



Why are dominant females not always showing higher reproductive success? A preregistration of a meta-analysis on social mammals

Matthieu Paquet based on reviews by Bonaventura Majolo and 1 anonymous reviewer

A recommendation of:

Shivani, Elise Huchard, Dieter Lukas. **Preregistration - The effect of dominance rank on female reproductive success in social mammals (2020)** *In principle acceptance by PCI Ecology of the version 1.2 on 07 July*

2020. https://github.com/dieterlukas/FemaleDominanceReproduction_MetaAnalysis/blob/trunk/Preregistration_MetaAnalysis_RankSuccess.Rmd

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In social species conflicts among group members typically lead to the formation of dominance hierarchies with dominant individuals outcompeting other groups members and, in some extreme cases, suppressing reproduction of subordinates. It has therefore been typically assumed that dominant individuals have a higher breeding success than subordinates. However, previous work on mammals (mostly primates) revealed high variation, with some populations showing no evidence for a link between female dominance reproductive success, and a meta-analysis on primates suggests that the strength of this relationship is stronger for species with a longer lifespan [1]. Therefore, there is now a need to understand 1) whether dominance and reproductive success are generally associated across social mammals (and beyond) and 2) which factors explains the variation in the strength (and possibly direction) of this relationship. In their preregistration, Shivani et al. [2] plan to perform a meta-analysis on 86 social mammal species to address these two points. More specifically, they will investigate whether the relationship between female dominance and reproductive success vary according to life history traits (e.g. stronger for species with large litter size), ecological conditions (e.g. stronger when resources are limited) and the social environment (e.g. stronger for cooperative breeders than for plural breeders). The two reviewers and I were particularly positive and enthusiastic about this preregistration and only had minor comments that were nicely addressed by the authors. We found the background well-grounded in the existing literature and that the predictions were therefore clear and well-motivated. The methods were particularly transparent with a nicely annotated R script and the authors even simulated a dataset with the same structure as the actual data in order to make sure that the coding of the

data handling and statistical analyses were appropriate (without being tempted to look at model outputs from the true dataset). Perhaps one limitation to keep in mind once we will have the chance to look at the outcome of this study is that the dataset may not be fully representative of social species with dominance hierarchies. For example, the current dataset contains only one aquatic mammal (*Mirounga angustirostris*) as far as I can see, which is likely due to a lack of knowledge on such systems. Furthermore, not only mammals exhibit dominance hierarchies and it will be interesting to see if the results of the proposed study hold for other social taxa (and if not, what may explain their differences). That being said, the proposed study will already offer a much broader overview of the relationship between dominance and reproductive success in animal societies and a better understanding for its variation. The reviewers and I believe it will make an important contribution to the fields of socio-ecology and evolutionary ecology. I therefore strongly recommend this preregistration and we are particularly looking forward to seeing the outcome of this exciting study.

References

- [1] Majolo, B., Lehmann, J., de Bortoli Vizioli, A., & Schino, G. (2012). Fitness-related benefits of dominance in primates. *American journal of physical anthropology*, 147(4), 652-660. doi: [10.1002/ajpa.22031](https://doi.org/10.1002/ajpa.22031)
- [2] Shivani, Huchard, E., Lukas, D. (2020). Preregistration - The effect of dominance rank on female reproductive success in social mammals In principle acceptance by PCI Ecology of the version 1.2 on 07 July 2020. https://github.com/dieterlukas/FemaleDominanceReproductionMetaAnalysis/blob/trunk/PreregistrationMetaAnalysis_RankSuccess.Rmd

Reviewed by Bonaventura Majolo, 2020-06-25 11:11

Dear Editor,

the authors have satisfactorily addressed my comments with clear and detailed answers. I have no further comments and I believe their plan of analysis is accurate and powerful, in relation to the available literature. I look forward to see the completed study.

Kind regards

Reviewed by anonymous reviewer, 2020-07-03 15:12

I want to thank the authors for their careful considerations of my previous comments. I am happy with the changes and I am looking forward to read about their results.

Revision round #1

2020-05-14

Dear Authors,

Your preprint entitled "Preregistration - The effect of dominance rank on female reproductive success in social mammals" has now been reviewed and the reviewers' comments are appended below. As you will see, both reviewers are highly positive about the study and I share their views. Yet they have several minor comments that need to be addressed carefully before I can recommend your preprint.

