Space Use and Leadership Modify Dilution Effects on Optimal Vigilance under Food-Safety Trade-Offs

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abstract: Dilution of predation risk within groups allows individuals to be less vigilant and forage more while still facing lower risk than if they were alone. How group size influences vigilance when individuals can also adjust their space use and whether this relationship differs among individuals contributing differently to space use decisions remain unknown. We present a model-based study of how dilution affects the optimal antipredator behavior of group members in groups where all individuals determine their vigilance level while group leaders also determine space use. We showed that optimal vigilance did not always decrease with group size, as it was sometimes favorable for individuals in larger groups to use riskier patches while remaining vigilant. Followers were also generally less vigilant than leaders. Indeed, followers needed to acquire more resources than leaders, as only the latter could decide when to go to richer patches. Followers still benefit from dilution of predation risk compared with solitary individuals. For leaders, keeping their leadership status can be more important than incorporating new group members to increase dilution. We demonstrate that risk dilution impacts both optimal vigilance and space use, with fitness reward being tied to a member's ability to influence group space use.

Keywords: group living, predator-prey relationships, model, decision-making, predation-starvation trade-off.

Introduction

Predation risk is an important driver of sociality (Krause and Ruxton 2002). Living in groups generally dilutes predation risk among group members (the so-called dilution effect of grouping; Lehtonen and Jaatinen 2016), and this immediate numerical effect can be complemented by other group-living benefits against predation, such as a collective vigilance that allows for early predator detection (the so-called detection effect of grouping; Dehn 1990; Bednekoff and Lima 1998). As a result, individuals living in groups can benefit from a lower predation risk, which allows them to decrease their own vigilance to increase foraging efficiency. While a decrease in vigilance with increasing group size is commonly reported (Elgar 1989; Lima and Dill 1990; Lima 1995; Roberts 1996; Beauchamp 2013), such a relationship is far from systematically observed. Beauchamp (2008) showed that approximately one-third of the relationships between group size and vigilance investigated in bird studies were not significant. The lack of relationship between group size and vigilance is also commonly noted in mammals. This is particularly clear in the taxa with which we have the most experience, primates and ungulates. Treves (2000) reviewed some examples in the primate literature and showed that in 9 out of 10 studies of nonhuman primates no group size effect on vigilance was found. Similarly, many studies of ungulates have failed to find a significant relationship between group size and vigilance (e.g., studies of African ungulates [Burger and Gochfeld 1994; Creel et al. 2014] and temperate ungulates [Fortin et al. 2004b]). These observations remain puzzling and go against current predictions (Beauchamp 2017). They highlight a gap in our understanding and the need to revisit our theoretical framework for the study of antipredator behaviors.

Grouping and vigilance are not the only behaviors that allow individuals to respond to predation risk. In particular, individuals also adjust their space use decisions—that is, their choice of patches or habitats and the time they spent in those—to resource availability and risk levels. Numerous examples exist: baboons (*Papio cynocephalus ursinus*) prefer low-quality/low-risk to high-quality/high-risk habitat (Cowlishaw 1997), black-tailed deer (*Odocoilus hemionus*)

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reduce the time spent near food patches scented with wolf (*Canis lupus*) urine by foregoing feeding (Chamaillé-Jammes et al. 2014), and elk (*Cervus canadensis*) alter their habitat selection when the risk of wolf predation increases (Fortin et al. 2005). These space use decisions influence resource intake and exposure to predators (Brown 1999), which in turn determine the survival of individuals. These decisions are particularly important as prey often navigate in a "landscape of fear" (sensu Laundré et al. 2001) where predation risk and food resources are not homogeneously spread and where prey face a trade-off between food availability and safety (Brown and Kotler 2004). This trade-off can emerge from resource depletion in the safest patches initially preferred by the prey or because the richer patches are those where the prey is more vulnerable or more likely to meet a predator. For instance, chacma baboons that forage in the rich riverine vegetation are more vulnerable to leopard or lion attacks than when foraging in poorer patches in the desert region because of reduced visibility in the riverine woodlands (Cowlishaw 1997). Such a trade-off between food and safety can also emerge if a predator benefits from tracking prey resources rather than prey themselves (Flaxman and Lou 2009). In the boreal forest, wolves select areas with the greatest resources for caribou (*Rangifer tarandus caribou*) and moose (*Alces alces*), thereby creating a food-safety trade-off for these species (Courbin et al. 2014). Therefore, space use decisions are a key component of an individual's antipredator strategy, and as such they should be adjusted in interaction with other behaviors, such as vigilance and grouping.

The interaction between these three key antipredator behaviors—grouping, vigilance, and space use behavior—is not well understood. To the best of our knowledge, no empirical study has investigated in a single study how these three behaviors interact with the others, and only Beauchamp and Ruxton (2007) have provided theoretical insights into this issue. Their model shows that if individuals can move to a refuge after having acquired sufficient resources, the presence of conspecifics may lead to reduced vigilance. This outcome largely results from the fact that it pays to forage more quickly than other individuals, to return to safety earlier and pass the risk of predation to conspecifics that are still foraging. However, this process occurs less forcefully in large groups because individuals in these groups are less vulnerable to the departure of a single individual. Overall, in the modeled situation the relation between group size and vigilance could take many forms (increase, decrease, nonmonotonic change) depending on parameter values (Beauchamp and Ruxton 2007), demonstrating the potentially strong interaction among patch use, vigilance, and group size. In their model, Beauchamp and Ruxton (2007) considered individuals to be nonsocial and that there were no benefits for them to remain within groups after having acquired sufficient resources because they moved to a ref-

uge. The group was simply a temporary aggregation that animals could leave at no cost. Beauchamp and Ruxton's (2007) model would be adequate to study animals that aggregate passively while foraging in suitable areas. The model could, for instance, be applied to elk that aggregate in open areas at night and return solitarily or in much smaller groups to nearby forest to find cover from wolves (Creel and Winnie 2005). Beauchamp and Ruxton's (2007) model would not apply to social species that form long-term stable associations in which individuals travel and forage together for long periods. For these species, no theoretical model of antipredator strategies has yet been formulated.

