possible.

Absolutely. To make this clear, we have added "*as potential to help home recipients declines, diversion of altruism towards more-distantly-related recipients can satisfy Hamilton's rule (increase in benefit b more than compensates for the decrease in relatedness r)*" (lines 90–92).

122-124: Basic information on the breeding biology of this species is needed here. What is colony size? Single foundress or multiple? What do workers actually do – how do they help raise the brood? Are direct fitness benefits like parasitism or nest inheritance possible?

We have added this information on lines 145–151.

137: Fig 2. I understand the rationale behind the Markov model, but it's not clear to me why transitions to death are equivalent to transitions back to the egg stage.

The aim is to look at the individual nest cell, rather than the brood individual, as this is ultimately what the workers should care about: how frequently does a brood cell produce a new adult? There may be several cycles of larval death and replacement until a new adult is produced successfully in a cell, which means that minimising the level of brood death is important for workers. To avoid the analysis being confounded by any failures in egg-laying (which may be related to the fecundity or dominance status of the queen, rather than the efforts of the workers), we made the assumption in calculating the 'idealised' expected first passage time through the Markov chain of cell states that death leads directly to a new egg, which we take as a way of distilling out the plausible effects of workers from extraneous variation introduced by queen behaviour. We have added this point to the caption of Fig. 2 (lines 171–172). We describe the rationale for this analytical step in Section 4.5 of the Methods (lines 922–926), focusing on the "*per-cell efficiency without the confounding effect of variation between queens in the rate at which replacement eggs are laid following the death of larvae*". An important focus for future fieldwork would be consideration of the extent to which the value of a colony to drifters depends on queen variables (fertility, dominance, age, etc.).

144-162: The basic idea here – that the value of a worker to the brood diminishes as the number of workers increases – is straightforward enough, and the slopes of Fig 3d show the diminishing returns. But it is not clear how the empirical observations contributed to the simulations. I think lines 125-134, rather than emphasizing the large sample sizes of observations, should state more clearly that the aim was to use empirical data to correlate the rate of development in a brood (from egg to adult) to the size of the brood and the number of workers. I find the left panels in Fig 3 very hard to interpret; the right panels are much more illustrative, but the y axis labels could be more clearly explained (for example, the y axis "Payoff" in Fig. 3F – is this from the inclusive fitness perspective of the colony being helped? The individual worker who is added to the colony?)

At the start of the relevant paragraph (lines 152–153), we have added: "*We aimed to assess how a colony's success at producing new adults is associated with the numbers of workers and brood on the colony.*" To make the '*payoff*' term in Fig. 3 clearer, we have added (lines 185–188): "*The 'payoff' in Fig. 3e,f represents an empirical estimate of the benefit b in Hamilton's rule from working on a colony of the given size. An investment in a partner colony 2 is in the inclusive-fitness interest of a worker from a home colony 1 if $r_2 b_2 > r_1 b_1$ (assuming equal direct fitness costs from altruism on all colonies).*" Similarly, in the caption to Fig. 3, we more explicitly define '*payoff*': "*Slope of predicted whole-colony productivity with respect to group size, representing predicted effect of adding a new worker (the 'payoff' provided to the recipients), an empirical*

***estimate of the potential benefit 'payoff' b in Hamilton's rule"* (lines 242–245). To make the y-axes clearer in the caption, we have also added to the description of "*Adults per day*" in Fig. 3c: "*…given the eMFPT values*" (line 241), to highlight that the panels build iteratively on each other.**

171-177: Does this result come about because of kin structuring among nearby colonies? It would seem that the diminishing returns argument depends on some non-zero level of relatedness, such that correlations between mean colony-drifter relatedness and spatial distance would be very important.

We have expanded our description of the simulation model, making the role of spatial kin structuring clearer: mean colony–drifter relatedness and spatial distance are crucial, as long as spatial kin structuring does not bring close kin into so much competition (for nest sites and mating) with each other than it counteracts the effect of closer relatedness between neighbours (lines 223–227).

