

Is part of vigilance behaviour of alpine marmot subordinates (*Marmota marmota*) directed towards pups?

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In cooperatively breeding species, adult subordinated individuals can delay dispersal and provide alloparental care for their siblings instead of reproducing themselves. Typical care of young involves feeding, carrying, but also anti-predator defence. Defence can include vigilance behaviour, which involves scanning the environment for potential danger. This work seeks to understand whether alpine marmot (*Marmota marmota*) subordinates were more vigilant during a heightened risk situation, after the emergence of the pups compared to before, indicating a guarding function that could explain why dominant individuals tolerate the presence of subordinates in the group. Experimental results show that vigilance rates significantly increased after a disturbance, but this was regardless of whether pups were present. Furthermore, the number of pups did not influence the subordinates' vigilance rates, and there was no difference between males and females. Rather, vigilance tended to link with the number of alarm calls given by others during the same period. These results demonstrate that subordinate alpine marmots do not provide extra vigilance after the emergence of the pups, suggesting that they benefit the breeding pair in other ways.

Key words: vigilance, alpine marmot, helper, cooperative breeding, care of young

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Introduction

Cooperative breeding species

In cooperatively breeding species, non-breeder adults may provide care for conspecific young, which is an investment generally referred as alloparental care (Riedman 1982, Wilson 2000, Russell and Hatchwell 2001). Non-breeders help parents either directly by looking after their offspring or indirectly by reducing their workload (Riedman 1982, Crick 1992, Allainé and Theuriau 2004). Alloparental care is defined as any investment that increases offspring survival, such as feeding, carrying, protecting, grooming or playing with non-descendant infants (Trivers 1972, Gould 1992,

Briga, Pen et al. 2012). Many cooperatively breeding mammals show alloparental behaviour, particularly amongst the Carnivora (African wild dog *Lycaon pictus*, Malcolm and Marten (1982)), Chiroptera (greater spear-nosed bat *Phyllostomus hastatus* Bohn, Moss et al. (2009)), Primates (see for example Callitrichines, Digby, Ferrari et al. (2006)), or Rodentia (*Castor canadensis*, Busher, Warner et al. (1983)) Orders. Many birds and insects also breed cooperatively. Typical examples include eusocial insects, such as termites, ants, and many bees and wasps, all of which comprise sterile workers in their colonies (Keller and Chapuisat 1999). Birds display many types of cooperative breeding occur, showing a broad range of helping behaviours, mating strategies and group living forms (see for a review Arnold and Owens 1999, Koenig and Dickinson 2004). For example, helpers in the long-tailed tits species *Aegithalos caudatus* help provision juveniles in the nest with food, thereby increasing their probability of survival (McGowan, Hatchwell et al. 2003).

According to Solomon and French (1997), the three main criteria for defining cooperative breeding are alloparental care, delayed dispersal of adults and reproductive suppression (Blumstein and Armitage 1999, Allainé, Brondex et al. 2000). The latter criterion implies that only some individuals can breed. In many birds and mammals, dominants usually have improved access to food, mates, and nesting sites, while subordinates usually do not reproduce but provide help (Eberhard 1975, Briga, Pen et al. 2012). The seemingly altruistic acts of subordinates, detrimental for them as donor but beneficial for the recipient, may be explained by the increase of their inclusive fitness, i.e. the genetical rule explaining whether a trait will be favoured or not, by taking into account costs and benefits together with relatedness (Hamilton 1964). An altruistic act is favoured if the benefit for the recipient multiplied by the relatedness with the actor is greater than the cost for the actor.

Can kin selection explain cooperative breeding?

Kin selection has been invoked to explain why non-breeding helpers raise young of relatives to gain indirect fitness benefits (Bergmüller, Johnstone et al. 2007). Indirect transmission of copies of one individual's genes is transmitted to the next generation by helping relatives, since full siblings are as

equally related as a parent to its offspring (Keller and Chapuisat 1999). A lot of evidence has shown that kin selection is playing a role in the evolution and maintenance of cooperative behaviour (Russell and Hatchwell 2001, Clutton-Brock 2002). This is in large part supported in cooperatively breeding mammals, where the mean relatedness in groups is high, while group size is relatively small (Briga, Pen et al. 2012).

However, kin selection alone may not be sufficient to explain the stability of cooperative behaviour, especially for species with unrelated helpers (Bergmüller, Johnstone et al. 2007). There is a lack of evidence of cooperation regulation as offspring may stay in groups without being punished/evicted while not helping or continuing alloparenting tasks in the absence of dominants (Clutton-Brock 2002). In cichlid fishes (*Neolamprologus pulcher*), no evidence has been found for helpers receiving punishment when they did not help (Bergmüller and Taborsky 2005).

Along with kin-selection, three other mechanisms can lead to cooperative social behaviour, namely reciprocity (including pseudo-, negative-, positive-, and indirect- reciprocity), mutualism/by-product mutualism and parental manipulation (Trivers 1971, Alexander 1974, Eberhard 1975, Kokko, Johnstone et al. 2002, Bergmüller, Johnstone et al. 2007). Alexander (1974) defined parental manipulation as an adjustment of parental investment that reduces reproduction of some offspring but increases for other offspring, which ultimately increases the reproductive success of the parents.

Competition and direct fitness benefits partly explain cooperative behaviour

Living in groups may produce local competition between relatives, which can reduce or even suppress altruism towards kin (West, Pen et al. 2002). Male fig wasps display lower fighting levels with higher number of females representing future mating opportunities and developing in the same fruit, while no such correlation is found with relatedness between competing males (West, Murray et al. 2001). Since male competition occurred between foreigners and brothers as well, West, Murray et al. (2001) suggested that competition might explain failure of finding correlations between relatedness and altruism. For example, Arabian babblers (*Turdoides squamiceps*) non-breeders have

different social ranks in the nest, with dominants chasing subordinates or even stealing food from them to give it to fledglings (Carlisle and Zahavi 1986). Competition for guarding also occurs between a reproducing alpha male and beta males, where the alpha male takes sentinel duty more often than any other individuals (Dattner, Zahavi et al. 2015). Such competition between kinship suggests cooperative behaviour to increase social status (i.e. prestige) of the performers.

There is increased evidence for direct fitness benefits gained by helpers partly explaining their behaviour (West, Pen et al. 2002). Direct benefits include prestige (Zahavi 1995), protected territory (Balshine-Earn, Neat et al. 1998), territory inheritance (Hamilton 1963), group augmentation benefits (Taborsky 1984), parental experience (Brown 2014) and/or future dominance status acquisition ('*social queuing*') (Kokko and Johnstone 1999), which are not mutually exclusive.