Strong social cohesion is observed in many species, including some primate (e.g., van Schaik and Kappeler 1997) and equid (e.g., Rubenstein 1986) species, in which adult group members can stay together for years. It is a striking observation that individuals remain together for long periods of time—and thus use space similarly—even if their needs (given their age, sex, and nutritional condition) and vulnerability differ. Much research has been devoted to understand decision-making processes in such groups. Studies have revealed a wide diversity of situations, with decisions about when and where to move ranging on a continuum from being well distributed among group members (i.e., collective/shared decisions) to undistributed (i.e., despotic decisions by a leader; Bourjade and Sueur 2010; Conradt and Roper 2010; King and Sueur 2011; Strandburg-Peshkin et al. 2015). For instance, detailed studies of the behavior of group members during pre- and postdeparture periods in Tonkean macaques (*Macaca tonkeana*) and Przewalski horses (*Equus ferus przewalskii*) have revealed that virtually all individuals can successfully initiate movements (i.e., decisions are well distributed among group members) and that the actual decisions of moving result from a shared consensus (Bourjade and Sueur 2010). In other species, space use decisions appear much less distributed. For instance, in chacma baboons the dominant male acts as a despotic leader without coercive behavior, able to successfully lead a group to patches where only it could access the resource (King et al. 2008). Females that have developed social bonds will follow this dominant male because they can benefit from its protective behavior against predators or infanticide by other males (King et al. 2008). Other males will likely follow to maintain their status in the hierarchy and, possibly for high-ranking males, to obtain some share of the food (King et al. 2008). In vervet monkeys (*Chlorocebus pygerythrus*), older females often lead the group (Lee and Teichroeb 2016). This is also true in harem-forming equid species (Rubenstein 1986), although this may interact with female reproductive status (Fischoff et al. 2007). Stallions likely follow to secure mating opportunities.

Overall, even if some form of collective decision may often exist in stable social groups, in many instances some individuals have much more weight in the movement deci-

Table 1: Model assumptions

	Assumption
Groups	Group size is constant
Predation	Predator can kill only one prey when encountering a group of prey
	Vigilance decreases only the predation risk of the focal individual (no collective detection)
Foraging	Vigilance and foraging are exclusive
	Type II response in foraging
	The encounter rate with food items decreases with the time spent vigilant
Optimal strategy	Fitness equivalent to long-term survival (nonreproductive season)
	Followers know the probability of patch switching, given the patch they currently occupy

sion than others. This does not prevent the individuals that contribute less to the decision to remain within the group (Sueur 2012). Accordingly and irrespective of our understanding of the processes underlying decision-making and the persistence of stable associations, we note that followers have to cope with space use decisions that they did not influence. When space use decisions determine the risk of predator encounters, differences between leaders and followers in risk perception or in body condition affecting the food-safety trade-off could lead followers to places that are suboptimal relative to their own needs for resources and safety (Sueur and Pelé 2015). In such cases, followers can still adjust vigilance levels to deal with the food-safety trade-off. This suggests that vigilance levels and the relationship between group size and vigilance could differ among group members, depending on their contribution to space use decisions. These contributions will also likely drive differences in the costs of antipredator behavioral adjustments (vigilance, space use) across individuals, but this has been overlooked until now, and no theoretical predictions exist.

Here, we contribute a theoretical study as a first step toward understanding the interaction among group size, vigilance, and space use in social species that forage under predation risk and form stable associations in which individuals do not contribute equally to space use decisions. We developed a model to determine optimal vigilance and space use for solitary individuals and for leaders and followers in groups of various sizes. We assumed that increasing vigilance level reduces foraging rate (as observed in primates [e.g., Cowlishaw et al. 2004] and ungulates [e.g., Fortin et al. 2004*a*]) and that individuals forage in an environment made of two patches characterized by a trade-off between resource quantity and predation risk. We used our model to test the following predictions. First, for group leaders we predicted

that both optimal vigilance and space use may be affected by a dilution effect, with individuals spending more time in risky places and/or being less vigilant, depending on the relative costs and benefits of predator avoidance and vigilance. Therefore, we also predicted that a dilution effect on optimal vigilance with increasing group size should not always occur when individuals can also adjust space use to their perception of risk. Second, for followers we predicted that they could decrease their vigilance with increasing group size but also that this response can depend on the leader's behavior. However, followers face uncertainty about their future foraging opportunities because space use is decided only by leaders; hence, followers may need to forage more to maintain higher energy reserve. The increased foraging effort would come at the expense of vigilance, and we predicted that followers would maintain lower vigilance levels than leaders. Therefore, followers should experience higher predation risk than leaders.

Methods

The model is stochastic, and in this article we present the outcomes of simulations run with individuals following the optimal behavioral strategies (depending on their leader/follower status, group size, and other parameters; see the model description and "Results"). These optimal strategies are found using a dynamic programming algorithm (Houston et al. 1988) applied to the model. The dynamic programming procedure is described below in the section "Finding Optimal Strategies." Model assumptions can be found in table 1, while parameters and equations are summarized in table 2. The model was implemented in Julia (ver. 0.5.12; Bezanson et al. 2014), and the code is available on figshare (Patin et al. 2017) and as a zip file, available online.[1]

Model Outline and Mathematical Formulation

Outline. The model uses discrete time steps and simulates the behavior of individuals foraging either solitarily or in groups. Groups are made of a despotic leader, which decides at each time step where the group will forage, and one to seven followers that cannot leave the group. Status—solitary, group leader, or follower—is a fixed attribute of individuals. This simple situation (despotic leadership, stable group composition) was used to study the implications of group size and individual contribution to movement decisions on individual vigilance and group space use. The environment is made of two contrasted patches. The likelihood of being attacked is lower in one patch than in the other, but the safe

1. Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

patch is relatively poor in food resources (hereafter defined as safe/poor patch vs. risky/rich patch). No food depletion occurs in the patches. Our model can therefore be thought of as representing individuals living at low density and having little impact on the forage basis, compared with other, unaccounted for factors. Each individual is characterized by a nutritional state s that declines with time if no feeding takes place. An individual's probability of starvation increases with decreasing s, and individuals die immediately if s reaches 0. At each time step, a decision about where to forage is made by the solitary individual or the group leader. All individuals then decide on their vigilance level. Higher vigilance decreases foraging but increases the chance of surviving an attack. Attacks occur stochastically based on patch-specific, predefined probabilities. When foraging in a group, a given individual is attacked with a probability $1/N$, with N being the group size. Thus, individual vigilance level has no impact on the likelihood of being attacked, but it affects the chances of surviving. Note that we focused here on the dilution effect, and we did not include the detection effects that may result from collective vigilance.

Formulation. The following computations were performed at each time step.

Computation 1. Solitary individuals and group leaders chose in which patch $p(t)$ to forage, and all individuals decided on their vigilance levels $v(t)$. These state-dependent decisions—the main focus here—were determined during the optimization process. We assumed that individuals had perfect knowledge of the patch characteristics and that decisions were made to maximize long-term survival of foragers.