Reviewer 2 (Dr Petri Rautiala):

Up front, this paper deserves to be published in Nature Ecology & Evolution but not in its current state.

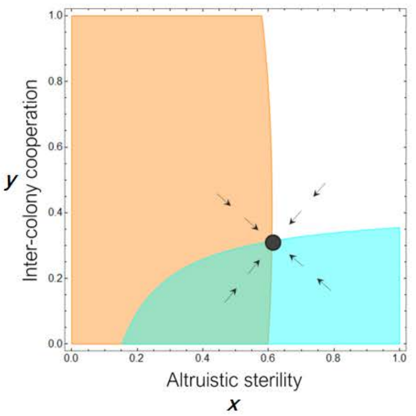
In this study the authors explore the conditions under which drifting of workers between haplodiploid colonies can evolve. According to their analytical modelling of three hypotheses, only diminishing returns can provide a selective environment where drifting can arise and back this qualitative result with experimental data. Being a theoretician, I refuse to comment on the validity of the experimental setup and its analysis. Paradoxically, the paragraph on lines 144-162 instantly convinced me of the value of this manuscript. This is a welcomed step away from the per-capita approach earlier studies have made and this is the paper I wish was published a few years ago when writing about diminishing returns in helping.

However, the paper is not ready to be published because of the way the models are explained and notated. I focused on the diminishing returns model but could not follow it through. The equations have either typos, pure mistakes, or are lacking explanations of what is being done. All in all, the paper felt very unpolished.

My main concern is whether the analysis considers if the size of the workforce is at a stable equilibrium before drifting evolves. It would benefit the reader if this were discussed and explained along with the requirement of variation in worker numbers for drifting to be beneficial in the main text.

With respect to whether workforce size is at a stable equilibrium, the level of altruism (x) is largely insensitive to the level of drifting (y) in the model. This is because altruism level (a choice individuals make during development in our model) evolves based on expectation of worker survival, but drifting (a choice workers make after development in our model) evolves based on between-colony variances in worker survival (which is set by ψ and g). Drifting offers workers a way to reduce this variance, but the expectation remains the same. Empirically, workers face high variation between colonies in the size of the workforce (and worker-to-brood ratio), which we document in the white points in Fig. 3.

For reassurance that the drifting rate is not likely to lead to surprising changes in the size of the workforce, we solved for the joint ESS of worker sterility (x^*) and worker drifting (y^*). They settle at an internal equilibrium (here shown for arbitrary trait values):



Selection favours higher altruism (x) in the orange zone, and higher drifting (y) in the blue zone.

Accordingly, explicitly coevolving x and y does not lead to substantial changes in the prediction equilibrium x or y. To avoid adding unnecessary complication (involving describing selection on x) to the paper (which already has several analyses), we have not added this analysis in the text, but we provide the plot in this response to confirm that group-size evolution is not dramatically affected. To explain and discuss in the main text, we have added the following:

> ***"Help (h) enjoyed by each brood depends on the worker-to-brood ratio ψ in their colony, which can vary stochastically between and within colonies through time."*** **(lines 95–96).**
>
> ***"Differences in worker and brood number arise easily among P. canadensis colonies (Fig. 3a), which are subject to several sources of stochasticity. These include fluctuations in worker number due to the higher attrition rate of foraging workers, the frequent loss of brood to parasitoids, the presumed loss of brood due to disease (based on workers' hygienic removal of larvae), episodes of queen replacement, and so on. Fluctuations in brood cohort size translate into fluctuations in workforce size once they pupate."*** **(lines 279–284)**

Finally, to provide a more complete picture of how drifting level depends on workforce size, we have also added a new figure (Fig. S2), which plots the candidate ESS drifting levels y^* across different sex ratios and levels of female altruism, which collectively determine workforce size.

I am confused about some of the variables and their definitions. While it is reasonable to have overlaps in notation, especially when so many are needed, I feel that some used variables should retain their unique definitions while some are needlessly relabelled between treatments. At least the symbols used in the main text should retain their uniqueness.