Costs of helping

Breeders and helpers usually do not exchange roles, but may reciprocally interact for food or grooming (Clutton-Brock 2002). Hence, helpers suffer from different costs. Not only do they infrequently produce their own offspring, but they also lose energy in providing services to conspecifics. In the subsocial spider *Stegodyphus lineatus* digestive enzymes are costly to produce for each individual during group feeding, and non-kin groups suffered from diminished prey digestive ability and individual weight mass loss (Schneider and Bilde 2008). The act of helping is physiologically costly, as described in Seychelles warblers (*Acrocephalus sechellensis*) where body condition levels of helpers were high prior to breeding and decreased in later stages with higher reactive oxygen metabolites production (van de Crommenacker, Komdeur et al. 2011). Cooperative mammals entail a high cost in lactation, as found in female subordinates meerkats (*Suricata suricatta*) who lactated dominant's pups and subsequently lost body mass, contrarily to mothers and non-lactating subordinates (Scantlebury, Russell et al. 2002). However, in fishes, costs are assumed to be low because alloparental care usually does not involve feeding and concerns only brood defence towards predators (see for a review (Wisenden 1999)).

Antipredator services in cooperative breeders

Time allocated to behaviours may vary according to life history of the species and environmental constraints but must guarantee growth, survival, and reproduction (Lenti Boero 2003). Vigilance consists of a visual scan of the environment for potential danger to assure survival of the performer and optionally its conspecifics. Cues of danger are then transmitted. Sentinel behaviour, a coordination in vigilance between individuals of the group performed in an exposed position and sometimes containing alarm features, allows detection of predators and conspecifics intruders (Bednekoff 2015). It is performed in some bird, mammal, and fish species, as routinely in gray jays (*Perisoreus canadensis*), or in subordinates dwarf mongooses (*Helogale parvula*) more than any other rank categories (Rasa 1989, Waite and Strickland 1997). In meerkats, “babysitters” did not feed when guarding pups (Clutton-Brock, O’riain et al. 1999). Instead, they provided predator protection by scanning the environment, warning of their approach, chasing away small predators and guarding the burrow (Clutton-Brock, Gaynor et al. 1998).

Alarm calls are acoustically distinct and often loud vocalizations produced in response to predator presence. They can function to deter predators, warn conspecifics, or create an escape opportunity (Blumstein 2007). Production of alarm signals and responses varies between cooperative breeding species, but may also vary between different categories of individuals. For example, in yellow-bellied marmots, both sexes paid attention to vulnerable young by increasing their vigilance and decreasing foraging (Blumstein and Daniel 2004). Many of other alarm signals exists, including tooth-chattering, quill-shaking, tail-slapping and food-thumping in rodents (Blumstein 2007). Signals are usually combined with visual cues, but their function is mainly for mobbing predators, which benefits directly the survival of the performer (Blumstein 2007).

Alpine marmots: the study species

Alpine marmots are large diurnal rodents living in family groups on defined territories in alpine open meadows with burrows, where they hibernate during winter (Barash 1976, Arnold 1990, Perrin,

Berre et al. 1993). A dominant breeding pair and their offspring, adult subordinates from 2 years old on, one-year old non-mature descendants called yearlings, and pups from the current year compose usual families (Perrin, Berre et al. 1993). Alpine marmots are considered a cooperative breeding species since dispersal in subordinates is delayed beyond maturity, their reproduction is partially suppressed and juveniles benefit from alloparental care (Allainé, Brondex et al. 2000). Particularly, pups' winter survival increases with the number of non-reproductive males in the hibernaculum until a certain threshold, although their survival also tends to decrease with the number of females subordinates (Allainé, Brondex et al. 2000, Allainé and Theuriau 2004). Male subordinates warm juveniles by grooming, covering them with hay and also producing heat during activity episodes (Allainé and Theuriau 2004). In summer, direct affiliative interactions, including nursing, and indirect interactions, such including burrow maintenance, environment scanning, and defence against conspecific intruder or predator are main behaviours thought to benefit pup's fitness (Blumstein and Armitage 1999).

Subordinates function still under investigation

Despite growing knowledge on the function, costs, and benefits of each age class, it is not clear why most adult individuals remain subordinated to the group instead of dispersing and founding a new family, thereby increasing their own fitness. Furthermore, from a dominant point of view, it is not clear why subordinates are allowed to stay and compete for resources (Allainé, Brondex et al. 2000). Male subordinates are considered as the helping sex because they increase juvenile survival, but at a certain threshold close to 1 added subordinate in the whole group, male subordinates reduce persistence of the dominant male, probably by competing for reproduction (Allainé and Theuriau 2004). Presence of subordinates females is more striking because they represent a reproductive cost by negatively affecting juveniles survival during hibernation (Allainé and Theuriau 2004). It has been hypothesised that females weak up less frequently than males but benefit from the heat produced by males (Allainé and Theuriau 2004). Although the mating system is monogamous, polyandry is not excluded and extra-pair paternity occurred in 30.9% litters on a studied population (Goossens,

Coulon et al. 1996, Cohas, Yoccoz et al. 2006). In addition, helpers do not provide delayed benefits in terms of body condition for the dominant pair by reducing their energy expenditure in raising young, as proposed in the load-lightening hypothesis (Crick 1992). However, helpers increase current reproductive success by adding to parental investment during hibernation (Allainé and Theuriau 2004).

Vigilance as an alloparental strategy

Studies on alpine marmots so far have not considered the hypothesis that vigilance functions as alloparental behaviour to benefit other group members, including pups, to the best of my knowledge based on an extensive literature search. Vigilance is a good intruder's detection strategy, because it is an active process for territory defence (Perrin, Coulon et al. 1993). Along with scent-marking behaviour by cheek rubbing, subordinates participate in territory defence by direct aggression towards conspecifics, and in warning by alarm calling. To be ready to perform anti-predator and defence strategies, marmots spent some time in vigilance, which consists of head raising while standing, sitting (Figure 1) or lying, also in-between foraging bouts (Armitage and Corona 1994).



Figure 1. Male alpine marmot being vigilant while sitting partly in a burrow (© Gabriela Cino).

An optimal duration of vigilance scan bouts has been suggested, which was independent from habitat characteristics (Ferrari, Bogliani et al. 2009). However, differences in vigilance rates were found, not only depending on environmental characteristics and intrinsic factors (Blumstein, Lea et al. 2010), but also on whether infants were present or not (Lenti Boero 2003). Previous studies on alpine marmots either did not take into account head-up scans during foraging as part of vigilance (“spotting” in Lenti Boero 2003), or did not investigate difference between age categories (Ferrari, Bogliani et al. 2009), or focused only on hibernation as a helping behaviour (Allainé, Brondex et al. 2000). Moreover, results of a study on yellow-bellied marmots suggested that adults may engage in vigilance to protect vulnerable young, because they increased vigilance and decreased foraging after hearing juvenile alarm calls (Blumstein and Daniel 2004).

Aim of the study and hypotheses

The present study investigates the vigilance behaviour of subordinates as an anti-predator strategy not only aimed at personal or group protection, but produced in extra to possibly protect juveniles of the current year, which are particularly vulnerable during their first weeks above ground (Loughry 1993, Armitage and Corona 1994). If infants influence the vigilance of subordinates, one might expect 1) a general increase in the rate of vigilance after pup emergence compared to before. If the vigilance of subordinates is a protection function of infants, 2) vigilance rate should increase in risky situations when in the presence of infants compared to baseline level situation. Even though many factors influence vigilance behaviour, such as the number of individuals in the group or distance to burrow (Armitage and Corona 1994), this study hypothesizes the presence of pups alone to influence a great part of subordinates’ vigilance, which will include subordinates being more vigilant after the emergence of pups regardless of those factors. In addition, 3) vigilance of subordinates should be higher when many pups emerged compared to no emergence on the current year.