Computation 2. All individuals had their nutritional state $s(t)$ modified. First, $s(t)$ decreased by $c(t)$, a metabolic cost that was drawn from a discrete normal distribution. The use of a distribution, rather than a set value, introduces some of the natural randomness observed in the energetic costs and gains of individuals, as done by Rands et al. (2003). Technically, a discrete normal distribution is the equivalent of a normal distribution for integer values, with the probability of a specific value proportional to the density of the corresponding normal distribution at this value. Here, the discrete approximation of a normal distribution was required by the use of a dynamic programming algorithm, which cannot operate on continuous values (Marescot et al. 2013). Second, $s(t)$ increased by $g(t)$, the amount of resources gained while foraging, drawn from a discrete normal distribution whose parameter depended on patch and vigilance level; $g(t)$ was drawn independently for each individual of a group. In a given patch, the mean amount

Table 2: Parameters and functional relationships

Variable	Definition	Formula or value
$v(t)$	Vigilance at time t	[0–1] (21 levels)
$p(t)$	Patch at time t	Risky and rich or safe and poor
$s(t)$	Nutritional state at time t	[0–40] (41 levels)
$c(t)$	Cost: state decrease at time t	$\mathcal{N}(2.5, 1, 4)$
$g(t)$	Gain: state increase at time t	$\mathcal{N}(G(p(t), v(t)), 1, M(p))$
$M(p(t))$	Maximum gain	Four in safe patch, eight in risky patch
$G(p(t), v(t))$	Mean gain in patch $p(t)$ with vigilance $v(t)$	$G(p(t), v(t)) = A \times \left(\frac{a(v(t)) \times R(p(t))}{1 + a(v(t)) \times h \times R(p(t))} \right)$
$a(v(t))$	Prey encounter rate with food items	$a(v(t)) = a_0(1 - v(t)^{a_1})$
a_0	Prey maximum encounter rate with food items	$a_0 = 1$
a_1	Cost of vigilance	$a_1 = 0$ if cost scales linearly with vigilance
		$a_1 = -0.25$ if cost is lower
		$a_1 = 0.5$ if cost is higher
h	Handling time	$h = 0.75$
$R(p(t))$	Patch resources	$R(\text{safe}) \approx 0.8$; $R(\text{risky}) \approx 2.54$
A	Duration of a time step	$A = 4$
$\text{Pred}(p(t), v(t))$	Probability of being killed by a predator	$k_0(p(t)) \times N^{k_2} \times 1/N \times \exp(-k_1 v(t))$
$k_0(p(t))$	Encounter rate with predator	$k_0(\text{safe}) = 0.001$; $k_0(\text{risky}) \in [0.004, 0.008, 0.016]$
k_1	Decrease of predation risk with vigilance	$k_1 = 1.5$
k_2	Increase of encounter rate with group size	$k_2 = 0$ if there is no increase in encounter rate with group size; $k_2 \in [0.25, 0.75]$ otherwise
n	Group size	$n \in [1–8]$
$\text{Starv}(s(t))$	Probability of dying by starvation	$1 - e^{s(t)f}$
f	Strength of starvation risk	$f \in [0.2, 0.25, 0.3]$; the larger f, the smaller the starvation risk

Note: $\mathcal{N}(\text{mean}, \text{sd}, \text{max})$ is for the discretized normal distribution of the mean, standard deviation, and maximum.

of resources eaten over each time step G was assumed to increase asymptotically with local resource biomass, as expected by a type II functional response (Stephens and Krebs 1986), with the resource level of the patch. The encounter rate with food items decreases with the time spent vigilant. It follows that

$$G(p(t), v(t)) = A \times \left(\frac{a(v(t)) \times R(p(t))}{1 + a(v(t)) \times h \times R(p(t))} \right), \quad (1)$$

where

$$a(v(t)) = a_0(1 - v(t)), \quad (2)$$

with a being the encounter rate with food items (equal to a_0 when vigilance $v(t)$ is 0). The term $R(p)$ is the level of resources in the patch, h is the handling time, and A is a scaling constant, equivalent to time spent foraging. See figure A1A (apps. A, B and figs. A1, A2, B1–B8 are available online) for a visual representation of the shape of this function. Note that this formulation of the functional response assumes no interference between individuals.

Computation 3. Individuals may die from predation. The actual presence of a predator in the patch at this time step was determined following a patch-specific predefined probability k_0. This probability was by definition higher in risky patches and remained constant throughout the simulations. If the predator was present it always attacked, but it could target only one prey. For groups, we assumed that the predator selected the group member to be attacked randomly. Thus, the likelihood of a specific individual being targeted was $1/N$. As we focus here on the dilution effect only, we did not integrate the detection effect. We also assumed that the likelihood that an individual died following an attack decreased with its vigilance level with a diminishing return, as in Dehn (1990). Specifically, the probability of dying from predation was

$$\text{Pred}(t) = k_0(p(t)) \times \frac{1}{N} \times \exp(-k_1 v(t)), \quad (3)$$

with k_0 being the patch-specific predator encounter rate and k_1 being a parameter influencing how vigilance affects the likelihood of dying following an attack. See figure A1B for a visual representation of the shape of this function.

Computation 4. Individuals may die from starvation, with a probability decreasing with its nutritional state $s(t)$, following

$$\text{Starv}(t) = \exp(-fs(t)), \quad (4)$$

with f being a parameter influencing how the nutritional state affects the likelihood of dying from starvation. See figure A2 for a visual representation of the shape of this function.

Finding Optimal Strategies

We determined optimal strategies for space use and vigilance for individuals aiming to maximize their long-term survival

using a dynamic programming algorithm (see details in app. B). The dynamic programming algorithm was chosen because it provided an easy and satisfying way of find prey optimal strategies under simple assumptions (Marescot et al. 2013). More complex assumptions (collective detection, for instance) would require a game theoretic approach, like a genetic algorithm (Ruxton and Beauchamp 2008).

Therefore, for solitary individuals and group leaders, we had to find, for any given environment, optimal state-dependent decisions on space use and vigilance. We assumed that individuals optimize their long-term survival, which is here a proxy for fitness. Individual optimal strategies ($p(s(t))$ and $v(s(t))$ for the leader and solitary individual, $v(s(t), p(t))$ for the follower) are calculated using a dynamic programming algorithm (see, e.g., Houston et al. 1988).

For the leader and the solitary individual. The term $J(S, t, T)$ denotes the probability of survival from day t until day T given that $s(t) = S$ and that the animal follows the best strategy. Maximizing long-term survival is equivalent to maximizing $J(S, t, T)$ with T being very large. We know that

$$J(S, T, T) = 1 - \Pr_{\text{starvation}} (T|s(T) = S). \quad (5)$$

The term $\Pr_{\text{starvation}}(T)$ depends only on S. Therefore, $J(S, T, T)$ is known.