Notably, reviewer one is concerned regarding the fact to incorporate together studies on both wild and captive individuals and suggest comparing estimates obtained from both types of studies. Also, both reviewers are concerned about the distinction between the effect of group size and the effect of population density and how to disentangle them. If I understand correctly the paragraph “Influence of study approach and other predictor variables”, both variables will be included in the same model (“For the variables reflecting the social environment, we will build multivariate models to assess potential pathways”). If so, this could be made clearer earlier on, for example in the beginning for the section “Analysis plan”, where it is stated “We will build separate models for each prediction”. Reviewer 2 also highlights that coalition formation and kinship likely covary. Would it be possible to include both variables in a single model in this case too to try to disentangle both effects? Both reviewers have a few other minor comments that you will find below.

Additionally, it was not clear to me from the document (although I highly appreciated the nicely annotated R script!) why two types of analyses are conducted (frequentist with the package Metafor and Bayesian with the package Rethinking). More particularly, it was unclear whether they are used to fit the same models (e.g. to compare results from both approaches) or if they are used to fit different models (e.g. because some types of models can be use with one approach but not the other) or to do different model checks. First it could be more precise what is meant by “estimating models”. Both estimating model fit and the effect of the predictor variables? Then what “subset of models” will be “estimated” using the Bayesian approach?

I look forward to read the revised version of this preregistration.

Best wishes,

Matthieu

Preprint

DOI: https://github.com/dieterlukas/FemaleDominanceReproduction_MetaAnalysis/blob/master/Preregistration_MetaAnalysis_RankSuccess.Rmd

Reviewed by [Bonaventura Majolo](#), 2020-05-13 17:33

The authors aim to analyse the effect of dominance rank on reproductive success in social mammals using a large data set based on published studies. Comparative analyses are a very effective tool to investigate biological phenomena and the authors have already published some excellent comparative work, so they are well equipped to achieve the goals of this study. The overall aim of the study and the need to investigate dominance effect across a large range of social mammals are well explained and would make an important contribution to socio-ecology. Their aims and predictions are very well grounded into the existing literature, interesting, and in several cases they will allow to have novel insights on the effect of dominance rank. The proposed methodology aims to use some of the most recent and powerful tools in meta-analytic and comparative analyses; the authors have clearly thought very carefully about their analyses and the variables to be included. I have only a few specific, but relatively minor comments:

In section C2, when the authors talk about “flexibility to quickly produce large numbers of offspring”, it was not clear to me whether they are referring to ‘flexibility’ in terms of short inter-birth interval, so that females can be pregnant multiple times if the ecological conditions are right, or to absence of breeding seasonality, or a combination of these two factors.

Prediction 3.3: I agree with the prediction, but I am curious to know whether the authors think they need to control for average group size when testing the effect of population density?

Prediction 4.5 & 4.6: these two predictions go in opposite directions, but kinship and coalition formation are often linked. I mean, if we look at what happens in primate species with female philopatry, where matrilineal play a key role on dominance rank, females from one kin group frequently form coalitions against members

of other matriline and often rank above (or below) members of other matriline. If so genetic similarity in a group and coalitions formation might not have opposite effects on reproductive success. Imagine, for example, a group where there are only two matriline (with low genetic diversity) and kin-biased coalitions are frequent: in these conditions both genetic similarity and coalition formation might have a positive effect of the benefits of higher dominance rank. This is something you might want to consider, depending on the taxa represented in the data set.

Methods: the authors list different measure of reproductive success to test their predictions, and reflecting data available in the literature. Maybe I missed this in the document, but I wasn't sure about what happens if they don't have enough data for a specific measure: would they combine multiple measures into one single reproductive benefit of dominance or would they exclude that variable from the analyses?

I hope these comments are useful. This looks a very interesting study and I look forward to see the results.