Since males are the helping sex (Allainé and Theuriau 2004), sex differences may be expected. 4) Males should perform higher vigilance than females because they are helpers and/or may sire their

own litter, as extra-pair paternity increase with number of subordinated males (Cohas, Yoccoz et al. 2006). Alternatively, females could compensate for their deleterious effect during hibernation by performing more vigilance than males.

Methods

Study site

The study site is located in La Grande Sassi re Nature Reserve, Vanoise National Park, in the French Alps at an elevation of 2350 m. During spring and summer 2016, an observational study was made concomitantly with the usual observation and marking-recapture survey of the Alpine Marmot Project conducted by the LBBE laboratory from the University of Lyon. Hence, territories boundaries, family composition, sex, dominant pair were known and useful for the present study (Cohas, Yoccoz et al. 2006). Age-categories were identifiable with telescopes: adult subordinates were the category of interest and easily recognizable by their substantially bigger size than yearlings or pups (Allain  and Theuriau 2004). They possessed only one metallic tag, either at the left ear for males or at the right ear for females and were distinguishable from dominants that had an extra plastic coloured tag. Additionally, some subordinates were recognizable after capture (occurring mostly prior pup emergence) because of a paint mark on the fur. Unfortunately, this paint mark quickly faded and metallic tags could be read without trapping, which is why individual identity of males and females within the same family group could not be inferred. Frequent predator-prey interactions are found in this large population, where natural predators are red foxes (*Vulpes vulpes*) and golden eagles (*Aquila chrysaetos*) (Perrin, Coulon et al. 1993).

Trials with emergence and disturbance conditions

Originally, I tested 8 family groups. Two of them in which pups were not conceived that year, presumably because of recent change in dominance (Allain  and Theuriau 2004), were removed from the first analyses. One of those two groups was kept for the second analysis, to compare the

vigilance level depending on the number of pups emerged on the current year, because the other group did not contain trials for the two season conditions. To find individuals for trials, I walked in the morning from 7AM to 12AM and in the afternoon from 3PM to 7PM along the tourist trail or somewhere outside the focal territory limit and watched adult individuals carefully with 10x42 binoculars and either 65x or 80x telescope. One focal adult subordinate was searched visually at least 5 minutes before a trial began and was tracked with a camera, set on the trail during the entire time of the trial. Date of emergence for each family group was reported as done each year for the survey (Allainé 2004) and allowed us to classify our video-recorded trials into two periods, the first one from 05/14 to 06/22 referred as “before emergence” and the second one from 07/03 to 07/10 referred as “after emergence”. Thus, all tested family groups had pups presumably born but remaining inside the burrows in the before emergence condition, and pups visible on their territory because going outside of the burrows during daily activities after emergence season.

As suggested by Lea and Blumstein (2011), one may gain insight into state-dependent antipredator response by studying both baseline and heightened risk levels. Hence, to create a standardized way for sampling and simulate a heightened risk situation, a disturbance was made after 10 minutes of filming. The disturbance consisted in a person running or walking rapidly towards the focal marmot until it fled into one burrow. The trial containing the following 10 minutes after and including disturbance were recorded by focusing on the same individual, but individual identity was later included as random factor in the statistical analysis for the reasons mentioned above. After pup emergence, the trial began when at least one pup was visible in addition to the focal marmot.

It was not always the same person creating the disturbance and sometimes the marmot did not go into the burrow, as the marmot retreat could not always be seen by the disturber, which caused the disturbance to end too soon. Alternatively, the disturber ran towards a slightly different direction than where the focal marmot stood. Although this may have had some variations in the disturbance, it has been assumed it had no influence on the general disturbance effect, because disturbance

always forced the focal marmot to flee somewhere else from where it was located before disturbance. Marmots from this area are used to tourist's passage on the trail, but they still pay attention to them, for example when a dog is accompanying, marmots alarm call and/or flee into their burrow (Mainini, Neuhaus et al. 1993). From the moment a disturbance entered their territory, their vigilance increased (Dominique Allainé, personal communication). Because marmots paid attention to humans, especially in proximity of their presence, it might reasonably be concluded that the experimentally induced disturbance created a heightened risk situation.

If the focal marmot was lost before the disturbance (during the 10 first minutes), trial was abandoned. Territory was always changed after a trial was performed, except one time, although the trials were performed at 5 hours of interval.

Video extraction

Video recordings were extracted with an HP Pavilion dm4 computer using Windows media player. From each trial, vigilance rate, quantity of environmental alarm calls (i.e. the number of notes per minute), and the latency (i.e. time) to come out of the burrow following the disturbance were extracted. For reasons of simplicity, I refer to vigilance rate and not proportion, which was calculated as follows (Equation 1):

$$Vr = \frac{T_{vigi}}{(T_{tot} - T_{oos})}$$

Equation 1. Calculation of the vigilance rate (Vr : vigilance rate). T_{vigi} : time spent in vigilance. T_{tot}: total trial duration time (600s). T_{oos}: time spent out of sight, including when in the burrow.

The factor pup emergence was coded as “before” for pups not emerged but presumably born and remaining in the burrow, and “after” for pups emerged thus visible on their territory during the period of activity. The factor disturbance was coded as “undisturbed” for 10 min trial before disturbance and “disturbed” for the 10 min trial after disturbance, disturbance comprised. In addition, sex of the focal marmot and number of pups emerged in each family group were reported. A marmot was considered vigilant when the focal marmot was looking while sitting, lying or standing

on both hind legs without doing anything else (“weariness” *sensu* Armitage & Chiesura Corona, 1994). It could happen during activities such as foraging, when the marmot stopped a while to raise the head up and look around. Counting time in vigilance began when the focal individual had straight head and stopped counting when it dropped the head to start another activity. Other activities were foraging, in the burrow and out of sight (see explicative table in Appendix A). The number of alarm calls notes was coded from the video-recordings with by counting any audible note with earplugs and with middle volume of the computer. Hence, I refer as to environmental alarm calls, as it included alarm calls coming from the trial territory as well as from the surroundings.

Statistical analysis

All models were fitted using R 3.2.2 (R Development Core Team 2015) package lme4 1.1.10 (Bates, Maechler et al. 2014). Generalized linear mixed models were build (GLMMs) with normal errors to take non-independence of replicate trials and include random effects (Bolker 2008). P-values were calculated for all models using log-likelihood ratio tests with the Anova function, using an $\alpha = 0.05$ level of significance (Keough and Quinn 2002). For the first analysis, vigilance rate was arcsin transformed (square root) and alarm rate fourth root transformed, while for the third analysis, latency time was arcsin transformed (square root) and alarm calls fourth root transformed, to fit the assumptions of normality. All figures show non-transformed data.