We also know that

$$J(S, t, T) = \max_{\pi, v}(P(S, \pi, v, t, T)), \quad (6)$$

with $P(S, \pi, v, t, T)$ being the probability that the animal survives until time T given that he chooses at time t level of vigilance v and patch π. This is known as the stochastic dynamic programming equation. More specifically, with $s_{\max}$ being the maximum nutritional state,

$$P(S, \pi, v, t, T) = 1 - \Pr_{\text{predation}} (t|p(t) = \pi, v(t) = v)$$

$$\times \left(1 - \Pr_{\text{starvation}} (T|s(T) = S) \right)$$

$$\times \sum_{\sigma=0}^{s_{\max}} \left(\Pr(s(t + 1) = \sigma) \times J(\sigma, t + 1, T) \right). \quad (7)$$

Thus, $J(S, t, T)$ is the maximum of the different $P(S, \pi, v, t, T)$ that we can calculate given that we know $J(S, t + 1, T)$. The optimal strategy at time t is the corresponding π and v. As we know $J(S, t, T)$, we can proceed by backward induction and find recursively $J(S, t, T)$ and the associated optimal strategy, that is, $\pi^*(s)$ and $v^*(s)$. Convergence is achieved when the optimal strategy becomes stable over t (see fig. B1 for convergence time).

For the follower. For followers, the optimal vigilance strategy depended on their current nutritional state and on the patch currently used. The optimal strategy of followers thus

depended on the sequence of patches used by the leader, but this sequence could not be known in advance because of the stochastic changes in the leader's nutritional status, which in turn influenced its patch use decisions. Thus, finding the optimal strategy for followers required making assumptions on their expectations for space use. We tested two different assumptions about their expectations.

First, we assumed that followers knew the probability of patch switching, given the patch they currently occupied (i.e., that they knew the average residence time in the current patch).

We now need to maximize $J(S, \pi, t, T)$, the probability of survival from day t until day T given that $s(t) = T$ and $p(t) = \pi$. The term $J(S, \pi, T, T)$ is known (as in eq. [5]), and we have

$$J(S, \pi, t, T) = \max_v (P(S, \pi, v, t, T)), \qquad (8)$$

with $P(S, \pi, v, t, T)$ being the probability that the animal survives until time T given its chosen level of vigilance v and its currently occupied patch π (imposed by the leader) at time t. We have then

$$P(S, \pi, v, t, T) =$$

$$1 - \Pr_{\text{predation}} (t | p(t) = \pi, v(t) = v)$$

$$\times \left(1 - \Pr_{\text{starvation}} (T | s(T) = S) \right)$$

$$\times \sum_{\sigma = 0}^{s_{\max}} \Bigg(\Pr(p(t + 1) = \text{risky}) \times \Pr(s(t + 1) = \sigma) \qquad (9)$$

$$\times J(\sigma, p(t + 1) = \text{risky}, t + 1, T)$$

$$+ \Pr(p(t + 1) = \text{safe}) \times \Pr(s(t + 1) = \sigma)$$

$$\times J(\sigma, p(t + 1) = \text{safe}, t + 1, T) \Bigg).$$

To calculate $P(S, \pi, v, t, T)$, we have to know the distribution of $p(t + 1)$, the patch used at $t + 1$ and chosen by the leader. Based on simulation of the leader behavior, we extracted the transition matrix with $p(t + 1) \vee p(t)$. This choice assumes that followers know the probability of patch switching given the patch they currently occupy. Said differently, followers knew what the optimal strategy of the leader was and have expectations about future space use. See below ("Analyses" and "Results") for an investigation of the effects of this assumption. Once we have $P(S, \pi, v, t, T)$, maximizing it over v gives $J(S, \pi, t, T)$ and the optimal strategy $v(t, s, \pi)$. By backward induction with T large enough, we can find the optimal strategy $v(s, \pi)$.

Simulations

Once the optimal strategies were found for solitary individuals, group leaders, and followers, we simulated their foraging dynamics over time and compared their behavior and overall performance. For each case (solitary, leader, follower), we ran 2,000 simulations for distinct individuals (in distinct groups for followers). For leaders and followers, in all simulations we assumed that group size remained constant, that is, individuals that died were immediately replaced. Thus, we assumed that the timescale over which group size could vary was longer than the timescale over which behavioral strategies were optimal. Strategies were optimized over 250 time steps, but optimal strategies emerged after ~50 time steps. As life expectancy was approximately 150 in the riskier situation modeled, this assumption was verified post hoc (see details in app. B). Individuals started simulations near the maximum state (app. B). During each simulation we recorded patches used, mean vigilance level, mean and standard deviation of the nutritional state, mean probability of dying from predation or starvation (calculated as the average of the instantaneous values from eqq. [3] and [4]), and the total mortality rate. These risks are presented as probabilities of dying per simulation time step.

Analyses

We calculated optimal strategies and ran simulations in three different situations. First, we tested that our model could reproduce the expected patterns emerging from a dilution effect when individuals cannot adjust their space use to deal with the food-safety trade-off and can rely only on vigilance adjustments. We did so by simulating the optimal behavior of individuals in an environment with only one patch (nonspatial model). In such cases, the only antipredator behavior was vigilance, and we expected that it should decrease monotonically with group size.

Then, in a two-patch context, we explored the different behavioral adjustments to dilution and despotic leadership by comparing solitary individuals, group leaders, and followers. The comparison between solitary individuals and group leaders showed the behavioral adjustments to dilution and their potential benefits. The comparison between leaders and followers informs how changes in optimal vigilance due to risk dilution were modified by the costs of imposed space use. We assessed how sensitive our conclusions were to changes in the strength of the following determinants of the food-safety trade-off: (i) the level of predation risk, which we modified by increasing risk in the risky patch (see "Results"); (ii) the level of starvation risk, which we modified by changing the value of parameter f in equation (4); and (iii) the cost of vigilance, which we modified by changing the shape of the relationship between encounter rate with food items and vigilance level. In this last case, equation (2) was modified so that the attack rate could vary nonlinearly with vigilance, depending on parameter a_1. This gives

$$a(v(t)) = a_0 (1 - v(t)^{1-a_1}). \qquad (10)$$

If $a_1 = 0$, the relationship is linear. If $a_1 < 0$, the encounter rate with food items decreases faster than expected under linear assumptions, thereby increasing the cost of vigilance. On the contrary, when $a_1 > 0$, vigilance is less costly. We also investigated how our results were influenced by the fact that the benefits of group dilution can be reduced if larger groups are more frequently encountered by predators, as reported in various predator-prey systems (Krause and Gaudin 1995; Hebblewhite and Pletscher 2002). Equation (3) was modified to

$$\text{Pred}(t) = k_0(p(t)) \times N^{k_2} \times \frac{1}{N} \times \exp(-k_1 v(t)). \quad (11)$$