Reviewed by anonymous reviewer, 2020-05-12 17:07

The study "Preregistration - The effect of dominance rank on female reproductive success in social mammals" is very well designed and the authors propose a very interesting study that will result in publications that will generate a lot of interest among evolutionary ecologists and beyond. I think the background, the predictions and the proposed methods are very clear and follow the logic of pre-existing studies. However, I would like to add three minor comments regarding the predictions. (1) I am a little bit concerned about the fact that the authors also propose to include captive studies. Although fully accounted for in the models, I wonder how much this will impact their estimates of reproductive success, population densities and number of females per social group. The latter is particularly difficult to compare in cases where group sizes might be artificially created. I would suggest to include another control analysis where effect sizes of the different variables are compared between "captive" and "wild" study populations. (2) I am confused about the distinction between the two predictions P3.3 (Effects of dominance rank on reproductive success will be more pronounced in populations with high densities of individuals) and P4.4 (In plural breeding species, dominance will have stronger effects on reproductive success when the number of females in the group is smaller). I understand that P3.3 refers to overall population density and P4.4 to group members but both aspects are linked (depending the way how its calculated) but doesn't larger group size naturally lead to higher densities? (3) Also, predictions P4.3 (Dominance rank will have stronger effects on reproductive success in populations in which females are philopatric in comparison to populations where females disperse to breed) and P4.5 (Dominance rank will be more strongly associated with reproductive success in populations in which average relatedness among female group members is high) are very similar in terms of their underlying biological relevance and could be merged into one prediction?

Author's reply:

Dear PCI Managing Board and Recommender,

We thank you for the opportunity to revise our preregistration for pre-study peer review. Our version-tracked version of this revision is available at [our github repository] (https://github.com/dieterlukas/FemaleDominanceReproduction_MetaAnalysis/blob/trunk/Preregistration_MetaAnalysis_RankSuccess.Rmd). For peer-review, we also provide [an html website] (<https://dieterlukas.github.io/PreregistrationMetaAnalysisRankSuccess.html>) and a [pdf copy at the repository] (https://github.com/dieterlukas/FemaleDominanceReproduction_MetaAnalysis/blob/trunk/Preregistration_MetaAnalysis_RankSuccess.pdf) Photo credit goes to Alecia Carter (CC-BY 4.0) Please let us know if you have any questions or need further information. Many thanks for your support!

All our best, Shivani, Elise, and Dieter

Dear Authors, Your preprint entitled "Preregistration - The effect of dominance rank on female reproductive success in social mammals" has now been reviewed and the reviewers' comments are appended below. As you will see, both reviewers are highly positive about the study and I share their views. Yet they have several minor comments that need to be addressed carefully before I can recommend your preprint.

Reply: We are grateful to the editor and the reviewers for the constructive and helpful feedback! In response, we have made changes to our predictions, added clarifications to the description of the variables, and adjusted our analysis plan. Please find our detailed replies below.

Comment 1: Notably, reviewer one is concerned regarding the fact to incorporate together studies on both wild and captive individuals and suggest comparing estimates obtained from both types of studies.

Reply 1: We had included a check whether samples from wild individuals might show different relationships between dominance and reproductive success than samples from captive individuals. We predict lower effect sizes for captive than for wild populations (P1.5 (i)). We have now made it clearer that, if we indeed find such a difference, we will include captive/wild as a covariate in the additional models. In addition, we now account for the possibility that the influence of some variables on the strength of the effect of rank on reproductive success might differ in captive as compared to wild populations. We added the following (see also our reply to Comment 9):

Analysis Plan: Influence of approach: To the base model, we will add random effects reflecting the differences in approaches across studies (wild/captive; agonism/correlate; linear/categorical rank).

Influence of predictor variables: Studies performed on wild versus captive individuals and using different measures of reproductive success might not only differ in the overall strength of the effect of rank on reproductive success, but also in how other variables influence this effect. We therefore will build models in which both the intercept and the slopes can vary according to whether studies were performed in the wild/captivity and to how reproductive success was measured.

Comment 2: Also, both reviewers are concerned about the distinction between the effect of group size and the effect of population density and how to disentangle them. If I understand correctly the paragraph "Influence of study approach and other predictor variables", both variables will be included in the same model ("For the variables reflecting the social environment, we will build multivariate models to assess potential pathways"). If so, this could be made clearer earlier on, for example in the beginning for the section "Analysis plan", where it is stated "We will build separate models for each prediction".

Reply 2: We realize that we had not explicitly considered and represented the potential interactions among some of the predictor variables. We have now expanded this in the predictions and the analysis section. In particular, we went through all variables to identify instances where variables might have influences that are in opposite directions (such as for population density and group size) and list them explicitly in the analysis plan. Please see our reply to Comment 6.

Comment 3: Reviewer 2 also highlights that coalition formation and kinship likely covary. Would it be possible to include both variables in a single model in this case too to try to disentangle both effects?

