# Allegato 2b_5

# How individual and environmental factors influence the activity of a wild population of Alpine chamois (*Rupicapra rupicapra rupicapra*)

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## Abstract

Optimal time allocation to foraging behavior may be constrained by individual and environmental factors making animals to adopt compromises to meet their daily energetic needs. Our goal was to determine the impact of those factors on the time budget of adult female alpine chamois Rupicapra rupicapra rupicapra. We compared the activity budget of lactating and non-lactating females, the age of each individual, the month of observation, the temperature and the two different valley of the Swiss National Park in which we conducted our study. Activity budget were built using focal animal sampling paired up with GPS data about 10 marked females during the month of May until July 2012. We found that lactating females rest less and move more than females without kids. Moreover, higher temperatures are correlated with less resting behavior and more moving behavior. Months were correlated negatively with the moving behavior and positively with the resting activity as they pass by. On another hand, older individuals tend to move less and rest more than younger individuals. Finally the valley of observation had an impact on all the behaviors. Our results underline the compromises in activity that an individual must face depending on its location, its age, whether it is lactating, but also on the time of the year and the temperature. Our findings allow a better understanding of how these trade-offs are interconnected and how they can vary through time.

## Introduction

The behavior of large herbivores has been widely studied as their foraging tactics impact greatly their fitness (White 1983). They can increase time assigned to foraging during summer to increase food intake (Shipley et al. 1994) in order to increase their winter survival rate or respond to a higher energetic need. However, individuals have not an unlimited amount of time and any increase of time allocated to an activity is at the cost of another one.

For mammals, lactation is the most energetic consuming stage of life-history traits, increasing energetic needs by up to five times the normal requirement (Oftedal 1985). Lactating females are therefore expected to modify their foraging behavior in order to increase nutrient intake (Ruckstuhl & Festa-Bianchet 1998, Arnold 1985), or to modify their metabolic expenditures by reducing the amount of locomotion activities (Miller & al. 2006). Overall, ungulate females with kids are expected to forage longer than non-lactating females. This is even more the case in the first weeks of lactation as it has been shown that there is a peek in milk production (Landete-Castillejos et al. 2000).

The Alpine chamois (*Rupicapra rupicapra*) reproduce in autumn and most kids are born in May (Couturier 1938). At that time female chamois and their young live in herds of up to 100 individuals. The presence of an offspring impacts the mother behavior as she will provide maternal care, which is any activity that increases children fitness. That leads to a rise in energy expenditures (Oftedal 1984). Therefore mothers should forage more during that time.

Toïgo (1999) showed that mothers have to provide protection for their offspring as they are more exposed to predation risk than adults hence more vigilance behavior can affect kids survival (Lima & Dill 1990). Lactating females therefore face a trade-off between foraging and vigilance behavior (Cowlishaw et al. 2004). Many individual factors or environmental factors will change the outcome of daily compromises faced by herbivores.

The temperature, an extrinsic factor, directly influences the activity of mammals. High temperature implies higher thermoregulation costs. Therefore, individuals often rest until the environment is colder (Dussault et al. 2004; Owen-Smith 1998). There are also intrinsic factors that influence the foraging behavior such as age and body mass (Pelletier & Festa-Bianchet 2004). Growing individuals have higher energetic needs and subsequently tend to forage longer (Bunnell & Gillingham 1985). It is known that, for behavioral biologist, observation of wild population is quite limited, whether it is in time or space. Indeed, it has been shown that the annual home range of adult chamois varies from 300 to 500 ha (Hamr 1984, Bögel et al. 1998, Clarke & Henderson 1984), in a mountain environment. It has also been shown that females with newborns prefer rocky areas to Alpine meadows until the kids have grown enough (the following autumn) (Grignolio et al. 2007). Those are reasons why building a time budget of a single individual based on observations is hard and time consuming.

At night observations are often limited, especially for wild populations, and it is almost impossible to accomplish. Fortunately the Global Positioning System (GPS) collars technology has greatly improved. Now they have accelerometer sensor integrated which allows long-term monitoring under natural conditions without disturbing the animals (Cooke et al. 2004). Heurich et al. (2011) showed that it is possible to correctly assign 88% of the behavior of roe dear (*Capreolus capreolus* L.) based on the activity sensor.

