

Online Supplementary 1: Results from the non-spatial model.

Space use and leadership modify dilution effects on optimal vigilance under
food/safety trade-offs

The American Naturalist

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This supplementary appendix presents results from the non-spatial model. The only patch available corresponds to the risky and rich patch of the spatial model. By definition there are no followers and leaders, because of the lack of space use decisions. All individuals in a group are therefore similar.

The different figures show the same variables that are presented in the main text (except patch use), that is vigilance (figure S1-1), nutritional state and its variations (figure S1-2), starvation risk, predation risk, and total risk (figure S1-3).

Figure S1-1: Relationship between time spent vigilant (% , median, lower and upper quartile, in the upper panel) and group size for individuals in groups exploiting only one patch, in situations where the likelihood of meeting the predator is medium (left, $k_1 = 0.004$), high (middle, $k_1 = 0.008$) or very high (right, $k_1 = 0.016$).

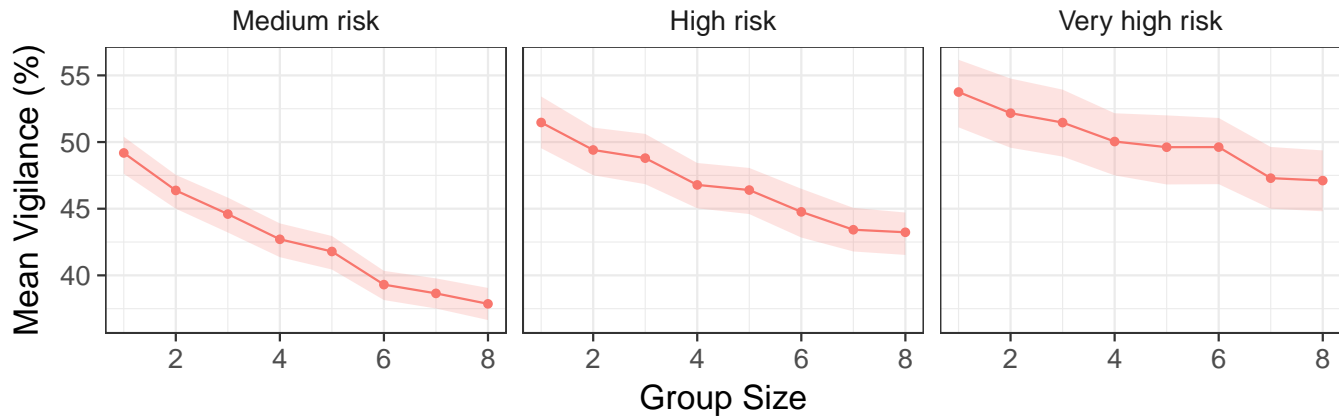


Figure S1-2: Relationship between mean nutritional state (% , median, lower and upper quartile, in the upper panel) or standard deviation of nutritional state (% , lower panel) and group size for individuals in groups exploiting only one patch, in situations where the likelihood of meeting the predator is medium (left, $k_1 = 0.004$), high (middle, $k_1 = 0.008$) or very high (right, $k_1 = 0.016$).

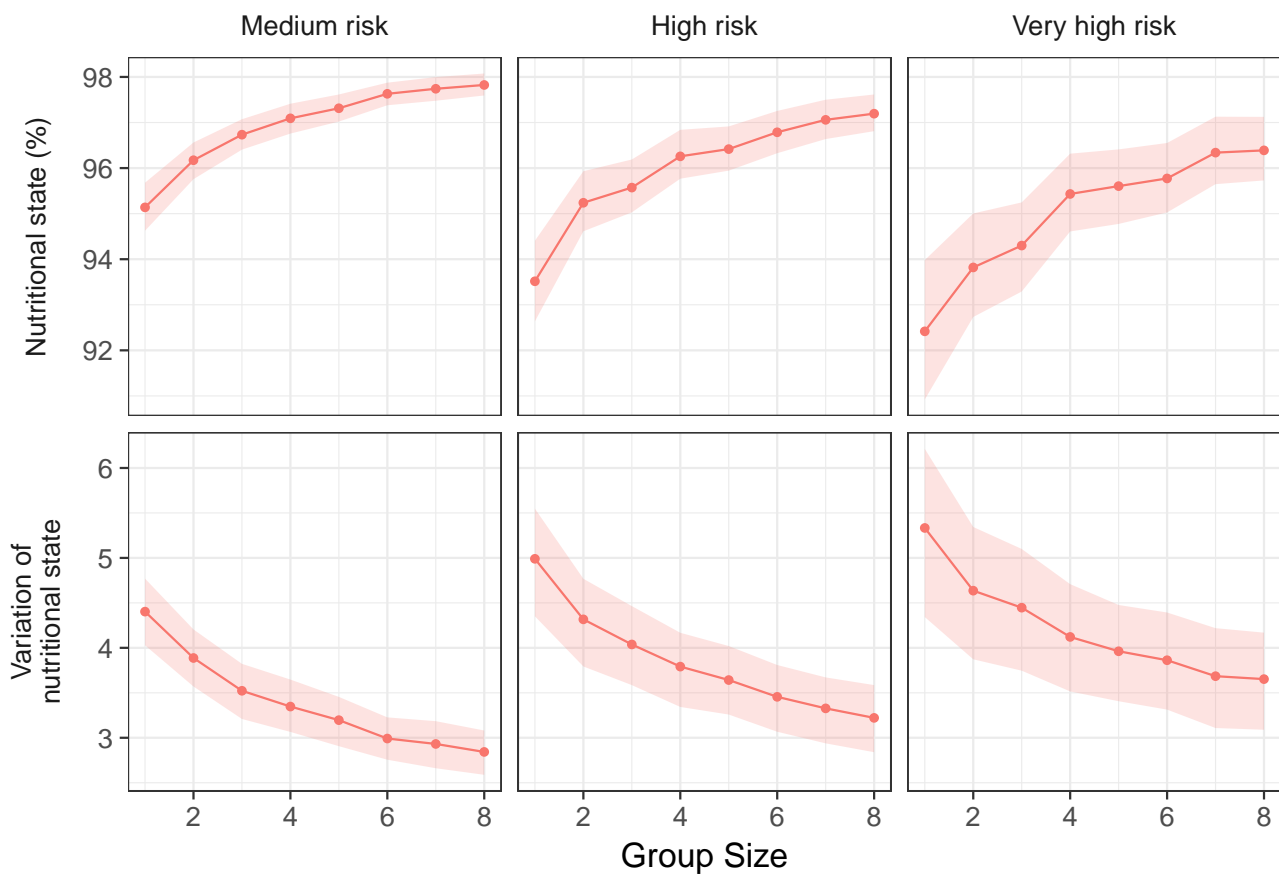
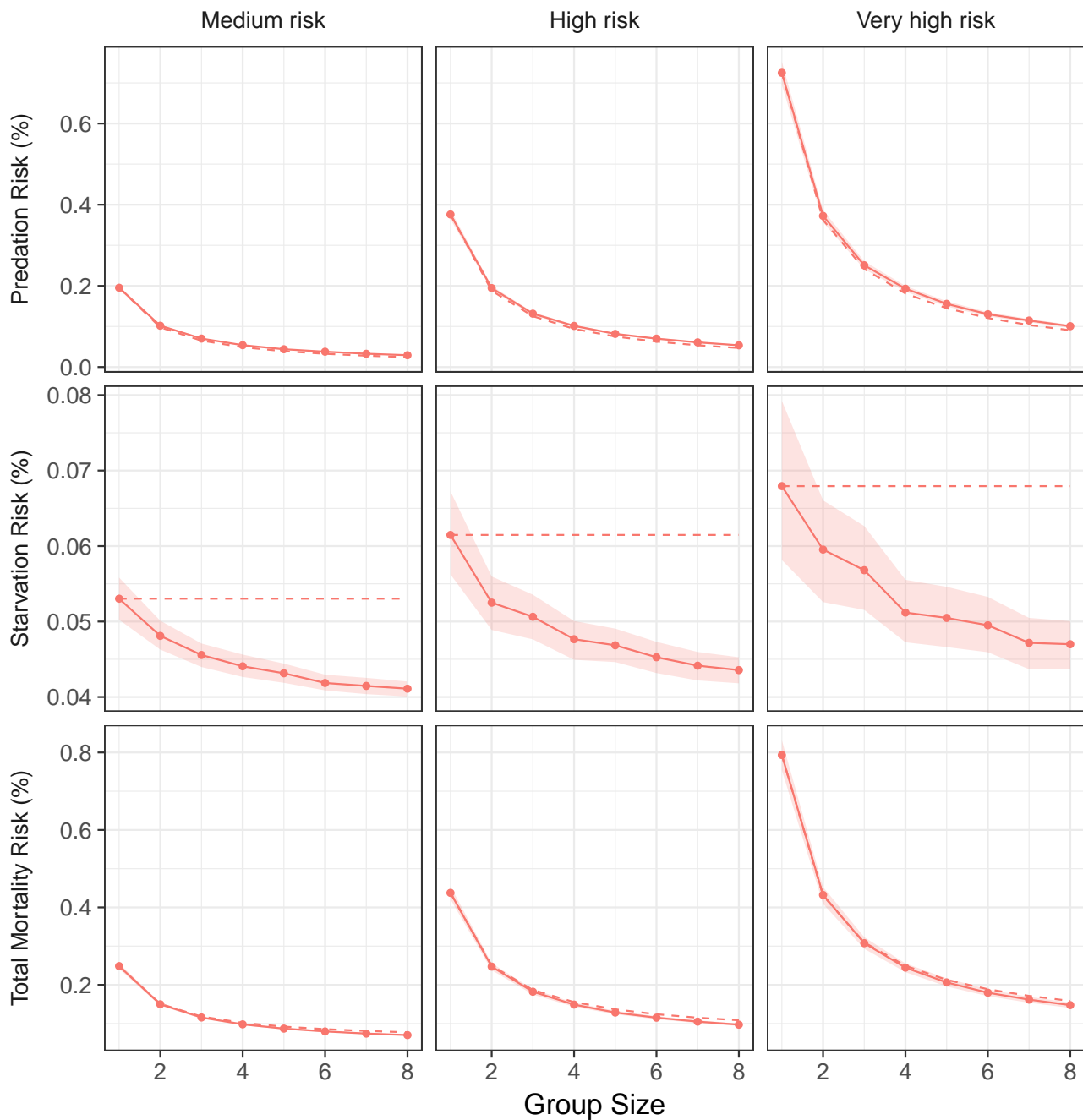


Figure S1-3: Relationship between mean suffered predation risk (% , median, lower and upper quartile, in the upper panel), mean suffered starvation risk (% , medium panel) or mean suffered total mortality risk (% , lower panel) and group size for individuals in groups exploiting only one patch, in situations where the likelihood of meeting the predator is medium (left, $k_1 = 0.004$), high (middle, $k_1 = 0.008$) or very high (right, $k_1 = 0.016$). Dashed lines show risk for an individual that would adopt the optimal behaviour of a solitary one. Percentages correspond to probabilities of death per simulation time step.



Online Supplementary 2: Additional model outputs.

Space use and leadership modify dilution effects on optimal vigilance under food/safety trade-offs

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This supplementary appendix shows additional outputs from the model:

1. Figure S2-1 shows mean vigilance across patches (as shown in main text), mean vigilance in the safe patch and also in the risky patch.
2. Figure S2-2 shows an example of 60 steps of model run for a follower and a leader, under condition of medium risk in risky patch.

1 Patch-specific vigilance

We can see on figure S2-1:

- that mean vigilance in the safe patch is either null or very low (lower panel).
- that relative differences of mean vigilance across patches (upper panel) follow the same pattern as relative differences of mean vigilance in the risky patch (middle panel).