First analysis: effect of pup emergence and disturbance

Generalized linear mixed models were built to determine whether vigilance rate of adult subordinates, the response variable, was different depending the emergence of pups (1), before and after a disturbance (2). In the initial model I included sex of subordinates and environmental alarm calls as additional fixed effects and an interaction between pup emergence and disturbance. Factors were removed if there was no improvement of the model fit as assessed by likelihood ratio tests. Trials number and family group (territory) in which trials were performed were entered as random effects, to control for repeated measures on the territories and individuals since individual identity

could not be inferred with certainty. This model was treated, and will be referred to, as the full model (i.e. model that included all predictor variables) as opposed to null models, which included the random effects and either none control variable or each of the variables at a time. Following (Keough and Quinn 2002), analysis began with the full model and efforts were made to simplify on the maximum and to see the significance of each variable.

Additionally, three-way interaction models were analysed to test the effect on the vigilance rate of the three joint variables being emergence, disturbance, and sex, with environmental alarm calls as a simple additional variable. Random effects contained trial number and territory.

Second analysis: effect of the number of pups after emergence

In order to investigate if the number of pups born on each family group had an effect on the vigilance rate of adult subordinates, I analysed data only after emergence with generalized mixed effect models similar to the previous analysis. One territory that had no pups on the current year was included. The number of pups (going from 0 to 5) was considered as a continuous variable and the rate of vigilance was kept at original scale. I included disturbance, number of pups, an interaction between number of pups and disturbance in the initial models. Sex was set as fixed effect while trials number and territory were included as random effects.

Third analysis: latency to come out of burrow after disturbance

As complementary information of vigilance rates, latency to come out of the burrow after disturbance was investigated. The latency to come out was defined as the time from the moment the marmot entered entirely in the burrow owing to disturbance, until the head was seen again out of the burrow. This latency allowed a direct measurement of the effect of disturbance. Trials were included only after a disturbance and trials where the marmot was out of sight during disturbance were removed. Furthermore, trials were removed where entry into burrow could not be inferred with certainty. Generalized mixed effect models were ran with initial model containing the number

of pups, emergence, an interaction between the number of pups and the emergence, with sex and environmental alarm calls as fixed effects and territory as random effect.

Results

1. Effect of pup emergence, disturbance, sex and environmental alarm calls

In 2016, 6 family groups comprising 5-10 total individuals prior pup emergence were tested. Each family had a range of 3-5 pups emerged between the 24 and 29 June.

Table 1

Results of the GLMM testing factors affecting vigilance rate of adult alpine marmot subordinates (Full model).

	Estimate	SE	Z	P
Intercept	0.442	0.063	7.025	< 0.01 ***
Pup emergence	0.054	0.060	0.903	0.368
Disturbance	0.178	0.049	3.657	< 0.01 **
Sex	-0.030	0.051	-0.594	0.553
Enviro. alarm calls	0.077	0.038	2.047	0.047 *
Pup emergence * Disturbance	0.046	0.069	0.671	0.50

Full model was significant, but final model excluded emergence-disturbance interaction (Table 1) and included emergence, disturbance, sex, environmental alarm calls and random effects (full model: $\chi^2 = 29.64$, $df = 5$, $p < 0.01$ Table 1, final model: $\chi^2 = 29.20$, $df = 4$, $p < 0.01$, Figure 2 & Table 2).

Table 2

Results of the GLMM testing factors affecting vigilance rate of adult alpine marmot subordinates (final reduced model).

	Estimate	SE	Z	P
Intercept	0.433	0.061	7.053	< 0.01 ***
Pup emergence	0.078	0.048	1.600	0.12
Disturbance	0.201	0.035	5.819	< 0.01 **
Sex	-0.030	0.051	-0.583	0.56
Enviro. alarm calls	0.075	0.038	1.982	0.054

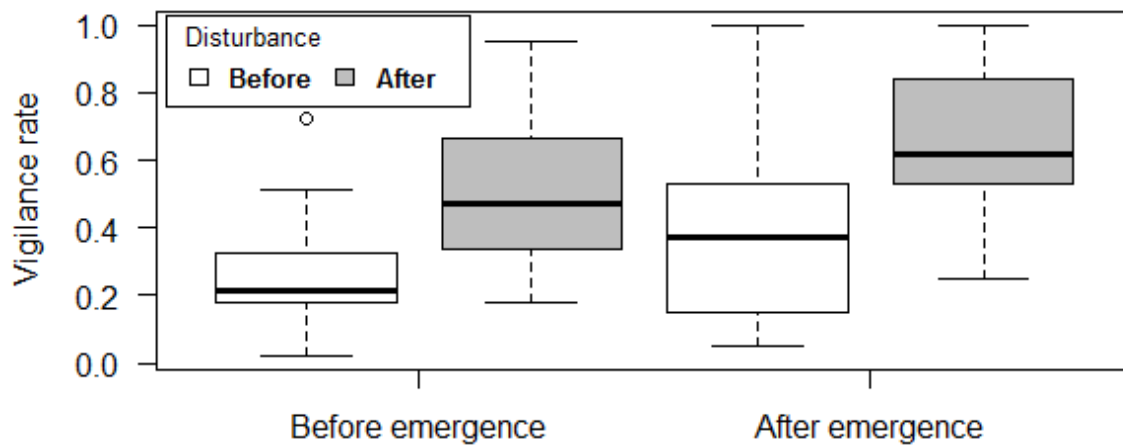


Figure 2. Vigilance rate of adult subordinates before (left part) and after emergence (right part), undisturbed (white) and disturbed (gray) conditions (N = 17 each). Although vigilance increased both in disturbed conditions and after emergence, the interaction in the model prediction was not significant, meaning that subordinates were not relatively more vigilant when pups emerged than before they emerged.

The vigilance rate was not significantly different before and after emergence (N = 34), although the effect went into the right direction (median before pup emergence = 0.326 vs. after emergence = 0.531; Figure 3), an increase by a factor of 1.63 ($\chi^2 = 2.45$, $df = 1$, $p = 0.12$).

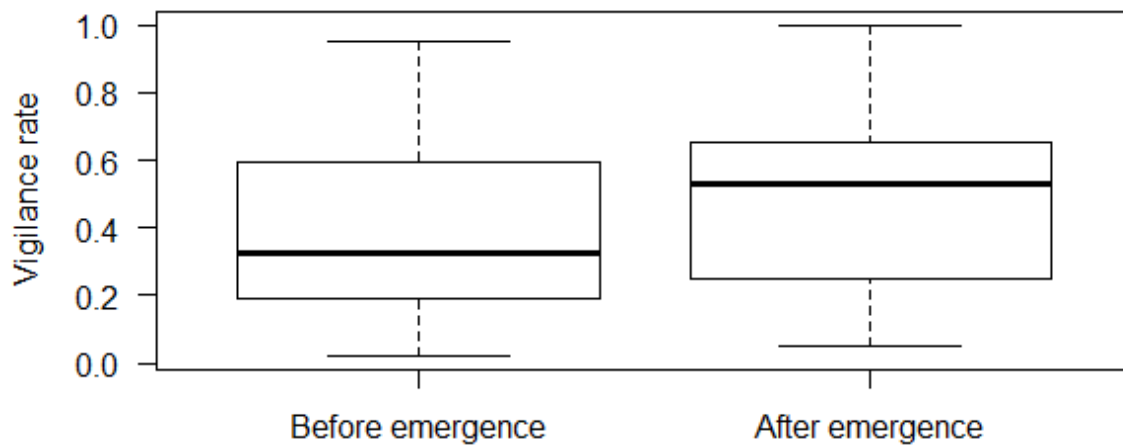


Figure 3. Vigilance rate of adult subordinates before and after emergence (N = 34). Although vigilance increased after emergence, the difference was not significant, meaning that subordinates were not more vigilant when pups emerged than before they emerged.