Thank you for highlighting that we needed to be much tighter on the notation. We have ensured that the notation is more consistent throughout the paper (for instance, y now refers to drifting throughout the models). We have removed unnecessary notation (e.g., X_{f}, X_{d}, and $\overline{x}$ are now all just x, since we assume a common x for all nests). We have also removed overlapping notation used for different parameters in different models (e.g., the previous manuscript's H, τ, g, N, d).

A table of notation used in the theoretical models is now provided in the Supplementary Information (Table S1), which shows the elimination of overlap in different parameters.

Rest of the comments are in no particular order and the numbers refer to lines.

66, 67, 89, 303, 511 A sentence should not start with a symbol.

These sentences no longer start with symbols (e.g., lines 63, 65, and 95).

It would benefit the reader if the values used for the example on lines 98-103 were the same as in one of the points in Fig. 1f. I also do not see why 3.5 should be considered as mild value for T.

We have changed the example (lines 116–122) to $T = 4$, $g = 0.5$, $\phi = 1$, $x = 0.75$, and $z = 0.25$, which also appears in the (now updated) Fig. 1f. We have changed Fig. 1f to a contour plot of the candidate ESS drifting level y^*, which more intuitively shows the results.

Avoid using superscripts (lines 634-635) as they can be confused with exponents, especially if they are left as italics.

We have changed the superscripts to subscripts. For instance, the previous $\beta^{w}_{ij,\text{workers}}$ is now $\beta_{ij,\text{workers}|\text{w}}$ (where w denotes the within-colony component) in Equation 4.3 (lines 867–873).

523 multiplying -> dividing

This has been changed to "dividing" (line 750).

Overbars, for example on line 485, should just be over the variable and not extend over the indexes.

We have moved the indices outside of the overbars (e.g., $\bar{K}_1$, line 726).

Table S3 states that $w_{x,j}$ is the absolute fitness of individual j **if** it develops as a female/male. However, the probability of developing as either female or male is embedded in the $w_{x,j}$ terms (S2.2 and S2.4), and the remaining part ($(1-x)K_j$ for the female for example) is the absolute fitness of individual j if it develops as a female.

We have removed the $(1-z)$ and z terms, which were unnecessary as they cancel out during the derivation, so that the w terms now refer only to absolute fitness (e.g., Equations 3.1 and 3.2, lines 715–716).

Symbol $\mathbb{C}$ is reserved for complex numbers and should not be used for covariance.

We have replaced □ with Cov (lines 485, 539, 540, 541).

Similarly, symbol π is reserved for pi and Π for a sequence product and should not be used for anything else.

We have replaced π and Π with ω and Ω (e.g., lines 484 and 496).

Symbol ϕ is defined in Table S3 as relative group size of the colony and on line 462 as relative worker number. Later, ϕ is used for transitions (line 589) and N as workforce size. Could these be somehow unified for clarity?

We have changed ϕ to ψ in the theoretical model (e.g., line 699), and left ϕ as the transitions in the statistics (e.g., line 824). We have also switched N to ψ in Equation 4.12 of the statistics model.

Some indexes should be upright instead of italics. For example, H and L used in equation 1.6 as they present words High and Low.

To reduce the number of notations, we have replaced H and L with '1' and '2', respectively (e.g., Equation 1.5, line 562).

Variable X_1 is the average level of altruistic sterility in the focal nest (line 475) and X_2 in the partner nest. Should Equation 3.1 have X_1 instead of $\bar{x}$ and Equation 3.2 have X_2 instead of $\bar{x}$ (like Equation S2.2 suggests)?

We have simplified the model by assuming a common x for all colonies (lines 707–708).

Should Equations 3.3 and 3.4 use z instead of $\bar{z}$ like in Equations 3.1 and 3.2?

Since we do not analyse selection on the sex ratio and assume a common sex ratio for all nests (lines 707–708), we have simplified the model by assuming a common z for all brood (e.g., lines 722–723).