2 Example of model run

Figure S2-2 shows a model run during 60 time steps. Groups alternate between the risky and the safe patch depending on the leader nutritional state. In this example, when the leader nutritional state is equal or lower to 95%, the leader switches to the risky patch. At some point, if the leader can maintain its state over 95% for a long time while in the safe patch (e.g. between time step 294 and 300). In the meantime, a luckless follower can see its state drops from nearly 95% to 80%, and its associated starvation risk rise. In other instance in the safe patch (time steps 275 to 278) a follower can maintain its nutritional state at nearly 100% while the one of the leader drops and force him to go with the group to the risky patch. The optimal strategy of a follower forces him to minimize the risk of a run of bad luck (as seen between time steps 294 and 300) that would increase highly its mortality risk. For that reason, a follower will be less vigilant than a leader to anticipate that it might not be in the risky patch when its states drops.

Note that the follower is sometimes more vigilant than the leader. Indeed when a follower is at maximum state in the risky patch, there is no need to be foraging at maximum capacity, because states cannot go higher. In opposition, a leader at maximum state would choose to go in the safe patch and be nearly non-vigilant.

Figure S2-1: Relationship between mean time spent vigilant (%; median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch. Time spent vigilant is shown across patches (upper panel), in the risky patch (middle panel) and in the safe patch (lower panel)

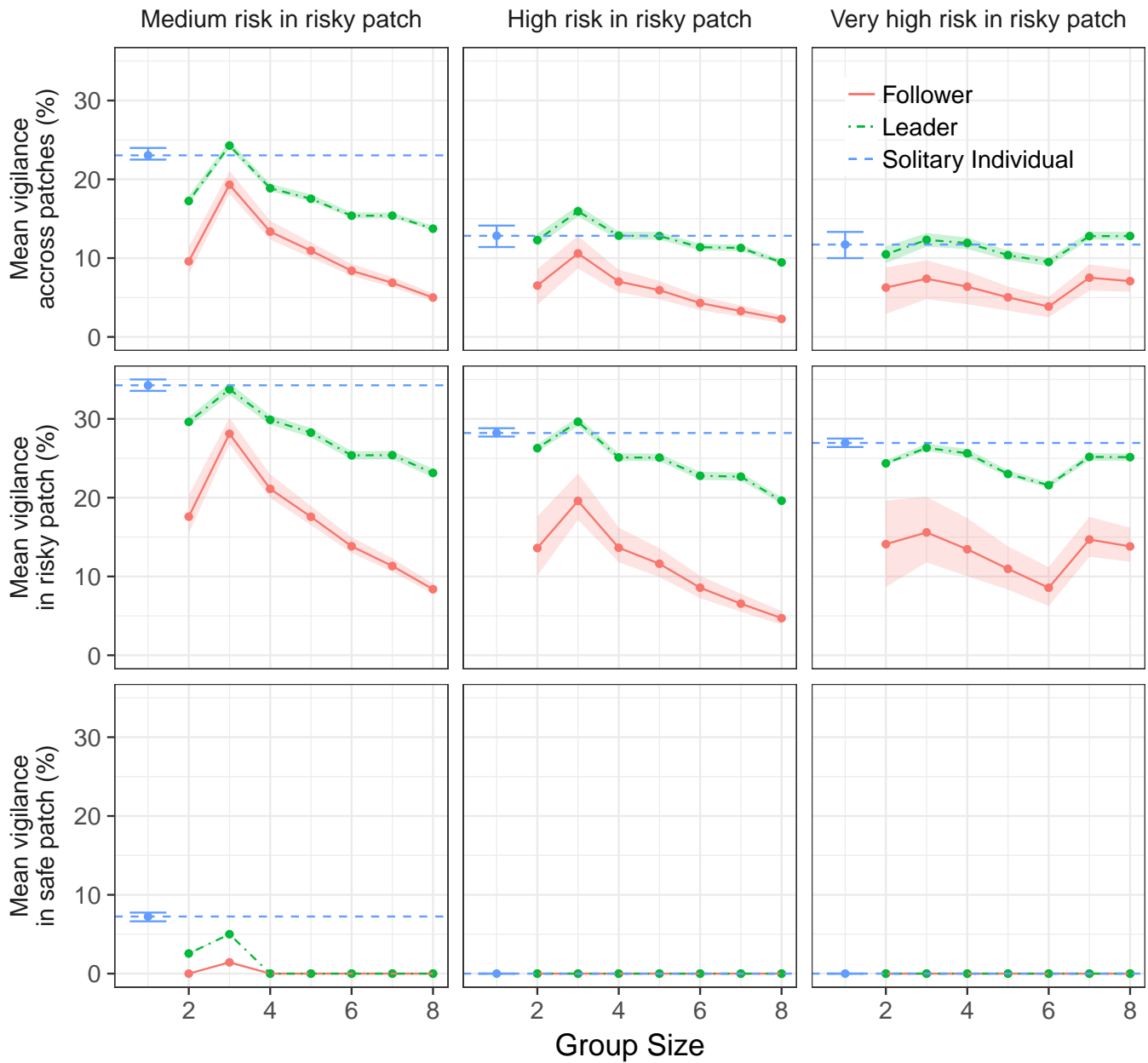
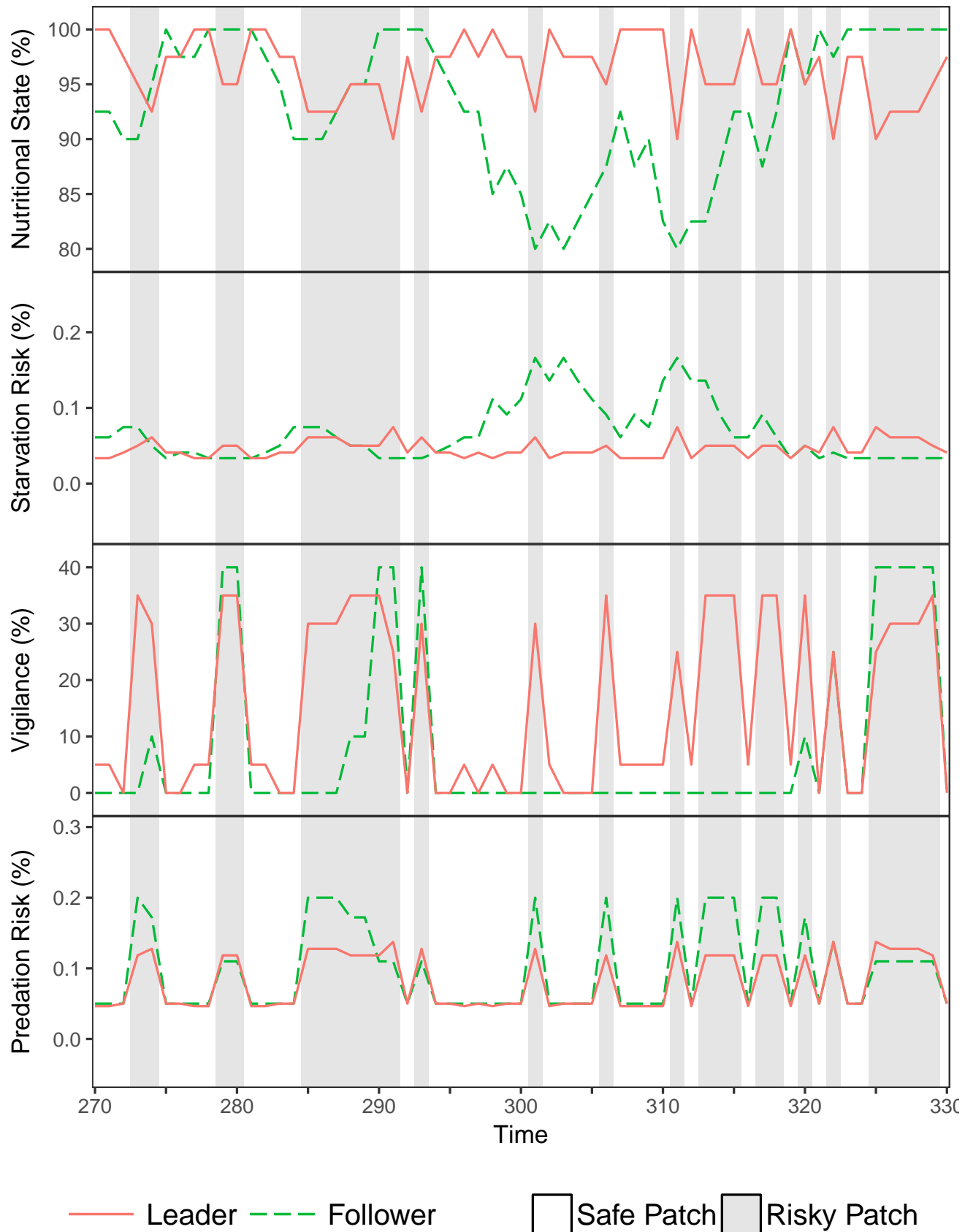


Figure S2-2: Example of a model run for 60 steps. Red lines shows leader behaviour while green dashed lines shows follower behaviour. Use of risky patch is shown by grey-shaded areas. Simulations were run considering a medium risk in the risky patch and a group of two individuals. Percentages for predation and starvation risk correspond to probabilities of death per simulation time step.



Online Supplementary 3: Results for different strength of starvation risk.

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This supplementary appendix presents results for different parameters of starvation risk strength (f , see equation 3). In the main article we showed results only for a high starvation risk ($f = 0.2$), but here we added results for medium and low starvation risk ($f = 0.25$ and $f = 0.3$). Under higher values of f , starvation risk was too low, and no dilution effect was observed (there were not enough benefits for increasing foraging).

The different figures show the same variables that are presented in the main text, that is vigilance (figure S3-1), patch use (figure S3-2), nutritional state and its variations (figure S3-3 and S3-4), starvation risk (figure S3-5), predation risk (figure S3-6) and total risk (figure S3-7).

See the main text for the presentation and discussion of these results.

Figure S3-1: Relationship between mean time spent vigilant across patches (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel).