The vigilance rate was significantly different over all individuals before and after disturbance ($\chi^2 = 23.50$, $df = 1$, $p < 0.01$, $N = 34$ each). Median of vigilance rate for undisturbed condition was 0.225 and for disturbed condition 0.576 (Figure 4), thereby being 2.56 times higher after disturbance.

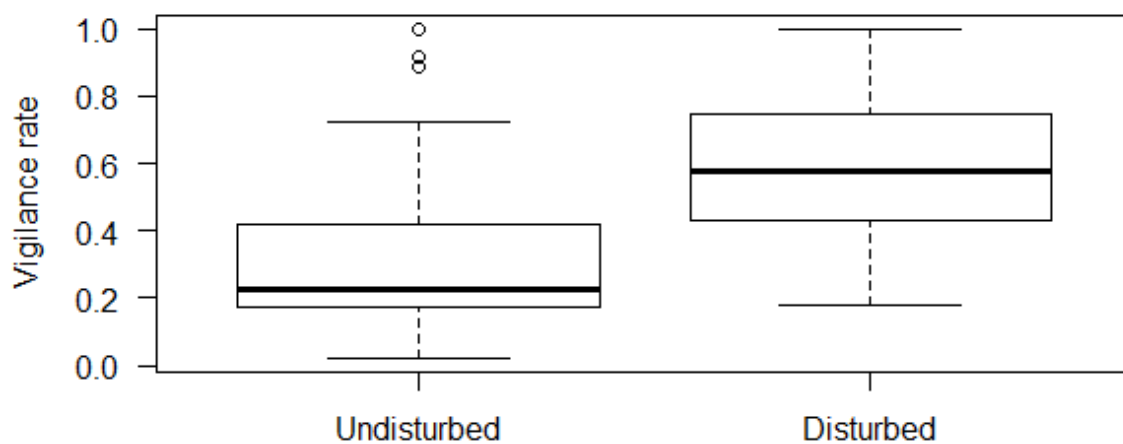


Figure 4. Vigilance rate of adult subordinates in undisturbed and disturbed conditions (N = 34). Disturbance increased significantly the vigilance rate.

There was no significant sex difference in the vigilance rates (N = 44 males, N = 24 females, $\chi^2 = 0.34$, $df = 1$, $p = 0.56$, Figure 5).

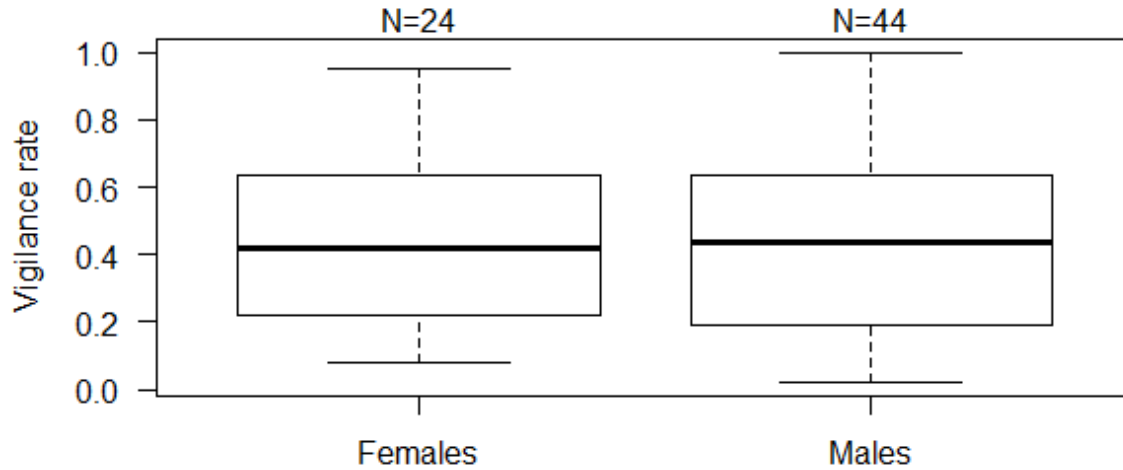


Figure 5. Vigilance rate of female subordinates (left, N = 24) and male subordinates (right, N = 44). There was no statistical difference of vigilance between sexes.

There was no significant difference in the vigilance rates depending environment alarm calls (N = 68, $\chi^2 = 3.72$, df = 1, $p = 0.054$, Figure 6).

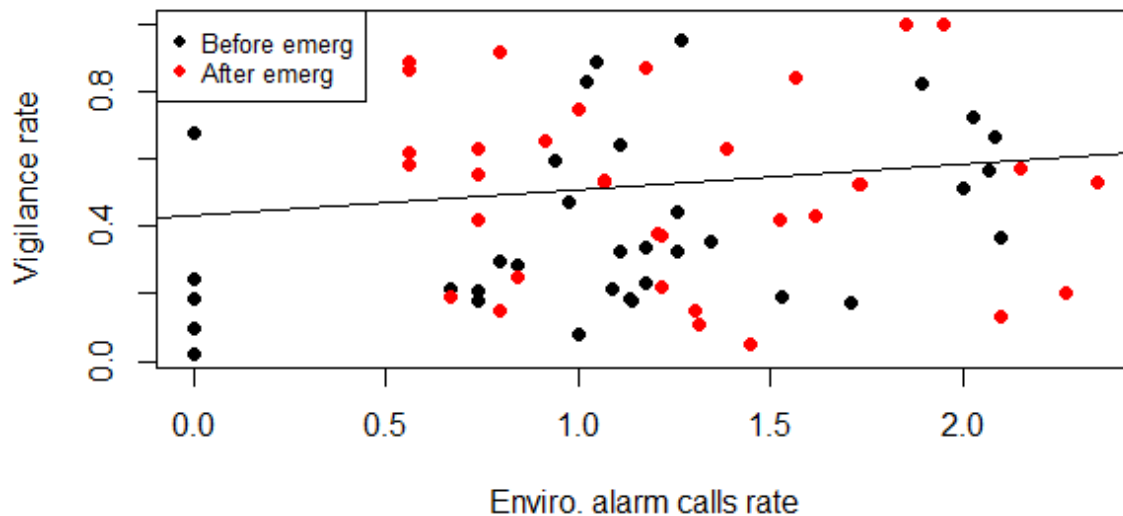


Figure 6. Vigilance rate of adult subordinates in function of environmental alarm calls (N = 68). Red points represent values after the emergence of pups and black points represent values before emergence. The black line represents the model prediction before emergence.