Reply 3: Our initial idea for this preregistration was to assess the possible direct influence of a variety of variables that had previously been suggested to shape the potential benefits that females might gain from high social rank. We recognize that there are likely several pathways that might link the various variables we are testing: for example, as suggested by the reviewer, coalitions are more likely to occur in species with a given kinship structure among group females; another example could be that species might adopt a specific social system depending on environmental harshness and/or the resources they feed on. Because there is a large number of possible pathways, we decided that, at this stage, we would narrow down the possibilities by first assessing simple associations before focusing on specific likely covariations (including those highlighted here and by the reviewers). We added the following:

Predictions: All our predictions consider the potential direct influence of a specific variable on the size of the effect of dominance rank on reproductive success. The predictions present the direction of the influence we consider a-priori most likely. We will report all results, but in instances where influences are opposite to what we predict further studies will be necessary to place these results in context. In addition, several of the variables we will include are likely to influence each other. Accordingly, analyses with single variables might not necessarily show the predicted direct influence even if it is present (e.g. there might not be a positive relationship between a social system and the size of the effects if species with this particular social system primarily occur in environments where the size of the effect is expected to be smaller). While deciphering all the potential relationships among the variables we include is beyond the scope of this study, we will also perform analyses accounting for these potential interactions among variables. We focus on instances where we expect that one variable might remove or change the direction of the influence of another variable, and present these at the end of the predictions.

At the end of the predictions we added a section on Potential interactions among predictor variables

Comment 4: Additionally, it was not clear to me from the document (although I highly appreciated the nicely annotated R script!) why two types of analyses are conducted (frequentist with the package Metafor and Bayesian with the package Rethinking). More particularly, it was unclear whether they are used to fit the same models (e.g. to compare results from both approaches) or if they are used to fit different models (e.g. because some types of models can be use with one approach but not the other) or to do different model checks. First it could be more precise what is meant by "estimating models". Both estimating model fit and the effect of the predictor variables? Then what "subset of models" will be "estimated" using the Bayesian approach?

Reply 4: There are different philosophies and possibilities with the two different types of analyses. A main reason why we decided to plan on performing both the frequentist and the Bayesian approach was to assess the robustness of any associations we might find. The 'metafor' approach is well established in meta-analyses, whereas Bayesian analyses are relatively recent (and we are not aware of any study that has used this particular implementation in stan) but in some parts offers more flexibility in modeling the relationships among variables and an assessment of the relative support. We have added this information to the manuscript:

Analysis Plan: To assess the robustness of the findings and whether modeling decisions might have an influence on our results, we will use a frequentist and a Bayesian approach to build the statistical models.

Reviewed by Bonaventura Majolo, 2020-05-13 17:33 The authors aim to analyse the effect of dominance rank on reproductive success in social mammals using a large data set based on published studies. Comparative analyses are a very effective tool to investigate biological phenomena and the authors have already published some excellent comparative work, so they are well equipped to achieve the goals of this study. The overall aim of the study and the need to investigate dominance effect across a large range of social mammals are well explained and would make an important contribution to socio-ecology. Their aims and predictions are very well grounded into the existing literature, interesting, and in several cases they will allow to have novel insights on the effect of dominance rank. The proposed methodology aims to use some of the most recent and powerful tolls in meta-analytic and comparative analyses; the authors have clearly thought very carefully about their analyses and the variables to be included.

Reply: Thank you for your positive comments!

Comment 5: In section C2, when the authors talk about "flexibility to quickly produce large numbers of offspring", it was not clear to me whether they are referring to 'flexibility' in terms of short inter-birth interval, so that females can be pregnant multiple times if the ecological conditions are right, or to absence of breeding seasonality, or a combination of these two factors.

Reply 5: Yes, you are right, flexibility in when to give birth is shaped both by ecological conditions and the ability of females to give birth to multiple offspring in short intervals. We considered including seasonality as a predictor variable, but there does (as yet) not seem to be suitable detailed breeding data for a large sample of species and the species in our sample likely differ in which ecological factor (rainfall, temperature, etc) shapes breeding patterns. Accordingly, we have clarified that we are focusing only on the life history part (short interbirth intervals) by changing flexibility to ability:

Objective: 2) We expect that dominants have higher reproductive success predominantly in species in which females have the ability to quickly produce large numbers of offspring.

Comment 6: Prediction 3.3: I agree with the prediction, but I am curious to know whether the authors think they need to control for average group size when testing the effect of population density?