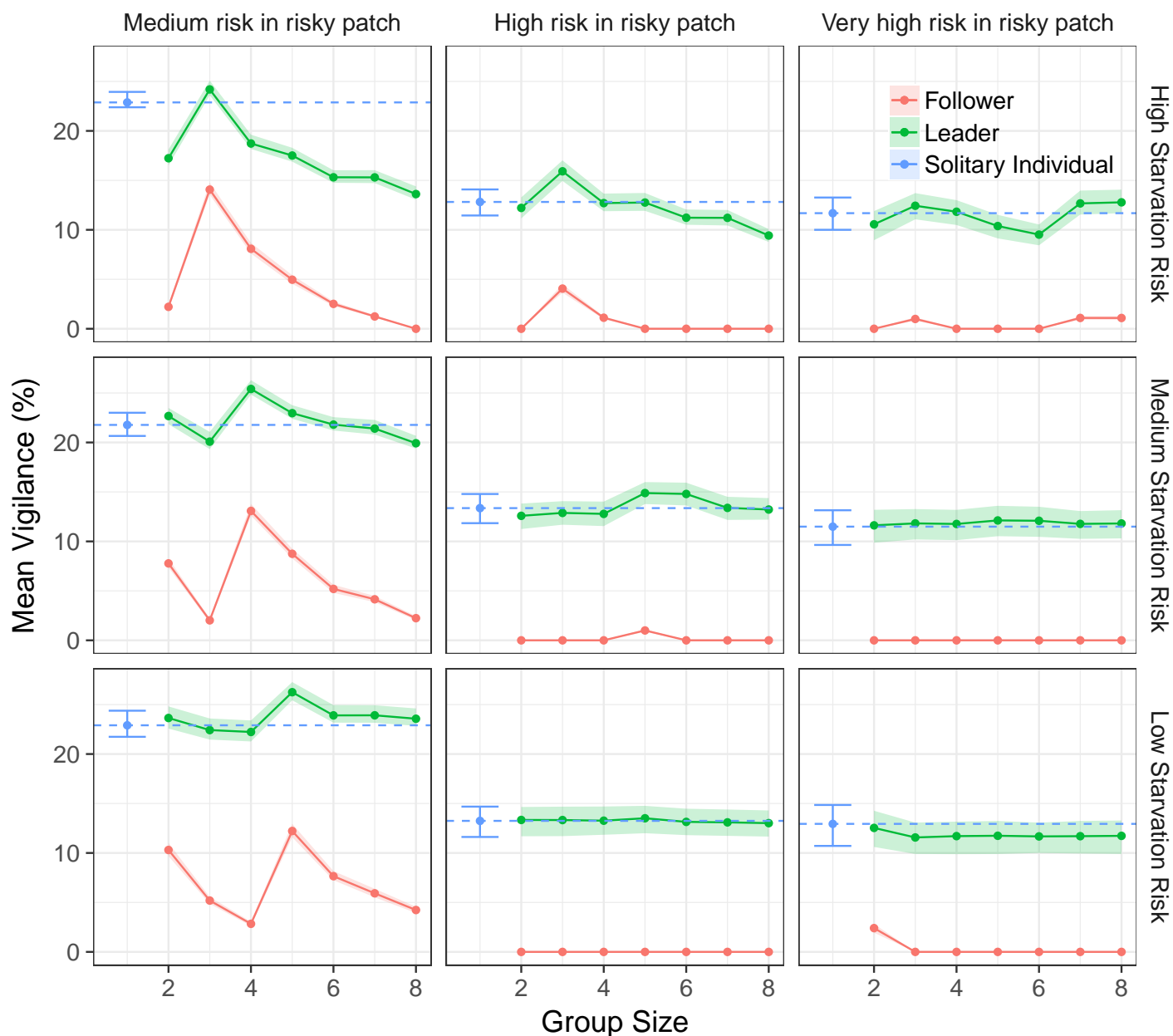


Figure S3-2: Relationship between time spent in the risky patch (% , median, lower and upper quartile) and group size for solitary individuals (blue) and group leaders (green), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel). Follower patch use is not shown because it is identical to the one of the leader.

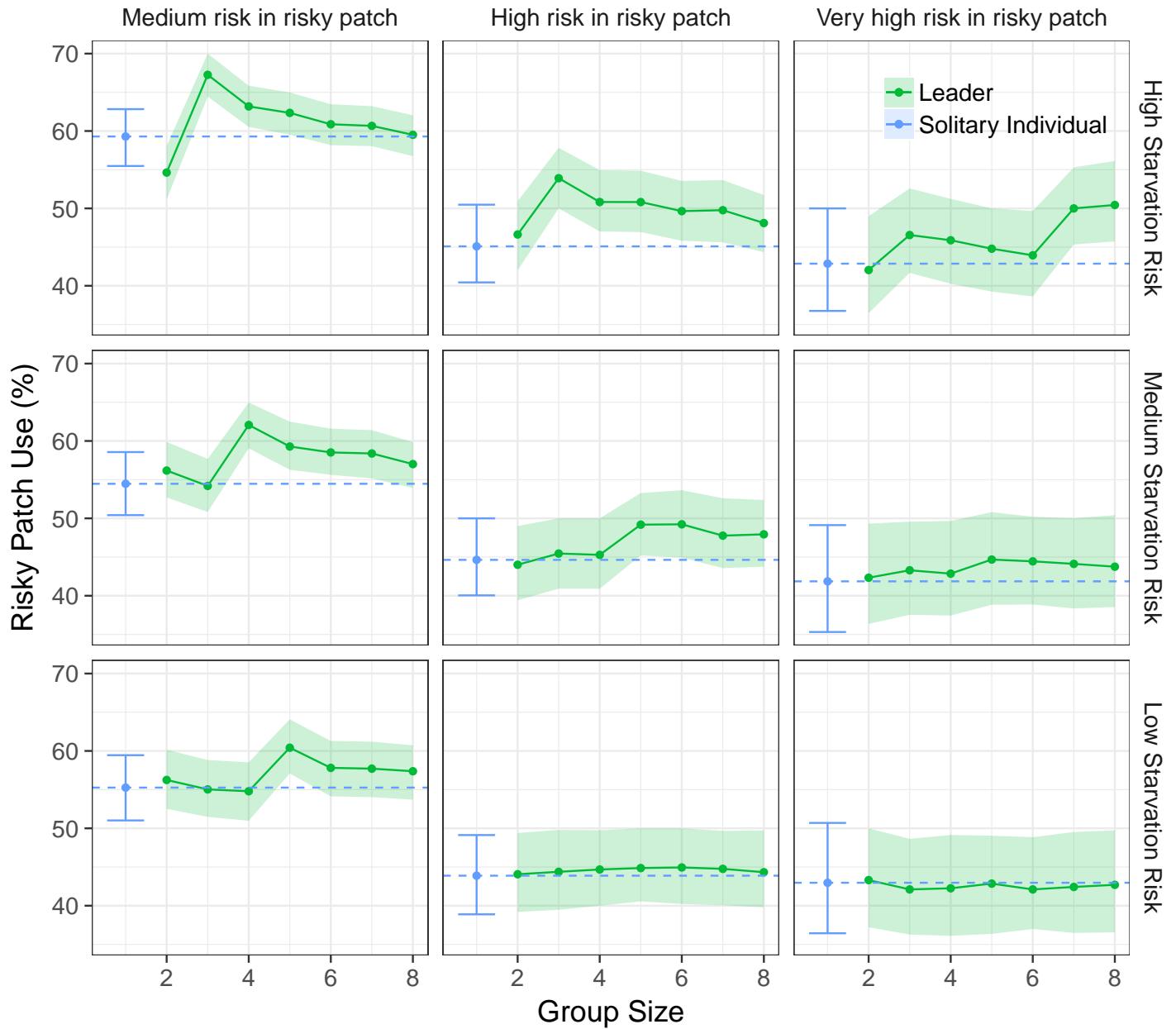


Figure S3-3: Relationship between mean nutritional state (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel).

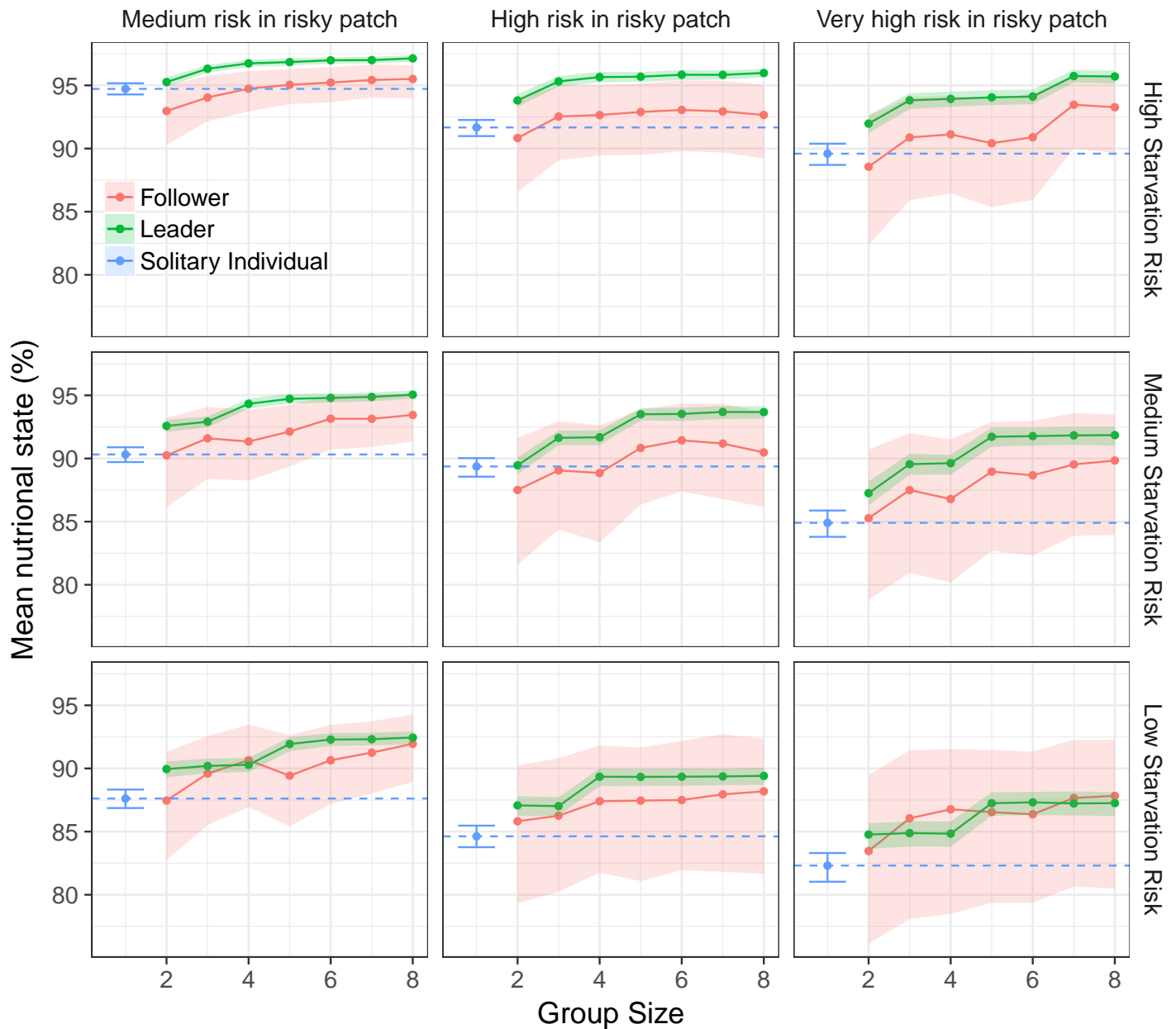


Figure S3-4: Relationship between standard deviation of nutritional state (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel).