Variable m is the focal individual's acceptance of drifters (Table S3). Should Equation 3.4 have $\bar{m}$ instead of m?

Since we do not analyse selection on acceptance rates in the diminishing returns model, this is equivalent to assuming $\bar{m} = 1$. To simplify the model, we have therefore removed m and $\bar{m}$ from this analysis (e.g., Equation 3.4, line 720).

Treatment of colony types versus individuals should be clearer. For example, in the Supplementary lines 42-46 j is said to represent both colony type and individual.

We now use s to refer to colony type (e.g., Supplementary line 34) and j to refer to the actor role when describing the Taylor-Frank method (e.g., Supplementary line 56).

In the Supplementary line 62 variable g is said to denote trait value, should this be genic value and then assume 1:1 genotype-phenotype mapping?

This should have said "*genic value for a trait of interest*", which we have updated (Supplementary line 57), and we have added *"for trait value, we assume 1:1 genotype:phenotype mapping"* on Supplementary lines 57–58.

Indexing and term usage for focal, donor, recipient, partner, and home should be unified and only one pair used throughout the manuscript if possible.

We now use 'home' and 'partner' as the pair throughout the manuscript (e.g., lines 116–118, 121, 645, 698–700, 708–709). The term 'donor' appears in the indirect reciprocity model as a different category (line 604).

757 Should the uppercase H be lowercase?

For consistency with the analytical models, we have changed it to h (line 983).

Use SetDirectory[NotebookDirectory[]]; instead of SetDirectory["/Users/patri/Desktop/rJAGS Output - 19-09-2019"]; in the submitted Mathematica code.

We have changed this to SetDirectory[NotebookDirectory[]].

Suggestions for the authors that can be ignored.
8 apparently -> seemingly

We have changed this to "seemingly" (line 7).

33, 36, 40, 202, 207 To me primitively eusocial is a more familiar term than simple eusociality. However, there has been debate on this terminology and I am happy with either as long as you have made a conscious choice.

We have changed "simple eusocial" to "primitively eusocial" wherever the term appears in the manuscript (e.g., lines 28, 32, 36, 40, 264).

Signed,

Petri Rautiala

Reviewer 3:

This is a well written and well executed ms presenting a theoretical exploration of the conditions that can favour 'drifting' or helping at multiple nests. The paper presents three theoretical analyses which suggest that diminishing returns provides the most plausible explanation for drifting. This is accompanied by a detailed analysis of one *Polistes* species in which drifting is very common. The empirical results show that the efficiency of nests in raising offspring to adulthood increases with group size at a decelerating rates. Thus the case study shows diminishing returns. Finally there is an exploration of spatial structure, showing that selection for drifting is stronger when helpers help at a smaller scale than the scale of at which competition occurs.

Each component of the ms is interesting and technically accomplished, and I feel that this is useful in helping to understand the conditions that favour drifting. However, the ms is slightly frustrating at present. The authors seems to me to oversell the drifting phenomenon at the outset, and then restrict their discussion to single underwhelming paragraph. I think the paper would be much stronger if a few things were tightened up.

We have tempered the Introduction (as described in the next response), and have expanded the Discussion to seven paragraphs, comprising (1) a statement of our main results (lines 262–267), (2) a discussion of predictions and the parameters in the models (lines 268–284), (3) the link to Michener's paradox (lines 285–292), (4) possible explanations for differences between species (lines 293–305), (5) the link to supercolonial ants (lines 306–319), (6) testing by experiments (lines 320–328), and (7) other effects of diminishing returns in biology (lines 329–339).

1. The generality of the phenomenon.
1.1 Line 32 onward seems like you want to imply that the idea that social insect colonies are fortresses is wrong in some way. Yet nearly all of your examples of drifting appear to be references to *Polistes* species, except one reference to a paper on unicolonial ants. But the unicolonial ant case doesn't seem to fit the assumptions of the systems that the authors are trying to model – at least in

the Helantera et al paper where it is argued that indiscriminate helping may be due to perceived high relatedness at foreign and home nests (the conditions that favour bet hedging in model 1).