A posteriori analysis included sex as another factor interacting with disturbance and emergence status. The full model containing a three-way interaction was significant ($\chi^2 = 30.60$, df = 8, $p < 0.01$), but none of the interactions were significant (Table 3).

The same conclusions were drawn from the linear generalized model, disturbance was significant while emergence, sex and alarm calls were not (Table 2).

Table 3

Results of the 3-way interaction GLM model testing factors affecting vigilance rate of adult alpine marmot subordinates (Full model).

	Estimate	SE	Z	P
Intercept	0.475	0.083	5.7	<< 0.01 ***
Pup emergence	0.044	0.099	0.445	0.118
Disturbance	0.145	0.081	1.788	<< 0.01 ***
Sex	-0.071	0.087	-0.811	0.560
Enviro. alarm calls	0.071	0.039	1.845	0.054
Pup emergence*disturbance	0.028	0.115	0.246	0.504
Pup emergence*sex	0.018	0.125	0.141	0.779
Disturbance*sex	0.053	0.101	0.521	0.360
Pup emergence*disturbance*sex	0.027	0.142	0.186	0.852

2. Effect of the number of pups after emergence

Only trials performed after pup emergence were kept and one family group which had no pups on the current year was included into the analysis to investigate the effect of the number of pups in a continuous variable, going from 0 to 5. Final model of vigilance rate included disturbance, number of pups, sex and random effects (full model: $\chi^2 = 17.91$, $df = 4$, $p < 0.01$).

The vigilance rate did not differ between the different number of pups ($\chi^2 = 0.53$, $df = 1$, $p = .47$, Figure 7, $N = 4, 8, 14$ and 12 trials with $0, 3, 4$, and 5 pups respectively), neither between males and females ($\chi^2 = 0.75$, $df = 1$, $p = .39$, Figure 8, $N = 24$ males, 14 females).

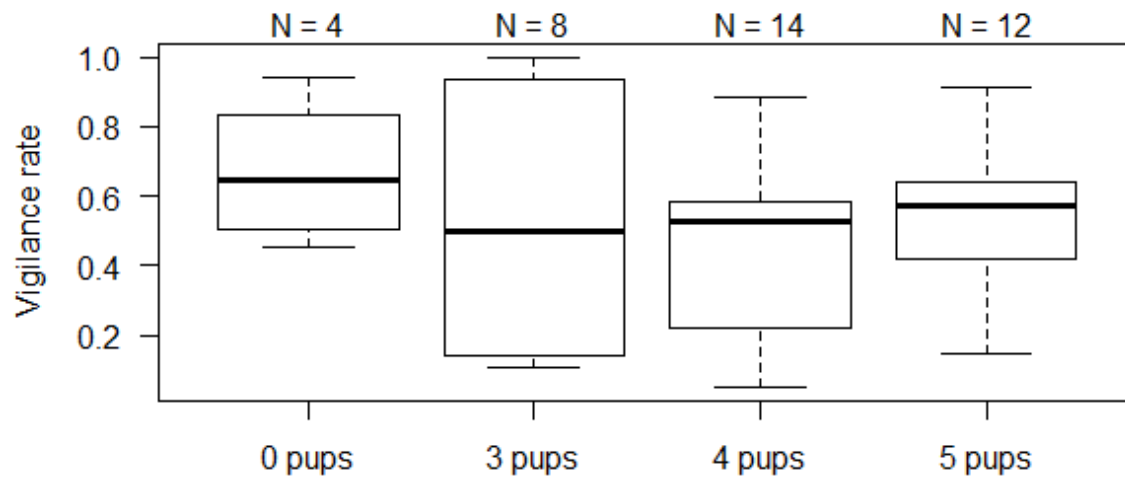


Figure 7. Vigilance rate of adult subordinates after emergence in function of the number of pups emerged on the territory (0 pups, N = 4; 3 pups, N = 8; 4 pups, N = 14; 5 pups, N = 12). The differences were not significant.

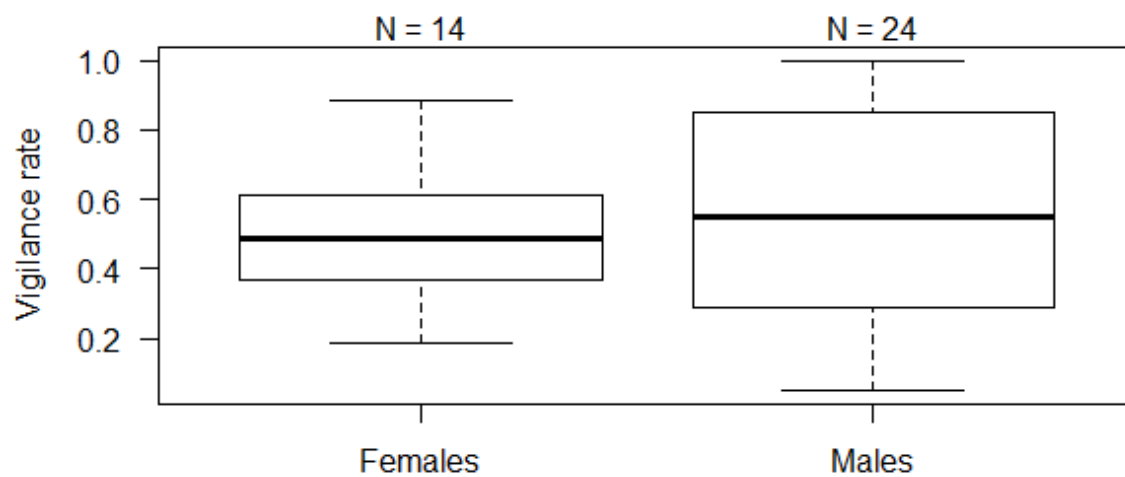


Figure 8. Vigilance rates of female subordinates (left, N =14) and male subordinates (right, N = 24) after emergence. The difference was not significant.

Disturbance had a significant effect on vigilance rate ($\chi^2 = 15.7$, $df = 1$, $p < 0.1$), with the median value increasing by 1.66 after disturbance (from 0.38 to 0.63, Figure 9).