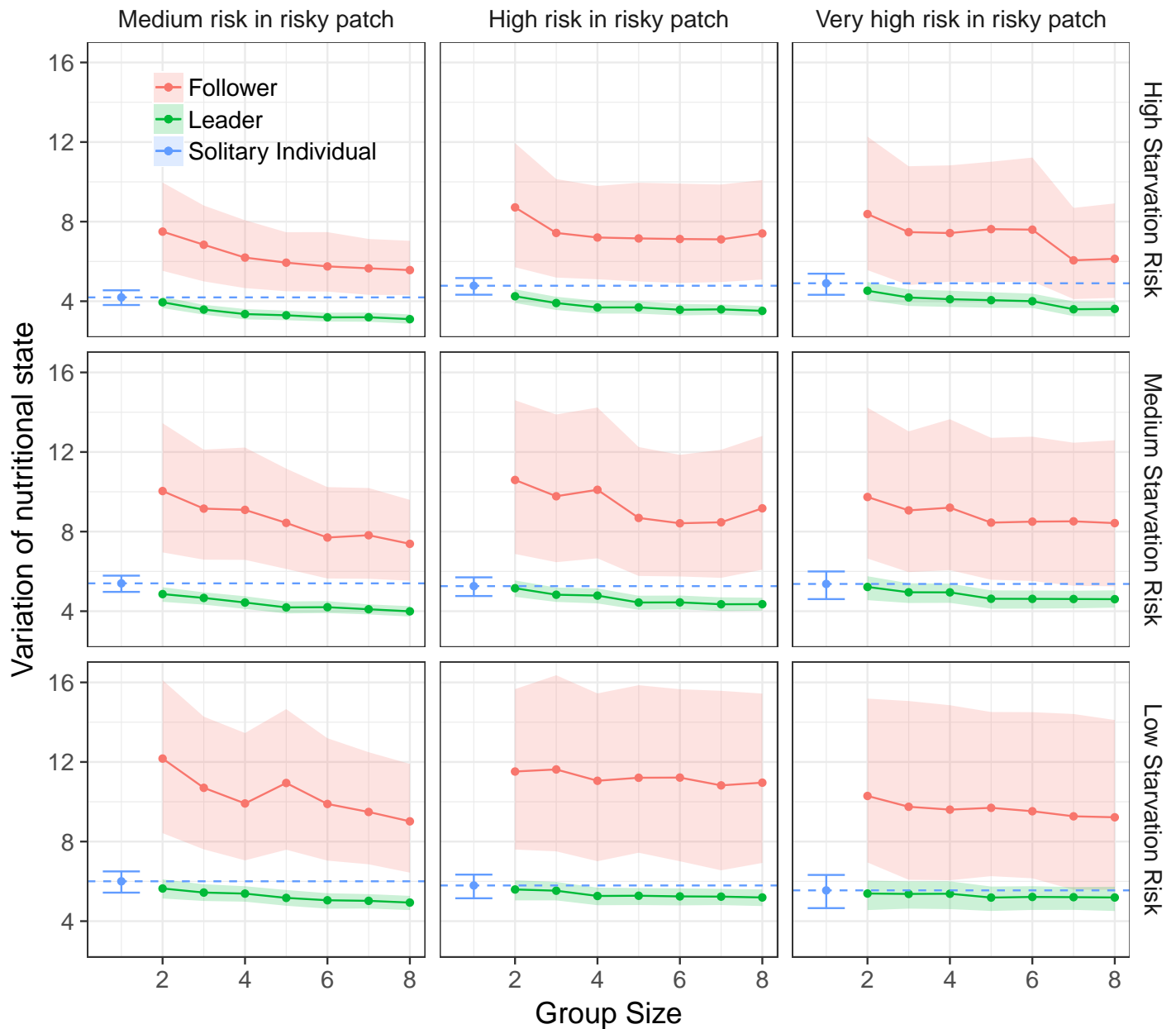


Figure S3-5: Relationship between mean suffered starvation risk (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel). Percentages correspond to probabilities of death per simulation time step.

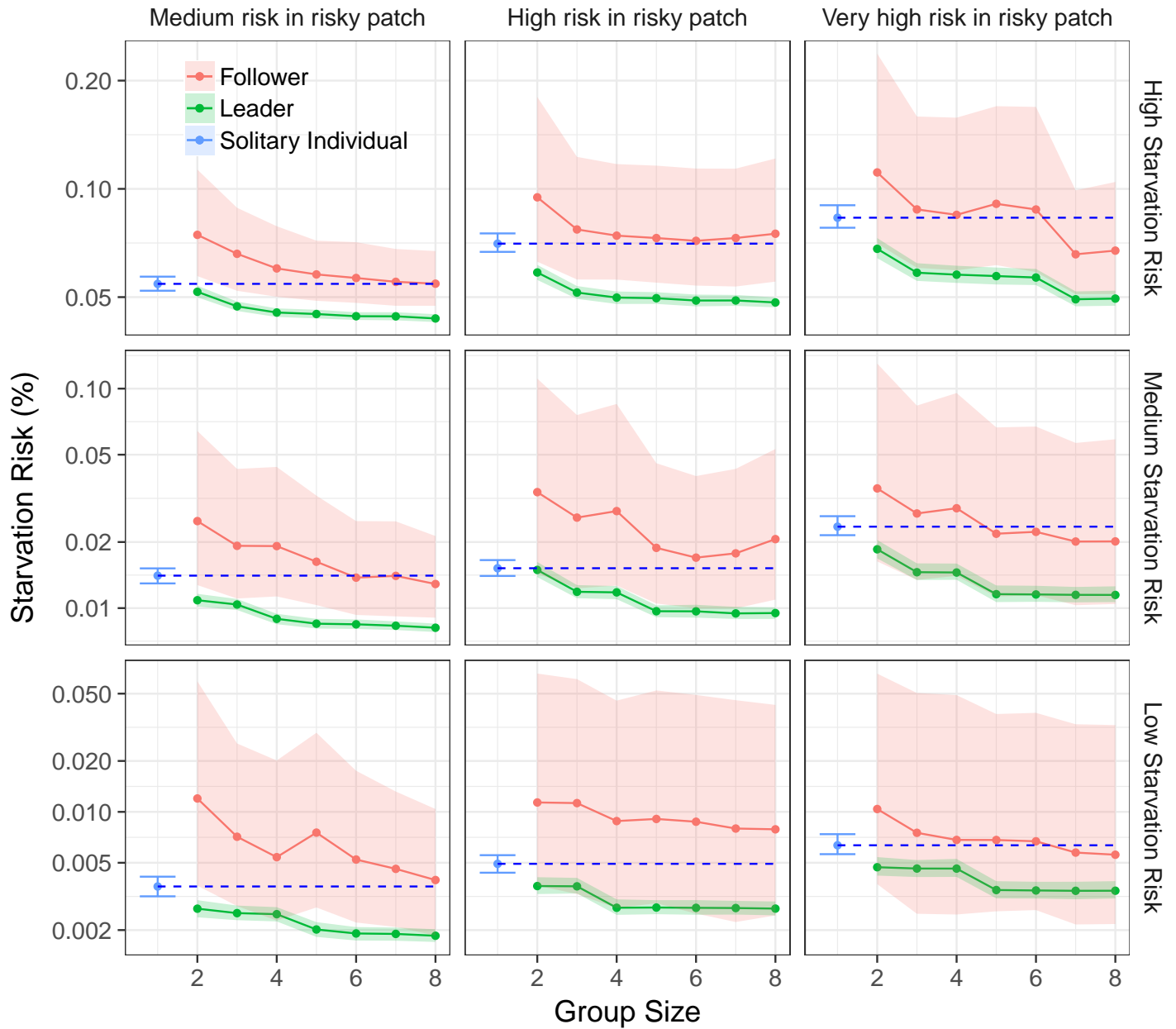


Figure S3-6: Relationship between mean suffered predation risk (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel). Dashed lines show predation risk of a leader that would adopt the optimal behaviour of a solitary individual. Percentages correspond to probabilities of death per simulation time step.

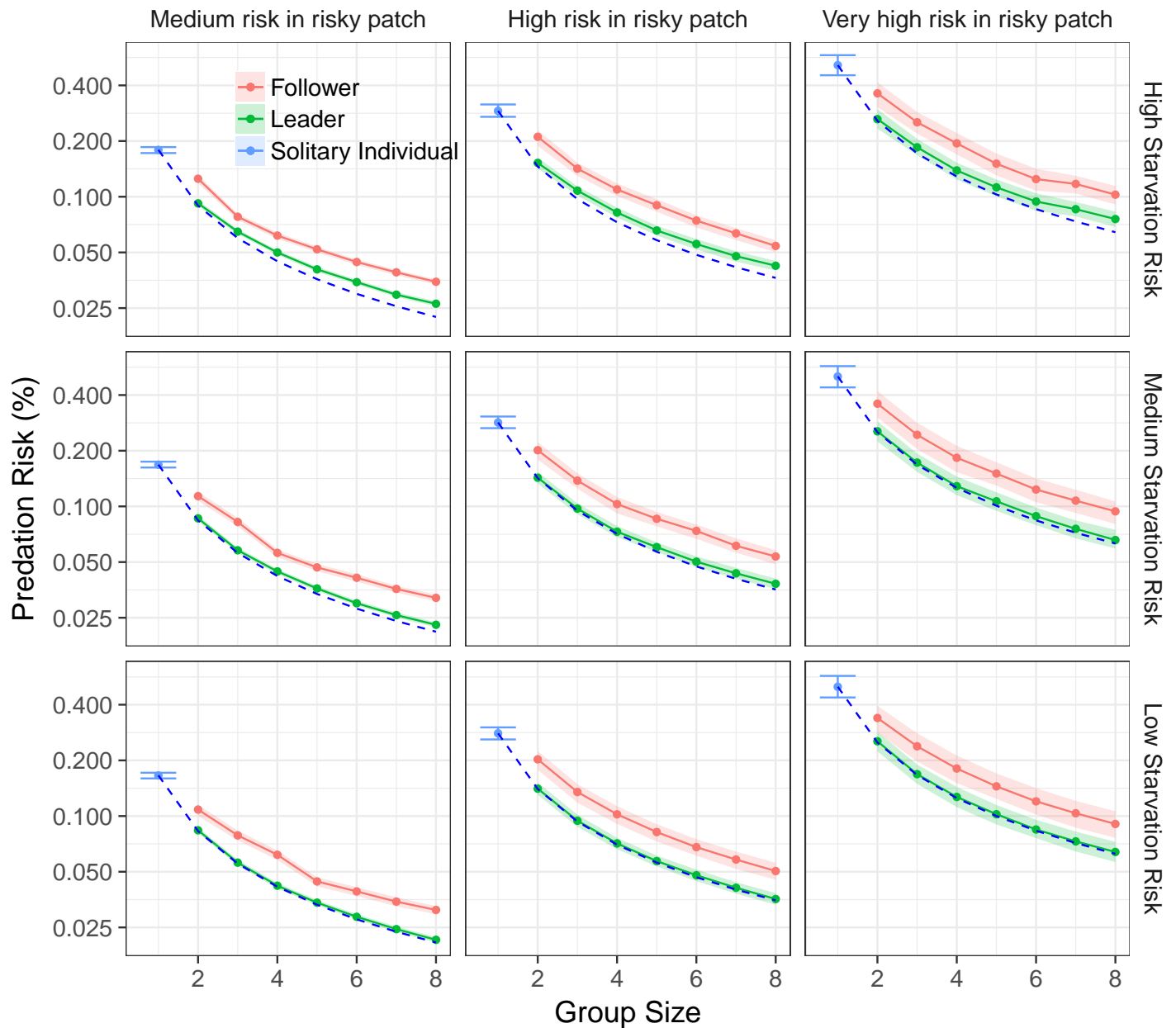
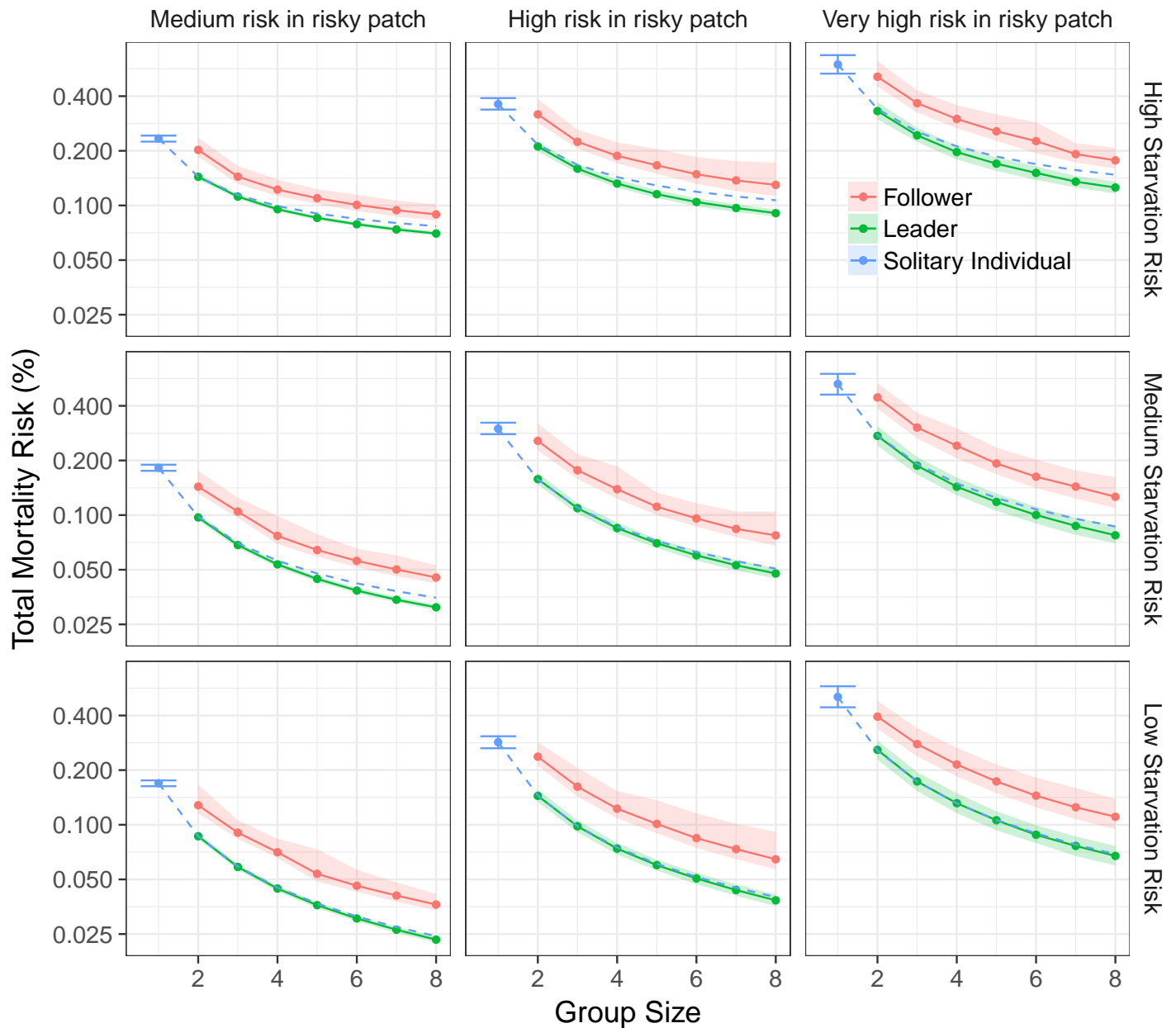