The basal encounter rate with predator k_0 is now multiplied by N^{k_2}. When $k_2 = 0$, the equation simplifies into equation (3), and the encounter rate does not change with group size. However, when $k_2 > 0$, the encounter rate increases with group size. When k_2 is higher, the benefits of risk dilution are reduced because the encounter rate with the predator increases with group size. Finally, in a last investigation of the effects of model assumptions, we compared the consequences for the followers to lack knowledge about the long-term patch use of their leaders. For this, we compared the followers' vigilance levels and their predation, starvation, and total mortality rate under the original model formulation and one where followers do not have expectation about future patch use and choose, at each time step, the vigilance level that maximized their survival to the next time step (i.e., short-term survival).

Results

Validating That the Model Can Reproduce Expectations about the Dilution Effect on Vigilance in the Absence of Space Use Decisions

In a model with only one patch where individuals took state-dependent decisions about their own vigilance level, the optimal strategies that maximized long-term survival always consisted of increasing vigilance with nutritional state (see fig. B3). In different situations, strategies differed in how much vigilance increased. Simulations using optimal behavior showed that, as expected, vigilance declined monotonically with group size (supplement 1, fig. S1-1; supplements 1–5 containing the supplemental figures are available online), allowing individuals to achieve a higher nutritional state (supplement 1, fig. S1-2). Accordingly, their risk of dying from starvation decreased with group size (supplement 1, fig. S1-3, *middle panel*) concurrently with predation risk, which followed the expected dilution of risk given by $1/N$ (supplement 1, fig. S1-3, *upper panel*). Therefore, we concluded that our model was adequate to study dilution effects and their consequences on the behavior of individuals.

Optimal State-Dependent Strategies in a Two-Patch Model

For leaders, in a model with two patches, finding the optimal state-dependent strategy consisted of finding in what patch and at what vigilance level leaders should forage, for each possible value of their nutritional state, to maximize long-term survival. We found that this optimal strategy was, below a certain nutritional state, to forage in the risky patch with no vigilance. As state increased above this nutritional state, the strategy was then to forage in the risky patch with an increasing vigilance level until the nutritional state reached a threshold value. When the nutritional state was above this value, the optimal strategy made leaders forage in the safe patch at a reduced vigilance level, which, however, increased as their nutritional state increased to its maximum value. An example of a leader optimal strategy is shown in figure B4. With different situations of risk level, starvation strength, or other parameters, the strategies differed in the nutritional states at which individuals became vigilant and switched patches and in the strength of the increase in vigilance with nutritional state, in both the risky patch and the safe patch (not shown).

For followers, finding the optimal state-dependent strategy consisted of finding at what vigilance level followers should forage, for each possible value of their nutritional state and for each patch type, to maximize long-term survival. We found that this optimal strategy was, in both patch types, to forage with no vigilance until the nutritional state reached a threshold value above which vigilance increased with increasing nutritional state. The threshold value at which followers became vigilant was lower in the risky patch than in the safe patch, in which followers were often always nonvigilant. An example of a follower optimal strategy is shown in figure B5. With different situations of risk level, starvation strength, or other parameters, the strategies differed in the nutritional states at which individuals became vigilant and in the strength of the increase in vigilance with nutritional state, in both the risky patch and the safe patch (not shown).

Consequences of an Increase in Predation Risk in the Risky Patch

Vigilance and patch use were complementary behaviors to deal with the food-safety trade-off. As risk in the risky patch increased (fig. 1 from left to right; see fig. S2-1 in supplement 2 for patch-specific vigilance), the optimal foraging strategy of solitary individuals or group members shifted from mostly using the risky patch while being highly vigilant to reducing both their use of the risky patch and their vigilance level. Independent of the general level of risk of the risky patch, vigilance and the time spent in the risky patch did not change monotonically or consistently with group size. For example, the optimal space use for groups of three individuals involved a stronger use of the risky patches than groups of two or six
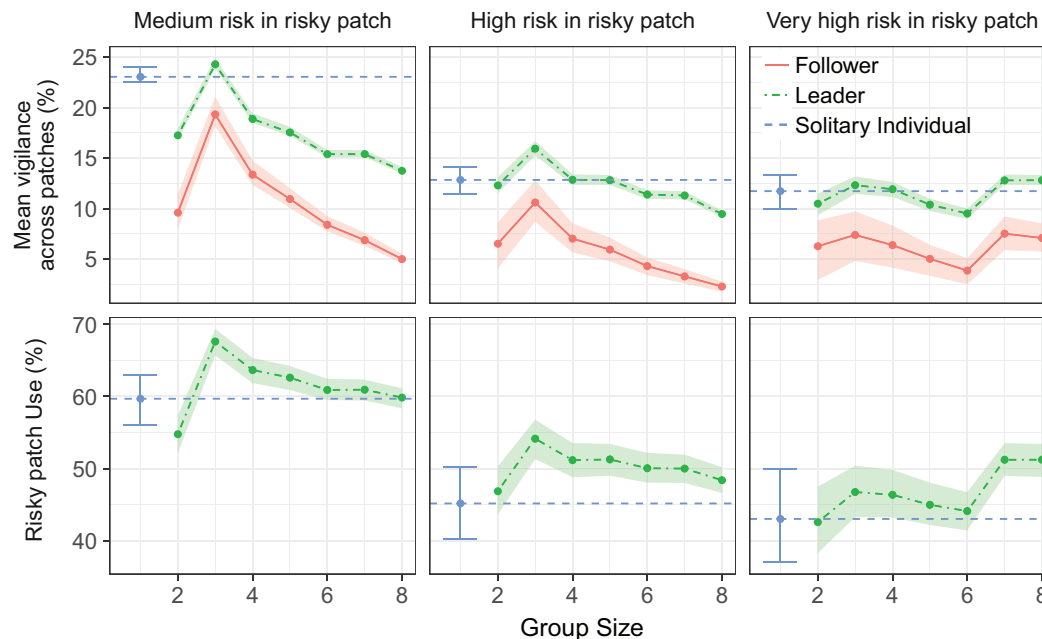
Figure 1: Relationship between time spent vigilant across patches (%; median, lower and upper quartiles; *upper panels*) or time spent in the risky patch (%; *lower panels*) and group size for solitary individuals (blue), group leaders (green), and followers (red), in situations where the likelihood of meeting the predator is four (*left*), eight (*middle*), or sixteen (*right*) times higher in the risky patch than in the safe patch. Patch use is displayed only for leaders because it is identical for followers and their leader. Patterns of how vigilance, averaged across patches (shown here), changes with group size match the patterns observed in the risky patch because vigilance levels are generally very low in the safe patch (see supplement 2, fig. S2-1).

individuals, with concomitant changes in overall vigilance levels (fig. 1).