Our aim was to estimate the activity budget of adult female alpine chamois, *Rupicapra rupicapra*, and to evaluate the influence of the age as an intrinsic factor and extrinsic factors such as the month, the temperature and the valley they were observed in on the time budget. The observations were conducted on wild individuals in two valleys of the Swiss national park and completed with GPS data. These two valleys have different touristic and noise exposure. Val Trupchun is where most of the tourists go hiking thus has a high human exposure. On the other hand, Val dal Botsch overlooks a road and is therefore much more exposed to noise disturbance than the first valley. We therefore predicted less resting behavior in val Trupchun as the individuals may be disturbed by tourists.

We also expected that the higher the temperature is the less likely they are to feed and allocate more time to the resting behavior. Adult female alpine chamois can start reproducing at the age of 2 and a half years but only reach asymptotic body mass at the age of 3 and a half years (Bassano et al. 2003). Therefore we predicted that older individuals have lesser energetic needs and thus will eat less. Finally, due to a peak in lactation for a few weeks after the kid is born, we expect less foraging behavior as the time passes.

## Material & methods

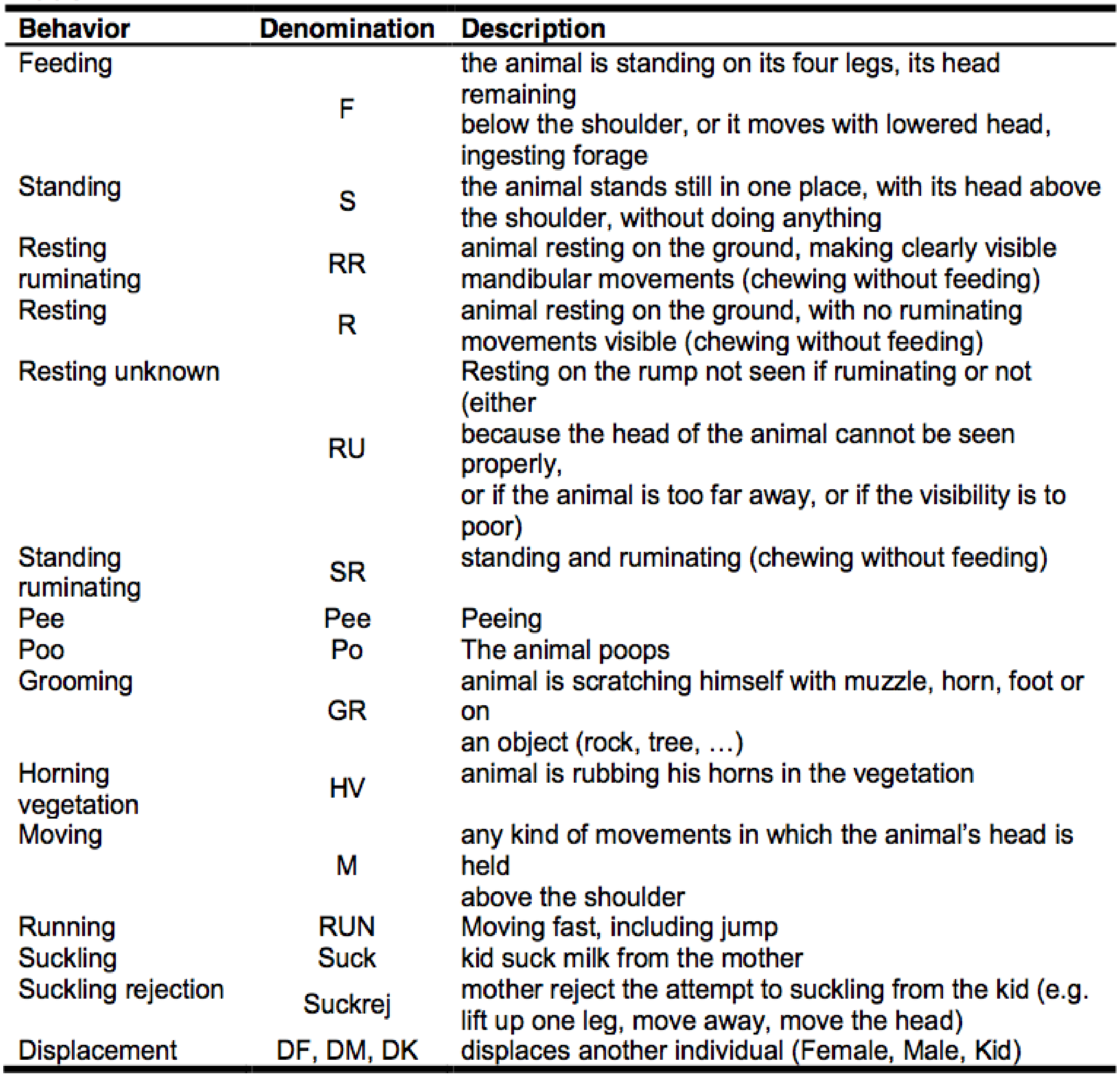
### *Study area*

The study was conducted in two valleys of the Swiss National Park. Val Trupchun where the altitude varies from 1840m to 2220m above sea level, and Val da Botsch ranging from 1836m to 2677m above sea level. The Swiss national park has a dry continental climate characterized by low precipitations (mean values of 54mm and 104mm in January and July, respectively), low humidity (0–10%) and large variations in diurnal and seasonal temperature (between −30◦C and 30◦C) (Haller 2006).

*Animal observation*

Chamois behavioral data was collected from May to July. To avoid an observer effect, only one person proceeded to the collection of the data using a Leica telescope (20 x 60) and located at least 100m away from the focal individual. As described by Altmann(1974), focal animal sampling was used on marked females to construct an activity budget (behavior presented in table 1) over continuous period of at least 4 hours depending on visibility. A 4 to 12 hour time budget was built for 6 different females that had kids. We limited our observations to marked individuals in order to have the age information.

Table 1:



| Behavior | Denomination | Description |
|---|---|---|