Figure S3-7: Relationship between mean suffered mortality risk (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch and starvation risk is either high ($f = 0.2$, upper panel), medium ($f = 0.25$, middle panel) or low ($f = 0.3$, lower panel). Dashed lines show mortality risk of a leader that would adopt the optimal behaviour of a solitary individual. Percentages correspond to probabilities of death per simulation time step.



Online Supplementary 4: Results under alternative assumptions about predator encounter rate and encounter rate with food items.

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This supplementary appendix presents results obtained under different assumptions about (i) the link between predator encounter rate and group size and (ii) the link between encounter rate with food items and vigilance.

Assuming that predator encounter rate increases with group size

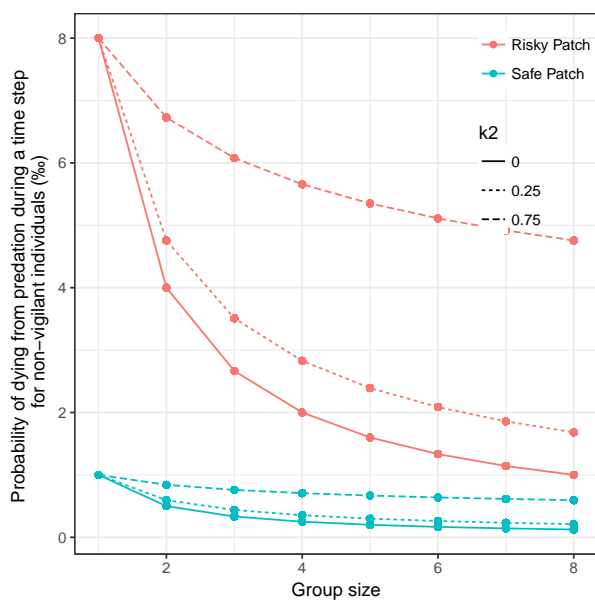
Increasing group size also incurs additional costs that we did not account for, such as coordination effort (see e.g. Sueur (2012)) or increased detectability by predator (Hebblewhite and Pletscher, 2002). In particular, we assumed that group size did not change the likelihood that the group meets the predator and that one individual is attacked. Although we studied the increase in group by only a few individuals, the validity of this assumption can be questioned. Previous modelling studies have sometimes relaxed this assumption (Turner and Pitcher, 1986), and empirical data suggests that indeed sometimes larger groups are more easily detected and targeted by predators (Krause and Godin, 1995), although not always (Quinn and Cresswell, 2004). Higher detectability of larger groups could lead to increased vigilance and increased use of safer patches in larger groups, compared to our results. As discussed in the main text, the specific changes in behavior (whether vigilance or space-use will change to a riskier behavior with increasing group size) are likely to be sensitive to exactly how group size affects encounter rate. Therefore, relaxing this assumption will certainly change the shape of the vigilance group size relationship in a context-specific way. The change in assumption, however, should not affect the differences of behaviour between leaders and followers.

In this appendix, we forced the predator encounter rate to increase with group size, following the equation below, which is modified from equation (2) in the main text.

$$Pred(t) = k_0(p(t)) \times N^{k_2} \times \frac{1}{N} \times e^{-k_1 v(t)} \quad (S1)$$

Basal encounter rate k_0 is now multiplied by N^{k_2} . If $k_2 = 0$ there is no increase of encounter rate, but if $k_2 > 0$, encounter rate increases with group-size. The higher k_2 , the lower are the benefits of risk dilution. Figure S4-1 shows how an increase of predator encounter risk with group size change the predation risk for a non-vigilant individual.

Figure S4-1: Relationship between probability of dying from predation and group size for a non vigilant individual in the safe and pour patch (blue) or the risky and rich patch (red), under different assumptions about the increase of predator encounter rate with group size : no increase of encounter rate with group size (plain line), large increase (dashed line), very large increase (double dashed line).



Assuming a non-linear decrease of food items encounter rate with vigilance

Instead of assuming that encounter rate with food items was linearly related to vigilance (see equation 1 in main text) we tested different non-linear relationship between encounter rate and vigilance, with encounter rate decreasing either slower or faster than with a linear relationship. We assumed that:

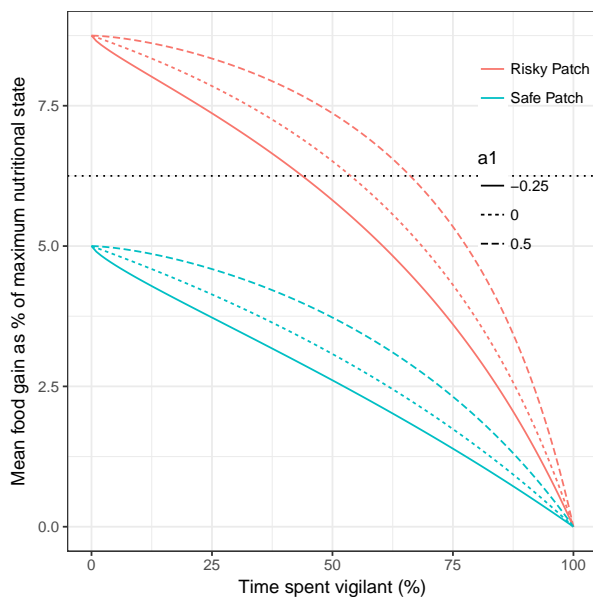
$$a = a_0 \times (1 - v^{1+a_1}) \quad (S2)$$

with a the encounter rate with food items, a_0 maximum encounter rate, v vigilance and a_1 the parameter controlling the non linearity of the relationship. If $a_1 = 0$ the relationship is linear. If $a_1 < 0$ encounter rate decreases faster than expected under linear assumptions. This makes vigilance more costly because an increase would decrease foraging more than expected under a linear assumption.

Also, if $a_1 > 0$ encounter rate decreases slower than expected under linear assumption. This makes vigilance more efficient because an increase would decrease foraging less than expected under a linear assumption.

The functional relationship between vigilance and food gain is shown on figure S4-2 for the different values of a_1 .

Figure S4-2: Relationship between food gain and vigilance for the safe and pour patch (blue) and the risky and rich patch (red), in situations where encounter rate with food items decrease either faster than linear (plain line, same as main text results), linearly (dashed line) or faster than linear (double dashed line).



Results

The different figures show the same variables presented in the main text, that is vigilance (figure S4-3), patch use (figure S4-4), nutritional state and its variations (figure S4-5 and S4-6), starvation risk (figure S4-7), predation risk (figure S4-8) and total mortality risk (figure S4-9).

See the main text for a presentation and discussion of the results.

References

- Hebblewhite, M. and Pletscher, D. H. (2002). Effects of elk group size on predation by wolves. *Canadian Journal of Zoology*, 80(5):800–809.
- Krause, J. and Godin, J.-G. J. (1995). Predator preferences for attacking particular prey group sizes: consequences for predator hunting success and prey predation risk. *Animal Behaviour*, 50(2):465–473.

Quinn, J. and Cresswell, W. (2004). Predator hunting behaviour and prey vulnerability. *Journal of Animal Ecology*, 73(1):143–154.

Sueur, C. (2012). Viability of decision-making systems in human and animal groups. *Journal of theoretical biology*, 306:93–103.

Turner, G. F. and Pitcher, T. J. (1986). Attack abatement: a model for group protection by combined avoidance and dilution. *The American Naturalist*, 128(2):228–240.

Figure S4-3: Relationship between mean time spent vigilant across patches (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate decreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance.