Overall, dilution reduced the risk of predation (fig. 2, *top panels*) and the total mortality risk (fig. 2, *bottom panels*) of members of larger groups. However, members of larger groups put themselves at greater risk of predation than what would be expected if they were using the optimal vigilance and patch use strategy of a solitary individual while remaining in the group (fig. 2, *top panels*, dashed line). However, this management of the food-safety trade-off and its consequences varied strongly between leaders and followers (fig. 2).

These differences are now described. Group leaders were not always less vigilant than solitary individuals because they sometimes increased their use of the risky patch instead (fig. 1). However, they benefited greatly from group living: they had a higher and generally less variable nutritional state than solitary individuals, and these differences increased with increasing group size (fig. 3). Accordingly, leaders experienced greater reduction in both starvation risk and predation risk as group size increased (fig. 2).

Followers were consistently less vigilant than solitary individuals but also less vigilant than their group leader (fig. 1). Still, their nutritional state was lower and much more variable than that of their leader (fig. 3). When in smaller groups (two or three individuals), the nutritional state of followers

was sometimes even lower than that of solitary individuals (fig. 3), indicating that individuals increase their safety at the expense of resource intake when joining a small group with a predetermined leader. The nutritional state of followers increased with group size, but it always remained highly variable (fig. 3), indicating that followers often experienced times of low nutritional state associated with high starvation risk (fig. 2; see fig. S2-2 in supplement 2 for an example of such an event). Followers had a higher predation risk than leaders, but it was still lower than that of solitary individuals (fig. 2). Compared with solitary individuals, followers maintained lower vigilance (fig. 1) but experienced lower total mortality risk (fig. 2), demonstrating that the benefit brought by dilution of predation risk within groups exceeds the cost of increased starvation risk.

Consequences of an Increase in Starvation Risk

Generally, the results presented above hold qualitatively when starvation risk increases. The dilution effect, however, becomes more beneficial when starvation risk increases (supplement 3, fig. S3-7, *upper panel*), as individuals have to be less vigilant to forage more (supplement 3, fig. S3-1), and changes in vigilance and risky patch use with group size are then more marked (supplement 3, fig. S3-1, S3-2).
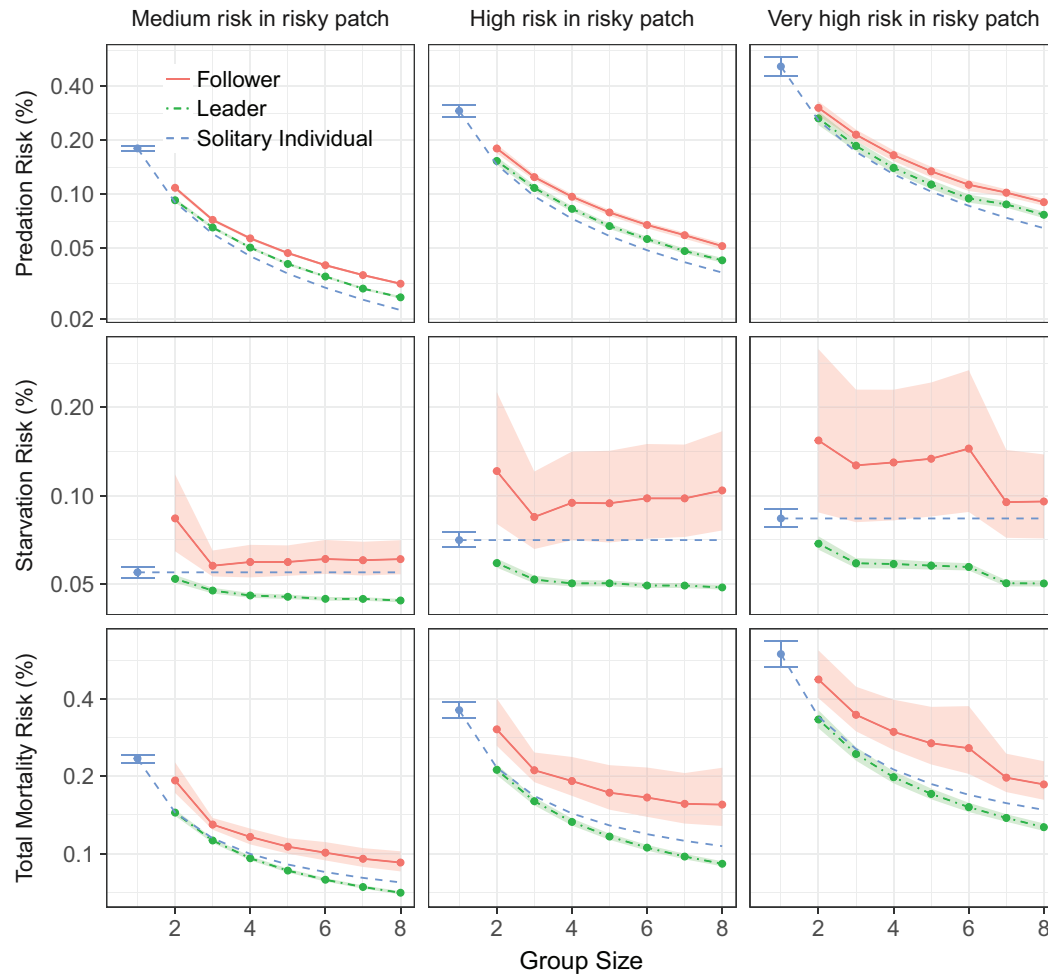
Figure 2: Relationship between mean experienced predation risk (%; median, lower and upper quartiles; *upper panels*), mean experienced starvation risk (%; *middle panels*), or mean experienced mortality risk (%; *lower panels*) and group size for solitary individuals (blue), group leaders (green), and followers (red), in situations where the likelihood of meeting the predator is four (*left*), eight (*middle*), or sixteen (*right*) times higher in the risky patch than in the safe patch. Dashed lines show the risk of a leader that would behave like an optimal solitary individual. Percentages correspond to probabilities of death per simulation time step.