Reply 6: As mentioned in our reply to Comment 3, our idea for this preregistration was to assess the possible direct influence of a variety of variables that had previously been suggested to shape the potential benefits that females might gain from high social rank. However, the reviewer is correct that this creates problems where the variables in a pathway might cancel each other out, as in this case: we predict stronger effects of high rank on reproductive success with increased population density, but increased population density might lead to larger group sizes which in turn could reduce the effect sizes. Accordingly, a model including only one of these two variables might not show an influence on the strength of the effect sizes. We went through all our variables to identify such potential cases of conflict, and added a plan to specifically assess their interactive influence on the strength of the effect sizes. We added the following: Prediction To answer these questions, we will assess the following predictions. All our predictions consider the potential direct influence of a specific variable on the size of the effect of dominance rank on reproductive success. The predictions present the direction of the influence we consider a-priori most likely. We will report all results, but in instances where influences are opposite to what we predict further studies will be necessary to place this result in context. In addition, several of the variables we will include are likely to influence each other. Accordingly, analyses with single variables might not necessarily show the predicted direct influence even if it is present (e.g. there might not be a positive relationship between a social system and the size of the effects if species with this particular social system primarily occur in environments where the size of the effect is expected to be smaller). While deciphering all the potential relationships among the variables we include is beyond the scope of this study, we will also perform analyses accounting for these potential interactions among variables. We focus on instances where we expect that one variable might remove or change the direction of the influence of another variable, and present these at the end of the predictions.

Potential interactions among predictor variables: Studies performed on wild versus captive individuals and using different measures of reproductive success might not only differ in the overall strength of the effect of rank on reproductive success, but also in how other variables influence this effect.

Higher population density [predicted to lead to larger effect sizes] might be associated with larger group sizes [smaller effect sizes predicted], leading to an interactive influence on the strength of the effect sizes of dominance rank on reproductive success.

Smaller group sizes [larger effect sizes predicted] might be associated with more intense intersexual conflict [smaller effect sizes predicted], leading to an interactive influence on the strength of the effect sizes of dominance rank on reproductive success.

Monopolizable resources [larger effect sizes predicted] might be associated with reduced population density [smaller effect sizes predicted]), leading to an interactive influence on the strength of the effect sizes of dominance rank on reproductive success.

Environmental harshness [larger effect sizes predicted] might be associated with reduced population density [smaller effect sizes predicted]), leading to an interactive influence on the strength of the effect sizes of dominance rank on reproductive success.

Female philopatry [larger effect sizes predicted] might be associated with increased group sizes [smaller effect sizes predicted]), leading to an interactive influence on the strength of the effect sizes of dominance rank on reproductive success.

Analysis Plan: Influence of predictor variables: For instances where we might expect covariation among variables that are predicted to influence the strength of the effect sizes in opposite ways, we will build models that include both variables and their interaction.

Comment 7: Prediction 4.5 & 4.6: these two predictions go in opposite directions, but kinship and coalition formation are often linked. I mean, if we look at what happens in primate species with female philopatry, where matrilineal play a key role on dominance rank, females from one kin group frequently form coalitions against members of other matrilineal and often rank above (or below) members of other matrilineal. If so genetic similarity in a group and coalition formation might not have opposite effects on reproductive success. Imagine, for example, a group where there are only two matrilineal (with low genetic diversity) and kin-biased coalitions are frequent: in these conditions both genetic similarity and coalition formation might have a positive effect of the benefits of higher dominance rank. This is something you might want to consider, depending on the taxa represented in the data set.

Reply 7: We recognize that we had built our predictions based on assuming only two extremes of species such as cooperatively breeding meerkats where all females are related and do not form coalitions versus species such as bonobos where females tend to be unrelated and form coalitions. This did not reflect species with matrilineal, as the reviewer correctly points out. To account for these species, we decided to change our approach to not only investigate average levels of relatedness among group females, but also variance in relatedness among group females. In both species we considered, variance in relatedness is low (either all are related or all are unrelated), whereas in species as described by the reviewer, variance in relatedness is high (females are closely related to other members of their matriline and less related to members of other matrilineal). We added the following:

Predictions: P4.6 Dominance rank will be more strongly associated with reproductive success in populations in which variance in relatedness among female group members is high.