| Feeding | F | the animal is standing on its four legs, its head remaining below the shoulder, or it moves with lowered head, ingesting forage |
| Standing | S | the animal stands still in one place, with its head above the shoulder, without doing anything |
| Resting ruminating | RR | animal resting on the ground, making clearly visible mandibular movements (chewing without feeding) |
| Resting | R | animal resting on the ground, with no ruminating movements visible (chewing without feeding) |
| Resting unknown | RU | Resting on the rump not seen if ruminating or not (either because the head of the animal cannot be seen properly, or if the animal is too far away, or if the visibility is to poor) |
| Standing ruminating | SR | standing and ruminating (chewing without feeding) |
| Pee | Pee | Peeing |
| Poo | Po | The animal poops |
| Grooming | GR | animal is scratching himself with muzzle, horn, foot or on an object (rock, tree, …) |
| Horning vegetation | HV | animal is rubbing his horns in the vegetation |
| Moving | M | any kind of movements in which the animal's head is held above the shoulder |
| Running | RUN | Moving fast, including jump |
| Suckling | Suck | kid suck milk from the mother |
| Suckling rejection | Suckrej | mother reject the attempt to suckling from the kid (e.g. lift up one leg, move away, move the head) |
| Displacement | DF, DM, DK | displaces another individual (Female, Male, Kid) |

Table 1: List of all behaviors used in the observation of animals

### *GPS data*

Vectronic Aerospace collars were previously attached to several individual of the Swiss national park by the rangers. They also aged every marked individual at that time. The collars are equipped with a dual-axis acceleration sensor. Axis X measures acceleration when the motion is forward or backward and axis Y measures acceleration when the motion is sideward rotary. Krop-Benesch et al. (2010) give more details on the collars. During the month of august, the data of 10 females was retrieved by the park rangers.

### *Statistical analysis*

The first step was to rearrange the behavioral data in 4 different categories: Resting, Feeding, Moving and Running. This step was mandatory because activity sensor can only discriminate between those states (for example, it cannot differentiate between suckling and resting as in both cases the individual doesn't move). We therefore assigned Standing, Standing ruminating, Resting ruminating, Resting unknown, Pee, Poo, Suckling in the Resting behavior. Also, Horning vegetation and Grooming were assigned to the Feeding category and finally the Displacement was assigned to the Moving category.