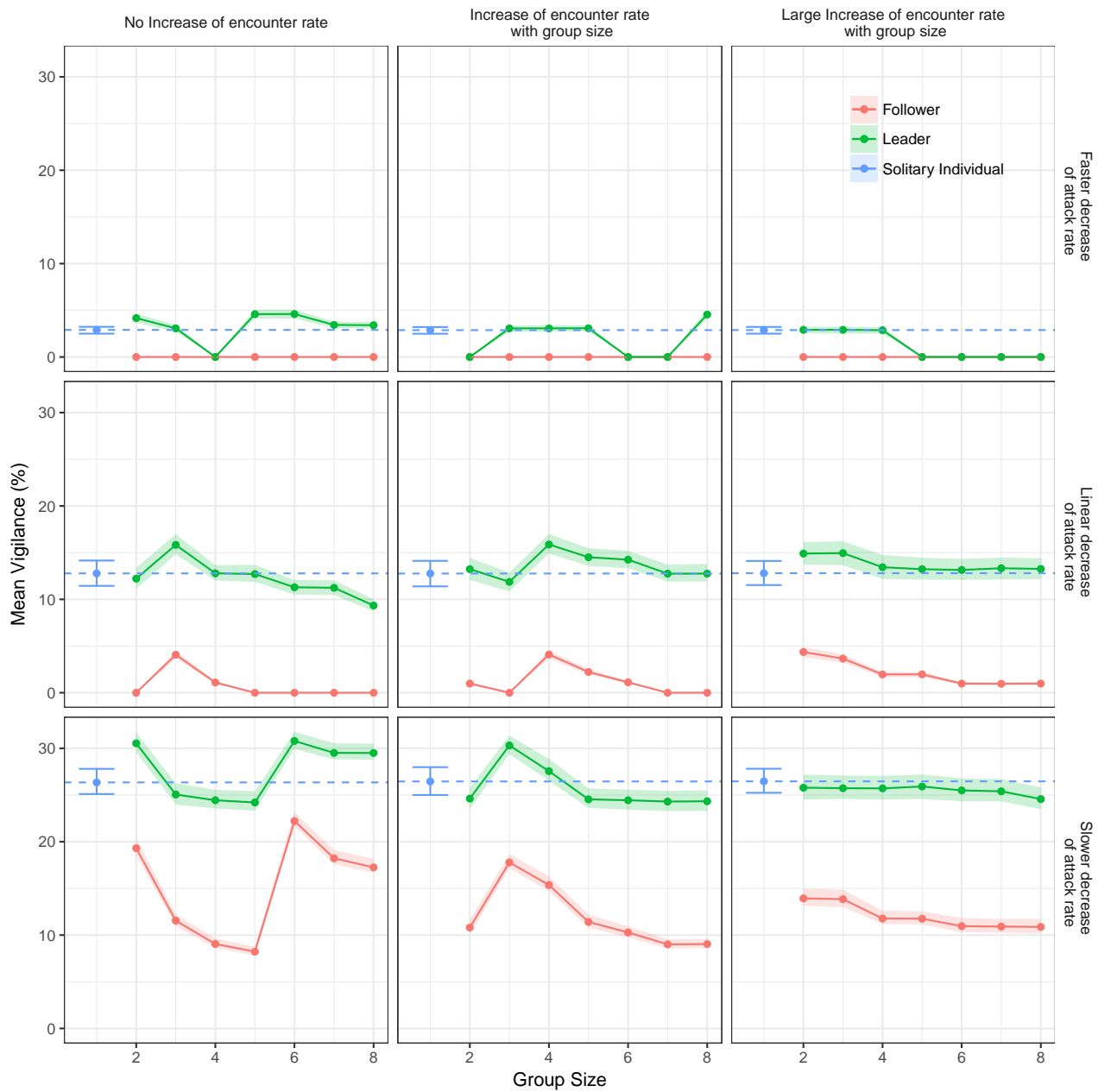


Figure S4-4: Relationship between time spent in the risky patch (% , median, lower and upper quartile) and group size for solitary individuals (blue) and group leaders (green), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate decreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance. Follower patch use is not shown because it is identical to the one of the leader.

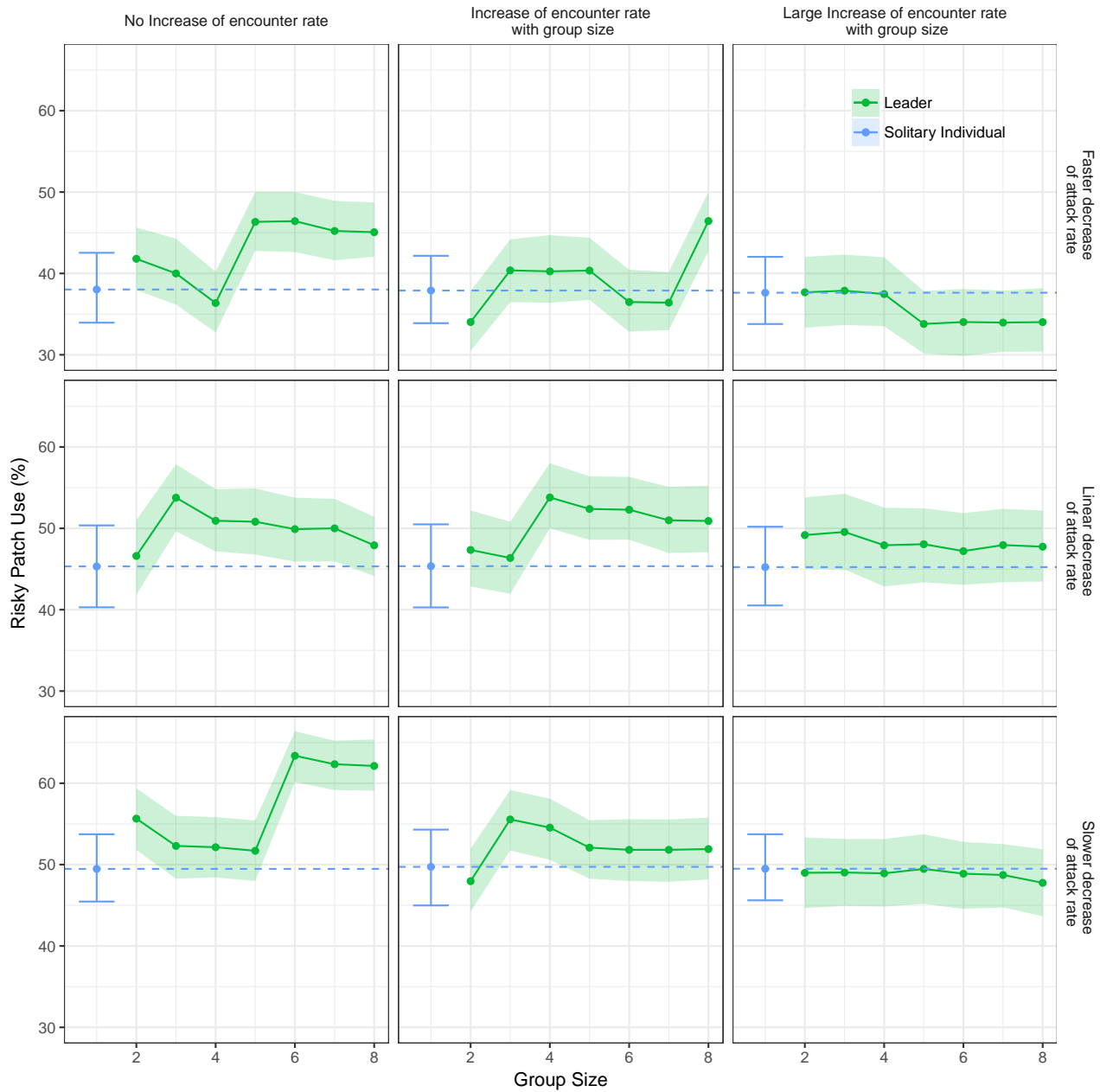


Figure S4-5: Relationship between mean nutritional state (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate decreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance.

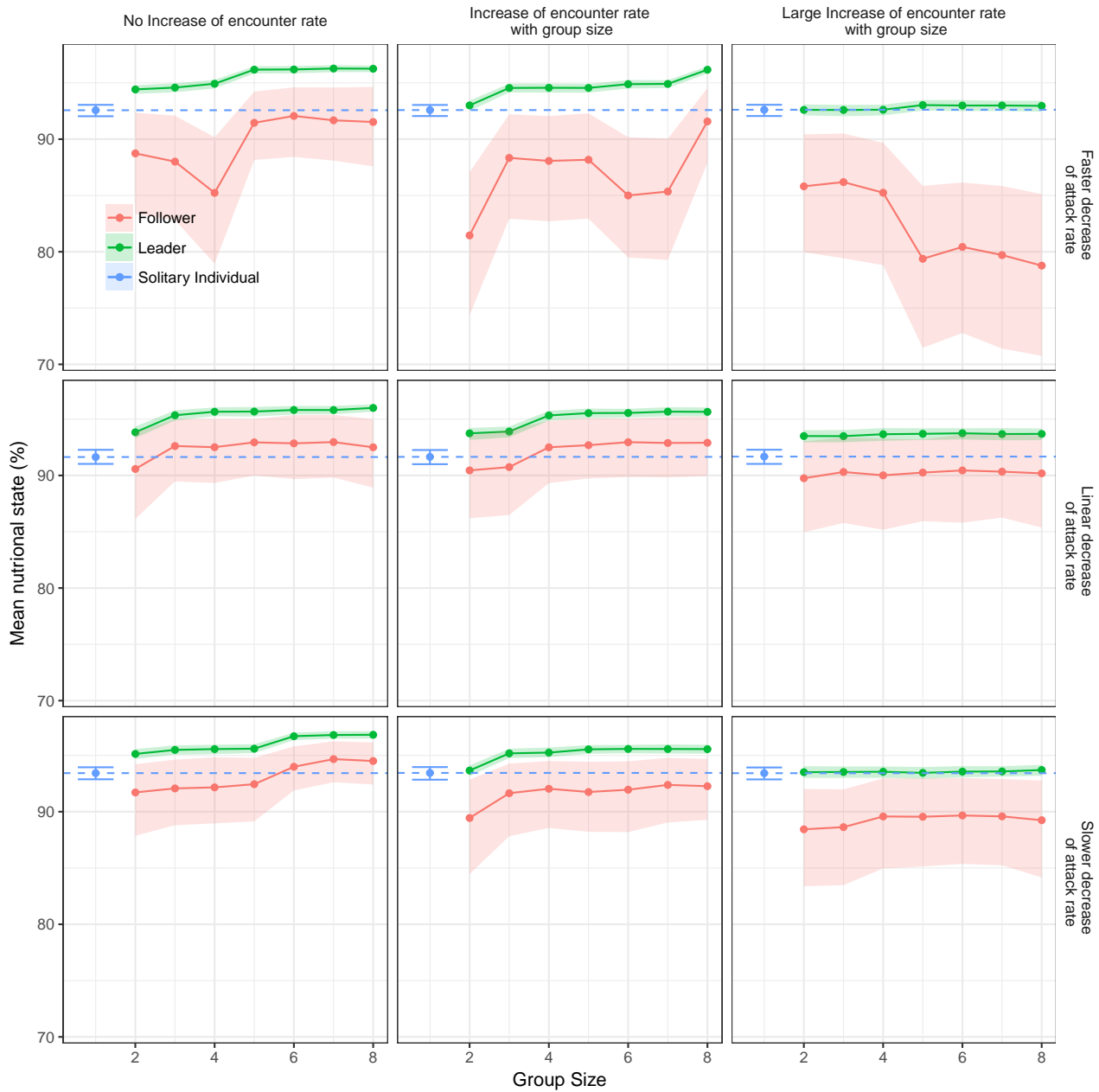


Figure S4-6: Relationship between standard deviation of nutritional state (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate decreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance.