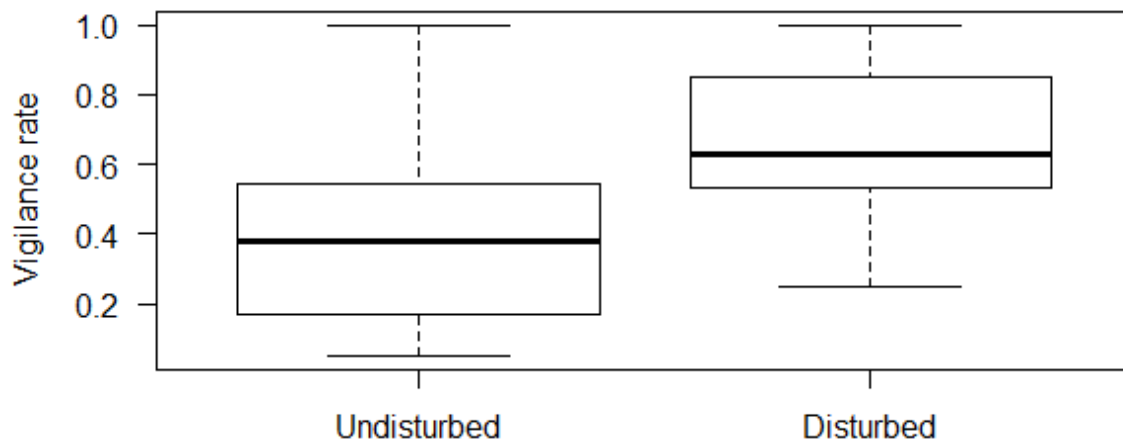


Figure 9. Vigilance rates of adult subordinates after emergence in undisturbed and disturbed situations (N = 19). The difference was significant.

3. Latency to come out of the burrow after disturbance

Only trials performed after disturbance were selected to analyse the latency to come out of the burrow after disturbance, and trials where marmots were out of sight during disturbance were excluded. Full model of latency to come out included pup emergence, number of pups, emergence-number of pups interaction, sex, alarm calls and a random effect but was not significant ($\chi^2 = 6.26$, $df = 5$, $p = .28$, Table 4). Median latency time was 185 seconds, ranged from 0 to 556 seconds, with 70% of trials (21 out of 30) coming out of the burrow before half of the trial (5 minutes). Before and after emergence, median latency represented respectively 162 and 193 seconds (N = 15).

Table 4

Results of the GLMM model testing factors affecting latency to come out of the burrow (Full model).

	Estimate	SE	Z	P
Intercept	0.611	10.754	0.057	0.282
Pup emergence	-12.72	13.723	-0.927	-
Number of pups	1.934	2.433	0.795	-
Sex	0.034	2.831	0.012	-
Enviro. alarm calls	3.523	2.123	1.660	-
Pup emergence*number of pups	3.157	3.314	0.952	-

Discussion

Vigilance rate generally increased after pup emergence, although not significantly

Contrarily to predictions, vigilance rate of subordinates did not significantly differ before and after emergence of the pups. This result was confirmed both by looking at differences in vigilance depending emergence status and vigilance in interaction with disturbance, where it could have been that disturbance increased the overall vigilance level, but this increase would be significantly higher after emergence of the pups. Hence, I refute our first hypothesis (1) that emergence of pups increased the vigilance behaviour of alpine marmot subordinates.

However, the data showed an increase in vigilance rate after emergence, from 32.6% of visible time prior emergence versus 53.1% after emergence, meaning that vigilance was 1.63 times higher after emergence. This increase may be a seasonal change in general vigilance level. As showed in a study on spotting behaviour of alpine marmots (Lenti Boero 2003), this activity decreased in August and augmented in September compared to July. Here, trials were performed on mid-May and mid-June before emergence, and from the beginning of July to mid-July after emergence. A study on yellow-bellied marmots revealed a considerable variation depending animal groups, time of the day, season and location from the burrow, which was not measured for the purpose of this study (Armitage and Corona 1994).

It was hypothesized that emergence itself would be a sufficient factor to influence significantly the vigilance level of subordinate marmots, which revealed to be inconclusive. The lack of emergence effect detection may be hindered by other factors that I did not consider, as for example group size, microhabitats (Ferrari, Bogliani et al. 2009), offspring activity (White and Berger 2001), distance to burrow (Loughry 1993) or relatedness of parents and offspring in the groups.

Firstly, the results suggested that in alpine marmots, even if the size of the family was higher after emergence, vigilance tended to increase. In black-tailed prairies dogs, to the contrary, individuals were less vigilant in larger colonies, and also when placed at the centre of the group compared to the

edge (Loughry 1993). More surprisingly, they were less vigilant after emergence of pups compared to before, which might be due to the increase in colony size (Loughry 1993).

Secondly, I did not expect microhabitat characteristics to interfere with the study design. Ferrari et al. (2009) showed that alpine marmots living in closed sites had greater rate of vigilance and spent more time being vigilant than marmots in open sites, although mean vigilance bouts did not differ in duration between the two sites. Closed sites were situated from 1870 to 2000 m of altitude, surrounded by mixed conifer forest while open sites began from 2100 m to 2500 m and both were characterized by alpine meadow (mainly *Festuca varia* and *Poa alpina*). This present study site was situated exclusively in open alpine meadow, and territories of the family groups investigated were close to each other in the same valley. In this population, combination of slope, territory exposure to sun, and plant cover are indications of territory quality, affect reproductive success and retention of subordinates (Allainé, Rodrigue et al. 1994), but I considered unlikely to find any differences in marmot's vigilance depending on the quality of their territory they lived in.

Thirdly, I did not control for offspring activity during the entire time of the trials. In Alaskan moose (*Alces alces*), mothers increased their vigilance level when their calf was active thus more vulnerable to predators (White and Berger 2001). A study on alpine marmots showed that the alert distance and flush distance and latency to come out of the burrow increased in presence of pups (Louis and Berre 2000). Here, the trials began after emergence only when I saw that at least one pup was above ground, but pups may have entered in burrows during the trial, thereby being out of predation risk. Moreover, when they were out, I couldn't control for their visibility to the focal adult subordinate, because their territory may have contained rocks, uneven heights of vegetation and ground, or several burrows and burrow's entries, for example.

Alternatively, the study design may have inadequately investigated subordinates' infant guarding by looking only at one breeding season. Lenti Boero (2003) found adult alpine marmots spotting less during years of skipped reproduction than in years of reproduction. The comparison between years

without and with pups may reveal a difference in the vigilance behavior, but pups being highly vulnerable during their first weeks after emergence (Armitage and Corona 1994), a difference within the same breeding season would make sense too. I also compared family groups with pups to one family group without pups, although it had a low number of trials ($N = 4$) and it was during one breeding season.

Finally, I may have gained insight by comparing age categories. In Lenti Boero's study, reproductive adults were the category which spent more time spotting compared to non-reproductive adults in presence of pups (Lenti Boero 2003). In yellow-bellied marmots, non-reproductive females spent more proportion of time in weariness than any other category, but only their difference compared to yearling females was statistically significant (Armitage and Corona 1994). This study was not designed to compare different age classes, though it focused on presence and absence of pups within the same reproductive season. Dominants may have increased their vigilance after the emergence of the pups, or their vigilance level may have been different from subordinates, which could indicate an effect of emergence on the vigilance.

Vigilance rate of subordinates increased significantly in heightened risk situations

After disturbance, vigilance rate increased by 2.55 compared to before disturbance's vigilance level and by 2.75 when data included only after emergence trials. Median levels of vigilance showed that subordinates spent 22.5% of the visible trial time in vigilance and 57.6% following disturbance. After emergence, subordinates were vigilant 14.3% of the visible trial time before disturbance and 39.3% following disturbance, and the difference was statistically significant. This reasonably confirms the second hypothesis (2) and concludes that the disturbance created a heightened risk situation, even though some individuals did not enter the burrow following disturbance. Cases where marmots did not enter a burrow were low (18%, 6 trials out of 34) and marmots responded to disturbance by fleeing from their initial position.