Two individuals for whom a time budget had been built appeared in the gps data. Recursive partitioning was therefore used, on the X axis activity, in order to find the activity values for each 4 behaviors. This is a statistical method for multivariate analysis that creates a decision tree that attempts to correctly classify my behaviors based on the activity variable. Unfortunately the running behavior is rare and didn't appear in activity data of those 2 individuals, so it has been decided that any activity on the X axis higher than 240 was part of the running behavior.

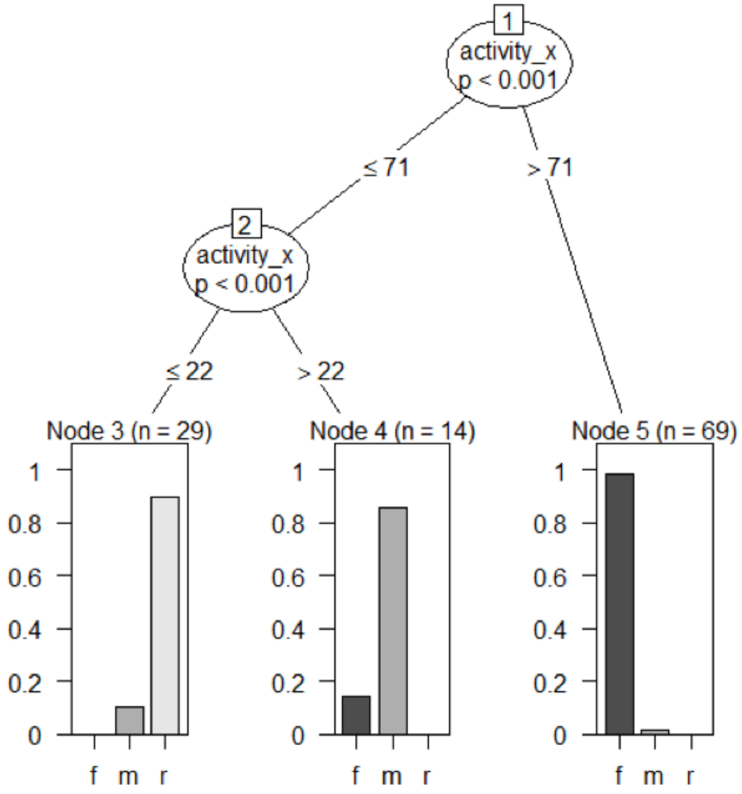
The next step was to transform all the activity data of the 10 individuals in behavioral data based on the recursive partitioning results. Finally, a multinomial logistic regression was run on several models to find the better fit (i.e.: the model with the lowest Akaike information criterion - AIC). For the analyses, the running behavior was ignored as it is linked with predator induced comportments. All statistical analyses were done with R 2.15.2

## Results

*Recursive partitioning*

The X axis thresholds were significantly established to separate resting from moving and feeding (P<0.001) and moving from feeding (P<0.01) using recursive partitioning (Fig.1). Values ≤ 22 indicated resting, values >22 and ≤71 indicated moving and values > 71 indicated feeding.

Figure 1. Result of the recursive partitioning based on 112 observations. Numbers showed on the lines linking the five nodes are the threshold for the activity. The behavior assigned for each final node (i.e.: Node 3, Node 4, Node 5) is the one most present in the barplot showed underneath the nod name (i.e: r, m, f respectively).



*Multinomial logistic regression*

Of all the different models tested (table 2), the best one explaining variations (AIC=518386.3, P<0.001), included the age, the valley, the temperature, the presence of a kid and the month. This model estimates are all significant (table 3) and the feeding behavior is the reference. It shows that for an increase in one unit of temperature, there is 1.54% (P<0.001) more chance of going from feeding to moving (Fig. 2) and 3.9% (P<0.001) less chance of switching from feeding to resting (Fig. 3). The age affects the log of the odd ratios between the moving category and the feeding category negatively (-1.10e-2, P<0.001) (Fig. 4) and affects the one between the feeding category and the resting category positively (1.95e-2, P<0.001) (Fig. 5). As we go in hotter month, we find a negative impact on the moving behavior (-0.205, P<0.001) and a positive impact on the resting behavior (2.41e-2, P<0.001) (Fig. 6). Individuals from val Trupchun move 30.34% (P<0.001) less and rest 3.94% (P<0.001) less than individuals in val dal Botsch (Fig. 7) at the at the benefit of the feeding behavior. Finally we can see that females with kids move 6.26 % (P<0.001) more and rest 34.06% (P<0.001) less than females without kids (Fig. 8).