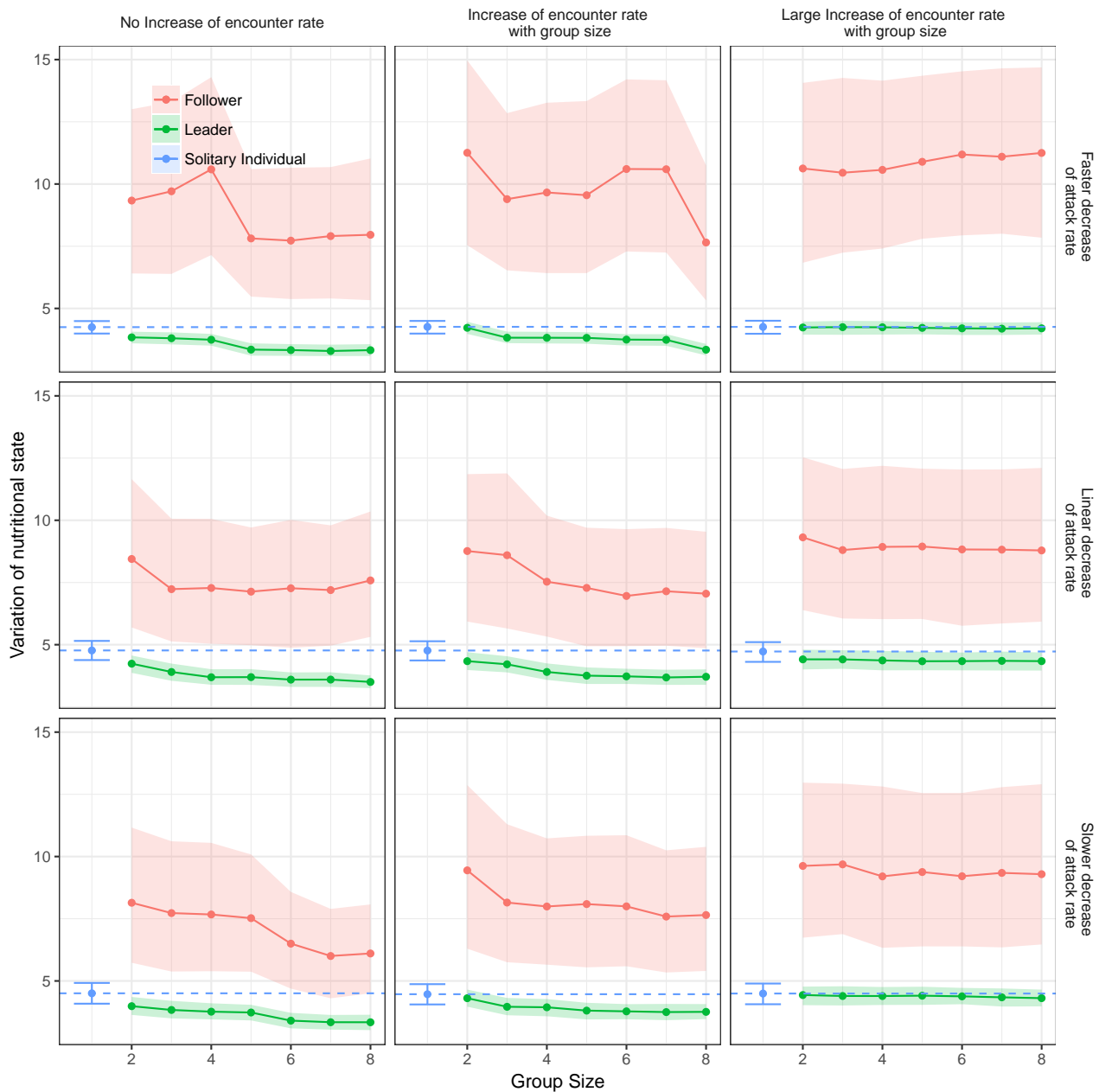


Figure S4-7: Relationship between mean suffered starvation risk (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate decreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance. Percentages correspond to probabilities of death per simulation time step.

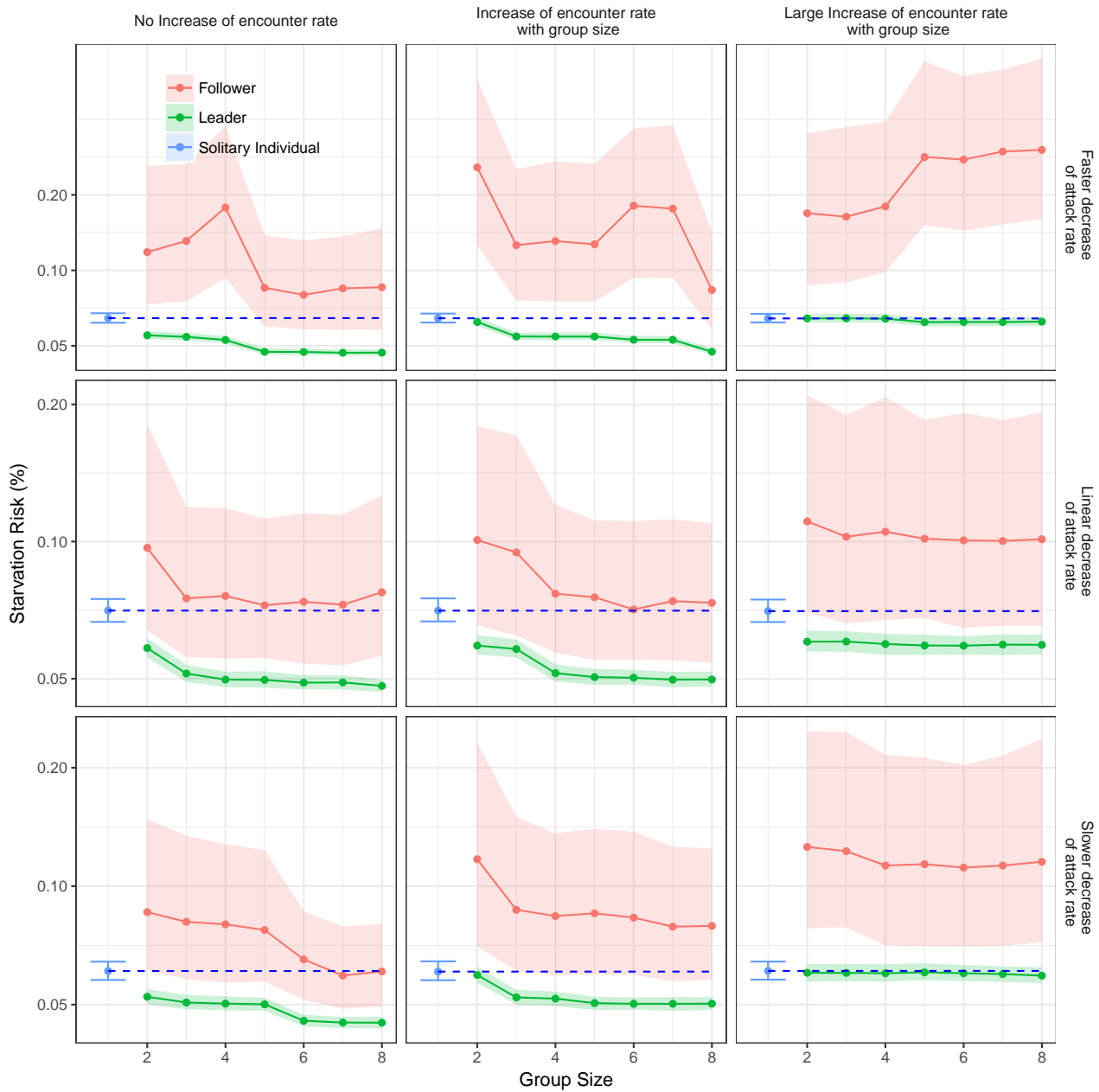


Figure S4-8: Relationship between mean suffered predation risk (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate decreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance. Dashed lines show predation risk of a leader that would adopt behaviour of a solitary individual. Percentages correspond to probabilities of death per simulation time step.

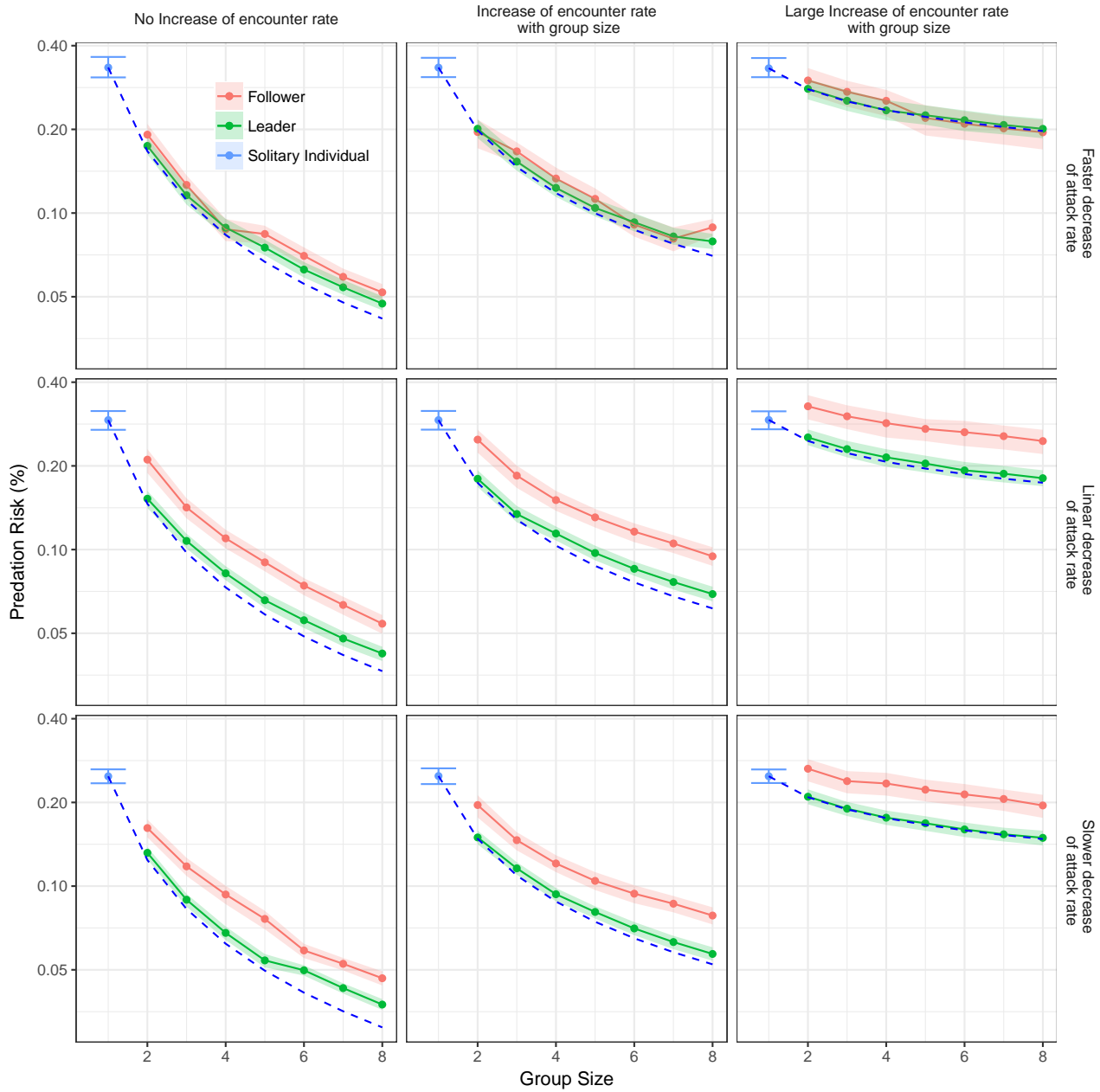
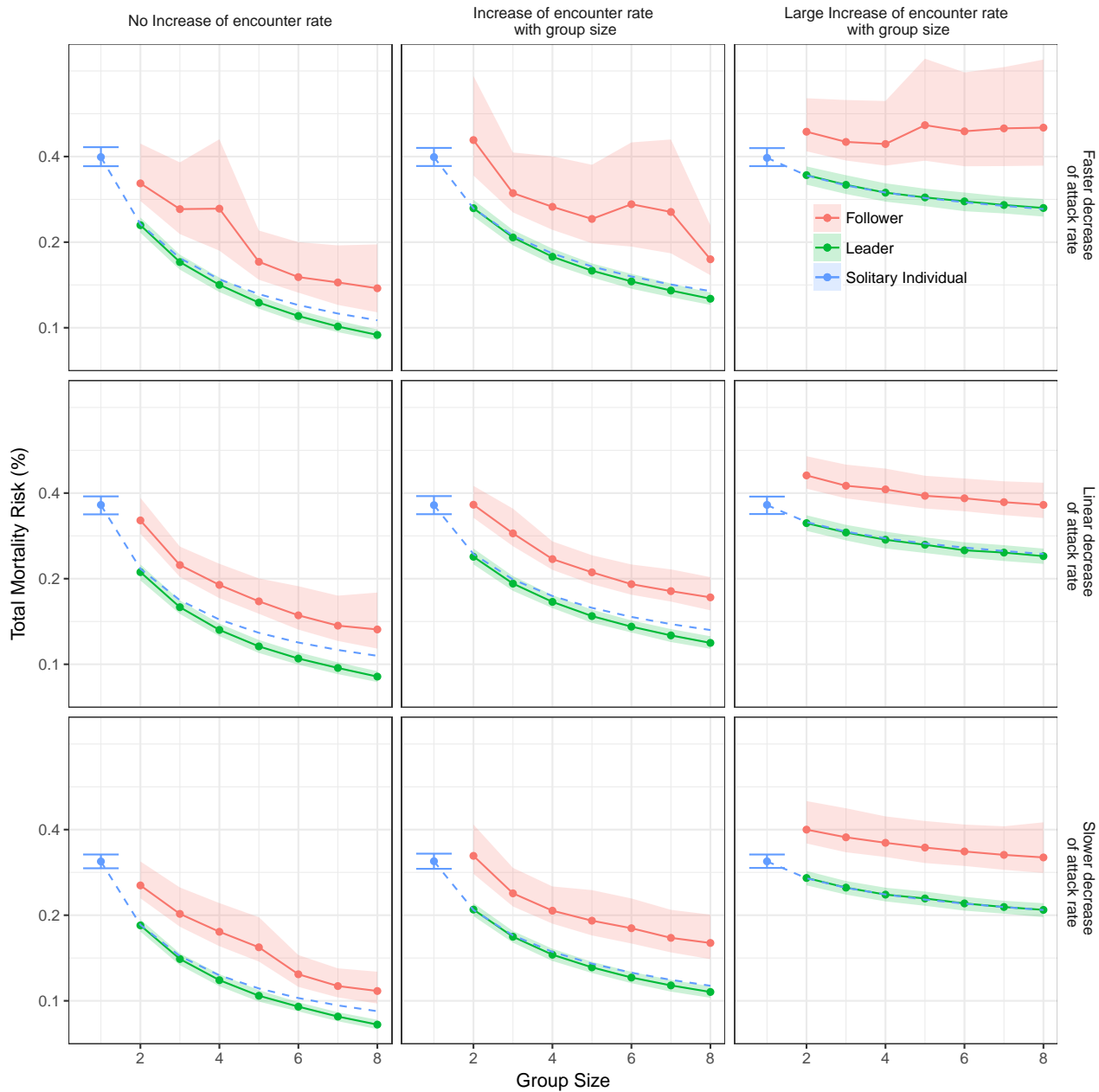