To avoid implying that we are criticising the (certainly correct) viewpoint that most social insect colonies are *"fortresses"*, we have removed *"are often viewed as"* and changed to "*Social insect colonies are often impenetrable fortresses*" (line 27). We have added "*However, in some species (especially primitively eusocial insects)...* " (line 27–28) before introducing drifting. We include a citation on unicolonial ants in the Introduction (line 28) to highlight the occurrence of general drifting-type behaviour before focusing on the primitively eusocial species in particular (line 32); accordingly, we have added "*in primitively eusocial insects*" (line 40) before introducing the three hypotheses we consider. We have also added a paragraph to the Discussion describing possible implications for the initial evolution of low-relatedness cooperation in unicolonial ants (lines 306–319), which is more likely due to polygyny (lines 316–318), and the difference between *Polistes*-style drifting and unicolonial ant drifting (lines 318–319).

1.2 Moreover, the introduction glosses over the observation that many (most) *Polistes* don't show drifting – group members are highly aggressive to intruders from neighbouring groups.

In the Introduction, we now say "*In some species...* " (line 27) and "*In some primitively eusocial Polistes paper wasps...* " (line 32). We now make the distinction with other *Polistes* much clearer in the Discussion, where we have added: *"However, the relatively high levels of drifting observed in Neotropical species such as P. canadensis contrast with, for example, the European wasp P. dominula, which also forms dense colony aggregations*[13] *but shows high aggression towards neighbours"* (lines 293–296). We have also added to the Discussion four potential reasons that may explain why drifting is not observed in species like *P. dominula* (lines 296–304), as detailed in the next comment.

Presumably you might predict on the basis of your model that these species (e.g. *P. dominula*) don't show diminishing returns? That would offer up a nice strong falsifying test, to go with your confirmatory one, wouldn't it? Or would you be wary of making this prediction? Note these other *Polistes* also nest in clusters as per your spatial model.

Thank you for pointing out that we should discuss why species like *P. dominula* lack drifting (lines 293–296) whilst species like *P. canadensis* have it. In the Discussion, we now suggest four (not mutually exclusive) hypotheses (lines 296–304), of which varying intensities of diminishing returns is one (lines 296–297). We also highlight the reviewer's point that *P. dominula* shows nest clustering (lines 295 and 303–304).

Obviously a much stronger test would be to include two or more systems, with and one without drifting, but I understand that this isn't data that you can just magic up from somewhere. However it would be good to point the way to a stronger test in your paper.

We agree that data from other primitively eusocial insects would be ideal, and we hope that these comparisons will be possible in the future. At the end of the paragraph discussing differences between *P. canadensis* and *P. dominula*, we say *"Direct comparisons between species with and without cooperative drifting are needed"* (lines 304–305). In terms of pointing towards stronger tests, we also include in the Discussion: "*Experimentally manipulating wild colony networks by adjusting worker-to-brood ratio (ψ) may offer future tests of whether workers make strategic adjustments to their investments (y)*" (lines 320–321).

1.3. I think you should point out that diminishing returns are extremely common in social insects – where it even has a name, the reproductivity effect. So why isn't drifting more common?

A stronger ms would be more transparent about the extent of this phenomenon, whether and why it is certain *Polistes* only that offer good systems for this modelling exercise. Just some better attempt to give biological context and perspective on this problem. It would not weaken the manuscript to be up front and honest about the frequency (or rarity) of drifting, and to provide some commentary as to why it is restricted to certain systems.

In the Introduction, we have added "*an effect first highlighted by Michener in 1964*" (line 50). We have added a paragraph to the Discussion on Michener's paradox (lines 285–292), highlighting that the reproductivity effect is common (lines 285–287, albeit not universal; line 287) but that previous analyses have tended to use snapshot estimates of per-capita productivity (line 289). Our Markov model instead incorporates the dynamic nature of brood development, and therefore offers a more realistic picture (lines 289–291). We now raise the question of why drifting is not more common on lines 293–296.