Consequences of an Increase in the Cost of Vigilance

Changes in the cost of vigilance mainly changed vigilance levels, but vigilance levels and patch use still varied nonmonotonically with group size (supplement 4, fig. S4-3, S4-4, *left panel*). Increasing the cost of vigilance led to lower vigilance levels and lower use of the risky patch (supplement 4, fig. S4-3, S4-4, *upper panel*). When the cost of vigilance was too high, followers were never vigilant, and leaders were vigilant only rarely (supplement 4, fig. S4-3, *upper panel*).

Consequences When a Higher Group Size Increases the Encounter Rate with the Predator

When group size increased the encounter rate with the predator, the relationships between behavior (vigilance levels, patch use) and predation, starvation, total mortality risks, and group size were attenuated (supplement 4, fig. S4-3 to S4-9, *right panel*). When the benefit of increased group size became too low, total risk could not be decreased much by trading predation risk against starvation risk (supplement 4, fig. S4-7 to S4-9, *right panel*). In such a situation, patch use and vigilance of leaders showed a slight monotonic decrease with group size, while risk was not very different compared with that for a solitary individual. However, followers experienced higher total risk, and they did not benefit anymore from being in a group (supplement 4, fig. S4-9, *right panel*).

Consequences of the Lack of Knowledge about Future Space Use by Followers

If followers had no expectations about future space use and were to maximize their short-term survival (i.e., their sur-
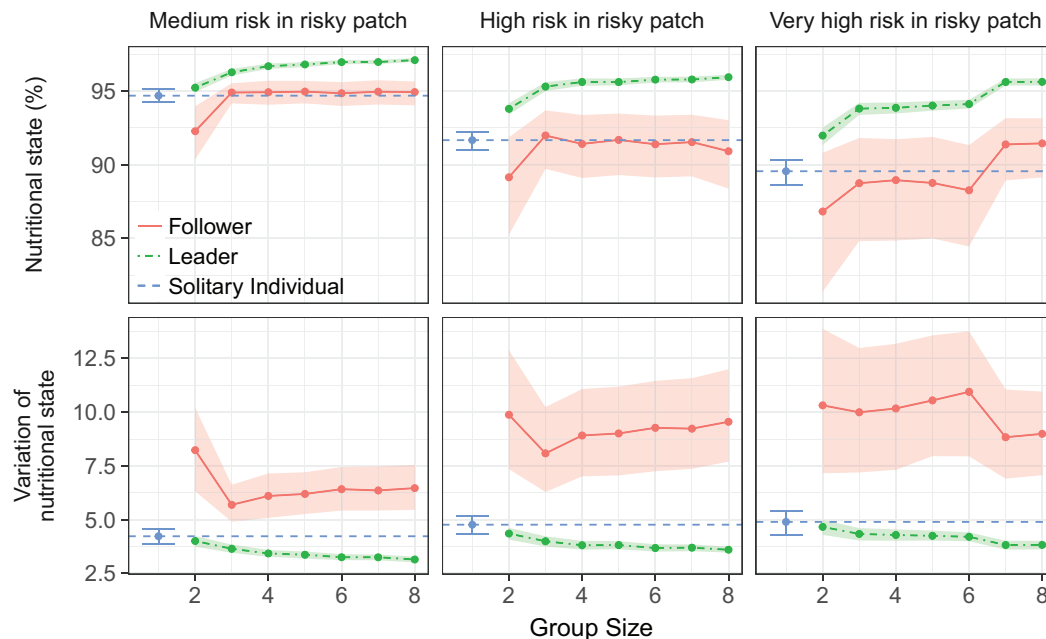
Figure 3: Relationship between mean nutritional state (% of maximum state; median, lower and upper quartiles; *upper panels*) or the standard deviation of nutritional state (% of maximum state; *lower panels*) and group size for solitary individuals (blue), group leaders (green), and followers (red), in situations where the likelihood of meeting the predator is four (*left*), eight (*middle*), or sixteen (*right*) times higher in the risky patch than in the safe patch.

vival until the next time step), their life expectancy would be really low (supplement 5, fig. S5-3). With the same nutritional state, followers without expectations about future space use maintained a higher vigilance and thus a lower foraging rate than followers with such expectations (compare figs. B4 and B5). In the situation of short-term maximization of optimal strategy, followers were more vigilant (supplement 5, fig. S5-1) and had a lower nutritional state (supplement 5, fig. S5-2/S5-1) than both leaders and followers, with the consequence that they had a lower predation risk but a higher risk of starvation. Ultimately, followers without expectations about future space use experienced a higher risk of mortality (supplement 5, fig. S5-3).

Discussion

Our study provides, to our knowledge, the first model combining dilution effects of predation risk, vigilance, and space use behavior in heterogeneous environments where a spatial food-safety trade-off exists. This comprehensive model provides multiple explanations, based on optimality principles, for the lack of relationship between vigilance and group size or for unexpected forms of this relationship found in many empirical studies (see the meta-analysis by Beauchamp 2008). Previous studies have shown that interference within groups

and scrounging behavior can alter the relationship between group size and vigilance (Beauchamp 2001, 2003; Fortin et al. 2004*b*). Here, we show that simply considering that individuals can also adjust their space use in response to risk leads to complex relationships among group size, vigilance, and space use. The decrease in predation risk from the dilution effect can be partially reallocated into resource acquisition either through a decrease in vigilance (and a concomitant increase in foraging) and/or an increase in the use of patches with high predation risk and food availability. Whether individuals will choose to invest more in riskier patch use or to reduce their vigilance depends on the relative efficiency of those two tactics in increasing resource gain while keeping predation risk relatively low. The sudden and erratic changes in vigilance and space use with group size indicate that optimal solutions shift rapidly between riskier space use and decreased vigilance with increasing risk dilution. Ultimately, we conclude that the lack of a consistent relationship between group size and vigilance levels is not in itself an indication of a lack of dilution effect on behavioral adjustments to predation risk by the prey. Together and independently of assumptions about leadership, vigilance and space use behaviors offer individuals a wealth of combinations to balance the food-safety trade-off (e.g., Brown 1999, this model). This was already noted by Cowlishaw (1998), who suggested that the lack of a relationship between group size and vigilance in chacma

baboons could be due to the fact that smaller groups spent more time in safer areas and therefore made different vigilance adjustments than larger groups. Cowlishaw (1998, p. 448) concluded that "variation in vigilance among individuals may be at least partially attributed to differential investment in other anti-predator behavior." Surprisingly, these interactions between antipredator behaviors remain poorly studied, both empirically and theoretically. Our work is a first step toward reducing this knowledge gap.