Figure S4-9: Relationship between mean suffered mortality risk (% , median, lower and upper quartile) and group size for solitary individuals (blue), group leaders (green) and followers (red), in situations where the likelihood of meeting the predator does not change ($k_2 = 0$, left), increases slightly ($k_2 = 0.25$, middle) or largely ($k_2 = 0.75$, right) with group size and attack rate decreases either faster ($a_1 = -0.25$, upper panel), at the same speed ($a_1 = 0$, middle panel) or slower ($a_1 = 0.5$, lower panel) than linearly with vigilance. Dashed lines show mortality risk of a leader that would adopt the optimal behaviour of a solitary individual. Percentages correspond to probabilities of death per simulation time step.



Online Supplementary 5: Results from simulations of followers that maximized their short-term survival.

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To estimate the optimal strategy of followers maximizing their long-term survival, we had to make the assumptions that followers, even if they had no information about when they would leave a patch, knew what the long-term rate of patch leaving was. Said differently, they knew what the optimal strategy of the leader was. An alternative approach would be to assume that, in the face of uncertainties about space use decisions, followers maximize their short-term survival (i.e. their survival until the next time-step). In this case their life expectancy was really low (figure S53), because these strategies were leading to higher vigilance level. Vigilance of followers was then a lot higher, than the one of the leader (figure S51), which contrasted with results obtained under the assumption of followers knowing the long-term patch leaving rates (see figure 1 in main text). Under the short-term maximisation assumption, followers traded-off long-term gain in survival for short-term gain in survival by increasing vigilance and decreasing predation risk. Followers that aim to maximize short term survival decrease their vigilance to increase their foraging at lower nutritional state than a long term maximizer. Thus, under the short-term maximization assumption, followers maintained a lower nutritional state (see figure S52) that made the individuals face higher risks of starvation and lower risk of predation, which led to a higher total mortality risk (see figure S53). Selection should therefore facilitate the evolution of cognitive mechanisms allowing to acquire knowledge about future space use. Understanding how this knowledge is acquired (learning, hard-wiring via selection) is an interesting issue. In line with work showing that despotic leadership is hardly viable (Sueur, 2012), this suggests that even despotic leaders could have interest in integrating the needs of the followers in its space use decisions, as the survival of the followers is an important driver of its own fitness through the dilution effect.

Figure S51: Relationship between mean time spent vigilant accross patches (% , median, lower and upper quartile, in the upper panel) and group size for leader (green), solitary individual (blue) or followers maximizing either long-term (red) or short-term survival (purple) in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch.

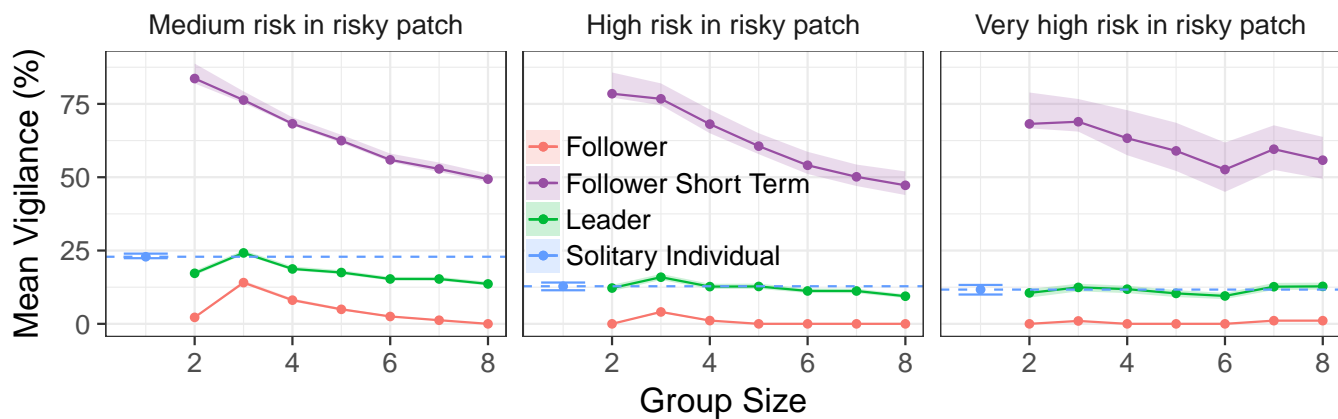


Figure S52: Relationship between mean nutritional state (% , median, lower and upper quartile, in the upper panel) or standard deviation of nutritional state (% , lower panel) and group size for leader (green), solitary individual (blue) or followers maximizing either long-term (red) or short-term survival (purple) in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch.

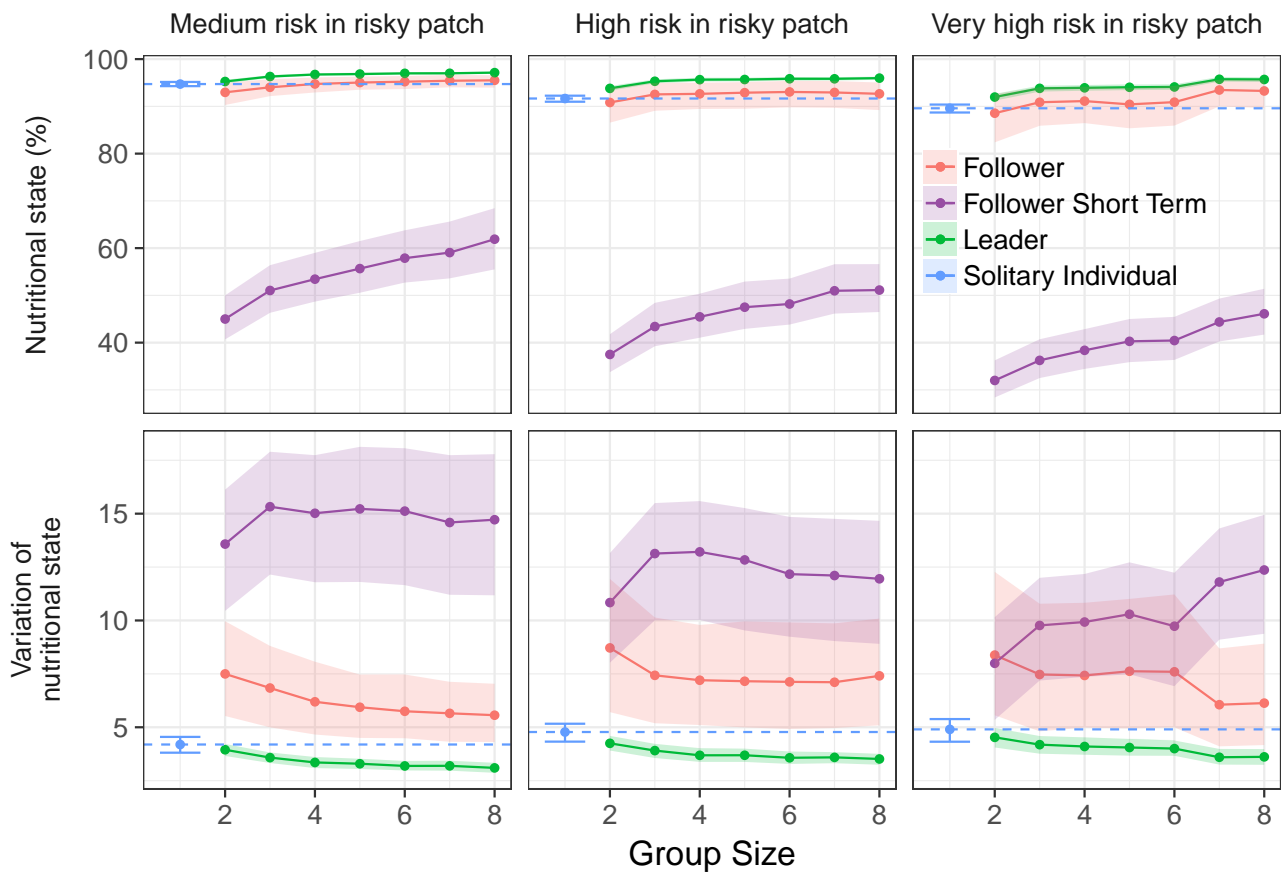


Figure S53: Relationship between mean suffered predation risk (% , median, lower and upper quartile, in the upper panel), mean suffered starvation risk (% , medium panel) or mean suffered total risk (% , lower panel) and group size for leader (green), solitary individual (blue) or followers maximizing either long-term (red) or short-term survival (purple) in situations where the likelihood of meeting the predator is four (left), eight (middle) or sixteen (right) times higher in the risky than in the safe patch. Dashed lines show risk for a leader that would adopt the optimal behaviour of a solitary individual. Percentages correspond to probabilities of death per simulation time step.