2. The broader importance of diminishing returns in models of social evolution. It might be nice to try to reach across to other areas in behavioural ecology where diminishing returns have been highlighted as important, e.g. reproductive skew theory (Cant & Johnstone 1999 Behav Ecol Costly young) and cooperation theory (Foster 2004 JEB Diminishing returns in social evolution). In both cases diminishing returns result in 'sharing' of benefits. The authors obviously have much theoretical strength – can you pull out the overarching principle at work here and comment on its generality in social evolution. In general I felt the last para was a bit short and rushed – maybe due to word limits– but the paper has a lot of ideas that are modelled, and could use more space to interpret the broader implications and place the results in context with what is known about the diversity of helping systems in social insects and other taxa.

The expanded Discussion now provides a stronger picture of the role of diminishing returns in biology, which has a broader scope than primitively eusocial workers alone (e.g., lines 263–264, 306–319, 329–331, and 336–341). We have added more context and links to other work on diminishing returns, including Cant & Johnstone (1999) and Foster (2004) in lines 329–331. In particular, we provide some additional historical context (which was cited in the original version, but not described in detail) on how in the 1980s Weigel and Schulman & Rubenstein developed ideas around diminishing returns as an explanation for divested altruism in response to Altmann's criticism of the 'proportional altruism' model (lines 336–339).

Decision Letter, first revision:

13th November 2020

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

Dear Patrick,

Your revised manuscript entitled "Diminishing returns drive altruists to help extended family" has now been seen by our reviewers, and in the light of their advice I am delighted to say that we can in principle offer to publish it. First, however, we would like you to revise your paper to ensure that it is as brief as possible and complies with our Guide to Authors at http://www.nature.com/natecolevol/info/final-submission.

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In particular, while checking through the manuscript and associated files, we noticed the following specific points which we will need you to address:

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2. Please include author names and affiliation in the article and indicate corresponding author(s).

3. Please include the heading 'Results'.

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We hope to hear from you within two weeks; please let us know if the revision process is likely to take longer.

Yours sincerely,
[REDACTED]

****
Reviewer Expertise:

Reviewer Comments:

Reviewer #1 (Remarks to the Author):

This paper, which I previously reviewed, provides an elegant test of three hypotheses to explain why Polistes workers occasionally "drift" to help at colonies containing less closely related individuals rather than staying to help closer relatives in their home colony. The revised version satisfactorily addresses all of the concerns I had about the first submission (including the overall framing of drifting behavior within an inclusive fitness framework, more detail on the natural history of Polistes, and expansion of the last section of the paper). The overall message of the paper -- that "r" is not the only term in Hamilton's rule; "b" also matters -- is eminently sensible. As with the first submission, I enjoyed the mix of empirical data, natural history, and theory, and think it will make a welcome contribution to the literature. I have no further suggestions. Signed, Christina Riehl

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Reviewer #2 was no able to review again but we have asked Reviewer #3 to check the responses to their comments.

Reviewer #3 (Remarks to the Author):

The authors have done an excellent job with this revision. I particularly appreciate the extended discussion where the authors have made made substantial additions to locate and explain their study in a wider context. The result is a very strong and rounded paper which is a valuable addition.

*******************END*******************

Final Decision Letter:

Dear Patrick,

We are pleased to inform you that your Article entitled "Diminishing returns drive altruists to help extended family", has now been accepted for publication in Nature Ecology & Evolution.

Before your manuscript is typeset, we will edit the text to ensure it is intelligible to our wide readership and conforms to house style. We look particularly carefully at the titles of all papers to ensure that they are relatively brief and understandable.

The subeditor may send you the edited text for your approval. Once your manuscript is typeset you will receive a link to your electronic proof via email within 20 working days, with a request to make any corrections within 48 hours. If you have queries at any point during the production process then please contact the production team at rjsproduction@springernature.com. Once your paper has been scheduled for online publication, the Nature press office will be in touch to confirm the details.

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