In addition to levels of average relatedness among group females, we also predict that the relationship between dominance rank and reproductive success will be more pronounced in species in which there is high variance in relatedness, with females being closely related to some group members but not to others, as compared to species in which group females are either all related or all unrelated. In several species with female philopatry, groups are structured into matrilineal (@fortunato2019lineal). Members of the same matrilineal tend to support each other in interactions with unrelated females, likely reinforcing differences among females.

Comment 8: Methods: the authors list different measure of reproductive success to test their predictions, and reflecting data available in the literature. Maybe I missed this in the document, but I wasn't sure about what happens if they don't have enough data for a specific measure: would they combine multiple measures into one single reproductive benefit of dominance or would they exclude that variable from the analyses?

Reply 8: In case the sample size for a specific measure of reproductive success is not sufficient, we will first try to combine measures as suggested, and exclude the variable if that's impossible. When combining measures, we would consider potential differences in effect sizes for the different measures of reproductive success, after assessing these differences, as explained below.

Analysis Plan: Influence of measure of reproductive success: To the base model, we will add a predictor variable reflecting the six classes of measures of reproductive success.

Influence of predictor variables : In case any of the previous models suggests dependencies among the measured effect sizes, we will add the predictor variables as moderators to models including covariance matrices reflecting the dependencies (e.g. if effect sizes are different for different measures of reproductive success).

Reviewed by anonymous reviewer, 2020-05-12 17:07 The study “Preregistration - The effect of dominance rank on female reproductive success in social mammals” is very well designed and the authors propose a very interesting study that will result in publications that will generate a lot of interest among evolutionary ecologists and beyond. I think the background, the predictions and the proposed methods are very clear and follow the logic of pre-existing studies.

Reply: Thank you for your positive comments!

Comment 9: However, I would like to add three minor comments regarding the predictions. (1) I am a little bit concerned about the fact that the authors also propose to include captive studies. Although fully accounted for in the models, I wonder how much this will impact their estimates of reproductive success, population densities and number of females per social group. The latter is particularly difficult to compare in cases where group sizes might be artificially created. I would suggest to include another control analysis where effect sizes of the different variables are compared between “captive” and “wild” study populations.

Reply 9: While we had predicted that effect sizes might principally differ between studies on captive and on wild individuals, we did not consider whether the influence of the other variables on the effect sizes might also depend on whether a study had been performed with captive individuals. We have now adjusted our analysis plan and our code to include models in which captive vs wild might not only influence the intercept of the effect sizes but also the slopes of the influence of other variables on the strength of the effect size. We added the following:

Influence of predictor variables: Studies performed on wild versus captive individuals and using different measures of reproductive success might not only differ in the overall strength of the effect of rank on reproductive success, but also in how other variables influence this effect. We therefore will build models in which both the intercept and the slopes can vary according to whether studies were performed in the wild/captivity and to how reproductive success was measured.

Comment 10: (2) I am confused about the distinction between the two predictions P3.3 (Effects of dominance rank on reproductive success will be more pronounced in populations with high densities of individuals) and P4.4 (In plural breeding species, dominance will have stronger effects on reproductive success when the number of females in the group is smaller). I understand that P3.3 refers to overall population density and P4.4 to group members but both aspects are linked (depending the way how its calculated) but doesn't larger group size naturally lead to higher densities?

Reply 10: The reviewer is right in that changes in population density are often associated with changes in group size. However, this is not the case in all species: in some, group size will stay the same but there will be more groups in a given area when population densities are higher. Accordingly, we expect that there might be independent influences of population density and of group size on the strength of the effect of rank on reproductive success. However, as population density and group size are likely to be linked with opposing influences on the effect sizes, we realize that we need to account for this - see our reply to comment 6.

Comment 11: (3) Also, predictions P4.3 (Dominance rank will have stronger effects on reproductive success in populations in which females are philopatric in comparison to populations where females disperse to breed) and P4.5 (Dominance rank will be more strongly associated with reproductive success in populations in which average relatedness among female group members is high) are very similar in terms of their underlying biological relevance and could be merged into one prediction?

Reply 11: Yes, average relatedness among females tends to be higher in species in which females are philopatric compared to populations where females can disperse. However, there is large variation in levels of average relatedness in species with female philopatry: in small groups of litter-producing cooperative breeders, average within-group relatedness tends to be high whereas in large groups where all females produce single offspring, average within-group relatedness tends to be very low, often not higher than in

species in which females disperse. Accordingly, we decided to keep both predictions and variables, to assess the relative influence of these two variables.