Irrespective of the actual complementarity occurring between vigilance and space use, our results show that dilution consistently allowed group leaders to obtain better and less variable nutritional states than solitary individuals, an advantage leading to lower starvation risk for a similar predation risk. Our results show, however, that followers benefit less than leaders from the dilution effect. Although by definition they have the same patch use and thus the same likelihood of being attacked as their leader, followers consistently display lower vigilance. This pattern emerged as a consequence of the followers' inability to adjust space use according to their current nutritional needs. Their optimal strategy anticipates that they will not be able to choose the rich patch when needed to maintain their state. When starvation risk is high, followers face the dilemma of reducing vigilance to increase foraging efficiency or maintaining vigilance to maintain low predation risk, particularly when the leader has led the group to the risky patch. This anticipation is consistent with Rands et al.'s (2003) model of optimal behavior for pairs of foraging individuals. In their model, individuals with a high nutritional state forage when their low-state partner forages, even if their own state is not at stake and if foraging is riskier than resting. This occurs because individuals anticipate that they will need to forage at some point in the near future and because it is safer to forage when the other forages than when the other rests (a model assumption). The importance of anticipation is also highlighted by the decreased survival observed when followers' strategies optimize short-term survival without any knowledge of long-term patch use. Overall, it is clear that optimal foraging strategies in a social context account for the future needs of the individual and for the uncertainty about the behavior of other individuals (timing of foraging in Rands et al. 2003; leader space use decision in our model).

However, our results suggest that in many situations the optimal strategy of followers, leading to reduced vigilance, does not enable them to compensate for the fact that they cannot select food-rich patches—the choice belonging to leaders—when their own nutritional state is low. Indeed, despite the increased foraging resulting from a decrease in vigilance, followers still show a lower nutritional state and thus a higher starvation risk than leaders or solitary individuals. Compared with leaders, the predation risk of followers is also elevated by the reduced vigilance, but it remains much lower

than for solitary individuals. Therefore, even if followers do not benefit as much as leaders from dilution effects, the benefits they experience may still be sufficient to promote group formation.

Generally, the differences in benefits brought by grouping between leaders and followers might provide a new explanation for why some individuals may try to prevent the arrival of new members in their group. This rejection of new group members by leaders has been observed in several primates species (Watts 1991; Kahlenberg et al. 2008) and equids (Rubenstein 1986) and has been most commonly attributed to individuals trying to reduce within-group competition. Our model does not include this within-group competition, and increasing group size reduces per capita predation risk. Therefore, immigration of new individuals into the group could only be beneficial except for the current leader if newly arrived individuals challenge its status. In this case, the leader could benefit from preventing the immigration of new members, to keep his status and enjoy lower starvation and predation risk than followers. For instance, in harem-forming equids (e.g., feral horses, plains zebras [*Equus quagga*]), it is generally accepted that foraging competition between members is low (Rubenstein 1994). Addition of a new member to the group should therefore be mostly beneficial to current members, as it will reduce their predation risk through the dilution effect. Older females, which generally are group leaders, will, however, often fight against other females trying to join the group (Rubenstein 1986). Our model suggests that this might be due to the importance of remaining in control of space use decisions. Interestingly, subordinate females are not observed engaging in these agonistic interactions with potential group joiners (Rubenstein 1986). This questions whether a conflict of interest between the leader and followers may exist. Depending on the costs of shifting from being a leader to a follower and on the relative benefits of an increased dilution effect, a leader might want to prevent a potential challenger from joining the group, whereas followers should always benefit from such an arrival, in situations where within-group competition is negligible. Such conflicts over acceptance of newcomers between group members of different status has been recently studied in cichlid fish in the context of reproductive dominance (Ligocki et al. 2015), and we call for similar studies focusing on status related to space use leadership.

Like any model, ours provides a simplified representation of real systems based on a set of assumptions. Two are particularly worth discussing here. First, group size remains fixed. This assumption was made because we were interested in understanding the relationship between group size and vigilance and how group size affects vigilance and space use behaviors. With this in mind, our choice of the dynamic programming optimization algorithm also made it a requirement, and fixed group size was enforced in the model by the imme-

diate replacement of dead individuals. We show in appendix B, "Examples of Optimal Strategies," that the algorithm is able to rapidly find the optimal behaviors that maximize the fitness of individuals (vigilance levels in safe and risky patches for followers, vigilance levels in safe and risky patches and time spent in safe and risky patches for leaders), usually well before any individual of the group died. Thus, the technical need to immediately replace dead individuals occurred only very rarely and should not have affected our results, which can be used to understand optimal vigilance and space use strategies at a given group size. Finally, to study how an individual contribution to space use decisions could affect its vigilance behavior given a specific group size, we used an all-or-nothing approach by modeling despotic leaders and followers. This simple situation, which may occur but is likely rare in social systems (Petit and Bon 2010; Sueur 2012), allowed us to use a simpler modeling framework and helped make clear that, in social species forming long-term stable associations, an individual contribution to space use decisions has a strong effect on its vigilance and ultimately its fitness. In systems where leadership is more distributed among group members—that is, when several individuals can lead the group, such as in horses (Bourjade et al. 2009) and macaques (Sueur and Petit 2010)—differences in vigilance and fitness between potential leaders might be reduced. In any case, our work highlights how a currently overlooked process in vigilance studies—the distribution of space use leadership within groups—can create heterogeneity in vigilance among group members.

Conclusion. In summary, using a behavioral model of prey foraging under predation risk integrating several well-known responses to predation risk (grouping, vigilance, and space use), we have shown that expectations for the shape and strength of the relationship between vigilance and group size are complex and in particular sensitive to how space use and vigilance affect foraging gains and predation risk. Overall, our results suggest that although dilution is likely to benefit all group members, the extent of this benefit differs between individuals depending on their contribution to space use decision-making. This emphasizes the need to understand how space use decisions are made. This is an active field of research and should allow a better understanding of how nonconsumptive effects of predators affect individuals in social species. However, equally critical is embracing a multibehavior perspective when studying antipredator responses. Individuals can deal with food-safety trade-offs using multiple behaviors, but covariation and linkages between these behaviors are still poorly studied empirically. This creates a gap between theory and data that must be bridged, possibly using the advances in telemetry that now allow tracking the movement, vigilance, and social behavior of individuals (baboons [Fehlmann et al. 2017]; ungulates [Lynch et al. 2015]), and provides an avenue for future fruitful research.

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A group of plains zebras (*Equus quagga*) with one vigilant individual. Photo credit: S. Chamaillé-Jammes.