It has been shown that alpine marmots react more strongly when a human walked off the trail than along the marked trail, mainly by retreating to burrow then returning within 10 min (Mainini, Neuhaus et al. 1993). However, humans may not be perceived as predators (Blumstein and Armitage 1997), especially in this nature reserve where marmots are not hunted. Thus, the disturbance in this study can be considered as an elicitor of a risky situation, not necessarily a threat to their survival. Trials with a predator model or a dog may have been more representative of a high danger, and is suggested for further studies with disturbances elicited by both humans and predator-like models or dogs.

Vigilance rate was not influenced by the number of pups emerged

No effect was seen by of the number of pups on the vigilance of subordinates or the latency to come out of the burrow after disturbance, thus the third hypothesis (3) can be refuted. Although median vigilance increased from three to five pups, subordinates in family groups where no pups were conceived had a higher vigilance median (64.5%, 49.8%, 52.8%, 57.3%, for 0 pups, 3 pups, 4 pups and 5 pups respectively). This result went against predictions, though the difference was not significant and may be explained by the low number of trials in the family group without pups (N = 4). However, the absence of pup number effect on vigilance was in agreement with a study on black-tailed prairie dogs, where the number of adults were more influential than the number of pups (Loughry 1993).

Vigilance rate between males and females did not differ

Male and female subordinates did not statistically differ in their vigilance rate, being in mean at 45.3% for males and 45.6% for females in the first analysis, and on after emergence condition at 55.3% for males and 49.1% for females. Male subordinates are called helpers and were expected to help by being vigilant for the protection of the pups, which are vulnerable above ground. Thus, the fourth hypothesis (4) that subordinate males are more vigilant than females, can be refuted. This result was similar to a study on yellow-bellied marmots which found no sex differences in the response - decrease foraging and increase vigilance - of marmots after hearing juveniles alarm calls

(Blumstein and Daniel 2004). A recent study on alpine marmots found males to perform more scent-marking than females, which is an intra-sexual competition and territory-defence behaviour (Pasquaretta, Busia et al. 2015). The frequency of this behaviour decreased in the season, particularly after the emergence of pups. However, the reason of persistence of female subordinates in alpine marmot families remains partially unknown. Since they did not perform more vigilance than males and that they represent a cost during hibernation, females should give some form of benefit to parents explaining why they are tolerated beyond maturity, whether it is an active or a passive process. Active suggested process for alloparental care includes maintaining of burrows, defending territory, look and warn for predators and pup nursing (Blumstein and Armitage 1999). Passive processes arise from benefit of sociality in general, as for example dilution effect from predation or social thermoregulation (Blumstein and Armitage 1999). To my knowledge, the investigation of some active processes performed by female (and male) subordinates in alpine marmots is still lacking, for example burrows maintenance or pup nursing.

Vigilance rate tended to be influenced by environmental alarm calls

Differences were expected in the rate of vigilance depending on environmental alarm calls level, because alarm calls have a function in warning and protection of conspecifics (Blumstein, Steinmetz et al. 1997). Hence, marmots should pay attention to the environmental alarm calls, which are audible up to 1km from emission site (Barash 1976, Lenti Boero, Gandini et al. 1988). Vigilance rate was not statistically dependent on environmental alarm calls, although near significant ($p = 0.054$). Subordinates tended to increase vigilance rate with the number of alarm calls heard. In alpine marmots, the quantity of alarm calls correlates with the level of risk: alarm calls with fewer notes are produced when a closer potential danger is detected with more notes when potential danger is far away (Blumstein and Arnold 1995). A high alarm calls level indicates many notes produced, thus a distant potential danger while a low level of alarm calls indicates fewer notes produced that might be more representative of a nearby danger.

A previous study showed alpine marmots to alarm call less when humans were closer and to close aerial stimuli (Blumstein and Arnold 1995). In this study, low alarm call rates and numbers were not associated with higher vigilance, perhaps because the location of the emitter(s) could not be controlled for, neither for their relatedness with the focal marmots. For example, alarm may have been either distant or near the focal marmots. In addition, emitters of the alarm calls may have been located in the same territory or in a distant territory from the focal marmot. A study on yellow-bellied marmots found that marmots were able to discriminate between juveniles and adult females, responding strongly to playback calls of juveniles, contrary to the statement that juveniles are less reliable individuals because of their degree of experience (Blumstein and Daniel 2004). Yellow-bellied marmots did not differentiate between calls of familiar and unfamiliar individuals.

Even if the degree of response may have changed depending the identity of the emitters, I did not aim at discriminate between the emitters. We assumed that environmental risk is transmitted through the alarm calls regardless of the emitters' identity.

Alternatively, even if the number of alarm calls indicates a degree of risk, it may not be directly linked to vigilance rate. Marmots could simply be vigilant for a long time without being seriously threatened. This seemed to be the case when passage of a fox elicited many alarm calls audible in the entire valley and probably coming from many distant family groups without representing urgent need for the focal marmot to hide into a burrow (personal observations).

Latency to come out of the burrow after a disturbance neither depended on the emergence or number of pups emerged

Since visible time after disturbance was reduced because of disturbance, which obliged marmot to enter a burrow in most of the cases, the latency to come out of the burrow following the disturbance was analysed to gain complementary information about the perceived risk of marmots. However, no conclusive information could be driven by this third analysis. Latency was explained neither by the emergence and the number of pups or sex and environmental alarm calls. I suggest that latency to

come out of the burrow may depend more on the degree of danger the marmot experienced with the disturbance, which I did not measure, as it was not the aim of this experiment. Alternatively, marmots may come out of the burrow after an optimum time in terms of risk.

Conclusion

With the present study, it could not be concluded that subordinates may help in pups guarding by being more vigilant in their presence, although an increase of the baseline vigilance level occurred after emergence. The role of alpine marmot subordinates is partially unresolved, especially for females, which are not considered as helpers but are still tolerated by the parents. I suggest further studies on subordinates and helpers in cooperative breeding species to compare the age-categories and test whether pups would indeed benefit from an increase in vigilance of their conspecifics. It may help to gain insights to compare the difference in years and territories with and without pups, with controlling for environmental, physical and biological factors, such as alarm vocalizations, visibility of the pups or presence of predators.

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Appendix A

Behaviour measured in time on focal alpine marmot subordinates.

Behaviour	Description
Vigilance	Looking while sitting/standing/lying. Can happen during feeding when the head is raised for a while and when the head moves to gaze at another direction. Do not include head raised when the marmot is walking/running.
In the burrow	When I see a marmot entering a burrow, I start to count time when the whole body is not visible anymore and until the head is visible again.
Out of sight	When the marmot is either out of the video frame or when I am not certain to follow the focal individual. In other words, each time the focal marmot is not visible but not in the burrow either.
Foraging	All other activities, including feeding, walking/running, digging, scent marking, relieving, grooming, being social.