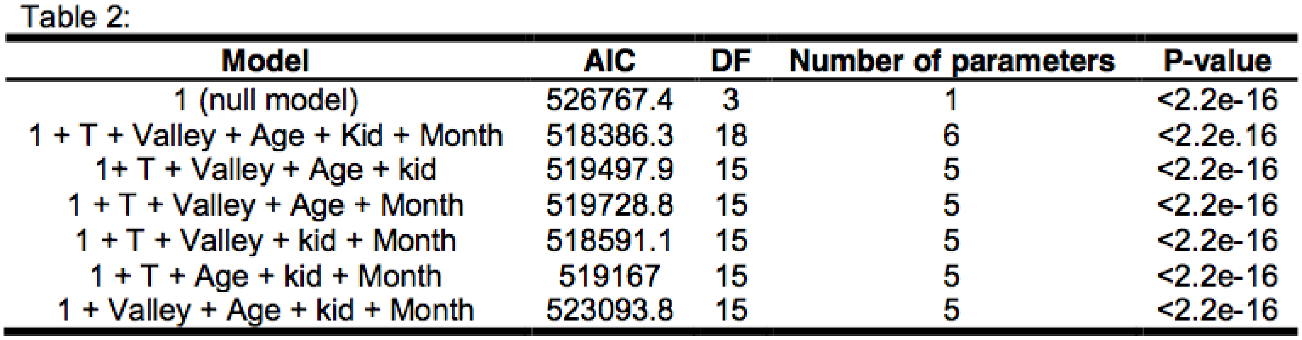


Table 2:

| Model | AIC | DF | Number of parameters | P-value |
|---|---|---|---|---|
| 1 (null model) | 526767.4 | 3 | 1 | <2.2e-16 |
| 1 + T + Valley + Age + Kid + Month | 518386.3 | 18 | 6 | <2.2e.16 |
| 1+ T + Valley + Age + kid | 519497.9 | 15 | 5 | <2.2e-16 |
| 1 + T + Valley + Age + Month | 519728.8 | 15 | 5 | <2.2e-16 |
| 1 + T + Valley + kid + Month | 518591.1 | 15 | 5 | <2.2e-16 |
| 1 + T + Age + kid + Month | 519167 | 15 | 5 | <2.2e-16 |
| 1 + Valley + Age + kid + Month | 523093.8 | 15 | 5 | <2.2e-16 |

Table 2: List of the model used with the Akaike information criterion, the degree of liberty, the number of parameters and the p-value for each model

Table 3:

| Variables | Estimate | Std, Error | t-value | Pr(>ltl) |
|---|---|---|---|---|
| M:T | 1,54E-02 | 9,87E-04 | 15,5764 | < 2,2e-16 *** |
| R:T | -3,99E-02 | 6,79E-04 | -58,6975 | < 2,2e-16 *** |
| M:ValleyTrupchun | -3,62E-01 | 1,64E-02 | -22,0968 | < 2,2e-16 *** |
| R:ValleyTrupchun | -4,02E-02 | 9,80E-03 | -4,102 | 4,096e-05 *** |
| M:Age | -1,10E-02 | 2,69E-03 | -4,0985 | 4,158e-05 *** |
| R:Age | 1,95E-02 | 1,65E-03 | 11,8119 | < 2,2e-16 *** |
| M:kidYes | 6,07E-02 | 2,26E-02 | 2,6807 | 0,0073460 ** |
| R:kidYes | -4,16E-01 | 1,24E-02 | -33,6024 | < 2,2e-16 *** |
| M:Month | -2,05E-01 | 8,44E-03 | -24,2346 | < 2,2e-16 *** |
| R:Month | 2,41E-02 | 5,23E-03 | 4,6157 | 3,917e-06 *** |

Table 3: Result of the multinomial logistic regression with the estimate and its p-value, the standard error associated and the t-value. We can thus see how each behavior is affected by the parameter

Figure 2. Percentage of time spent moving in relation to the temperature in adult female alpine chamois, at the Swiss national park in 2012. For the presentation, data is for all the females observed during the study. Blue regression line represents a linear fit of these data point.

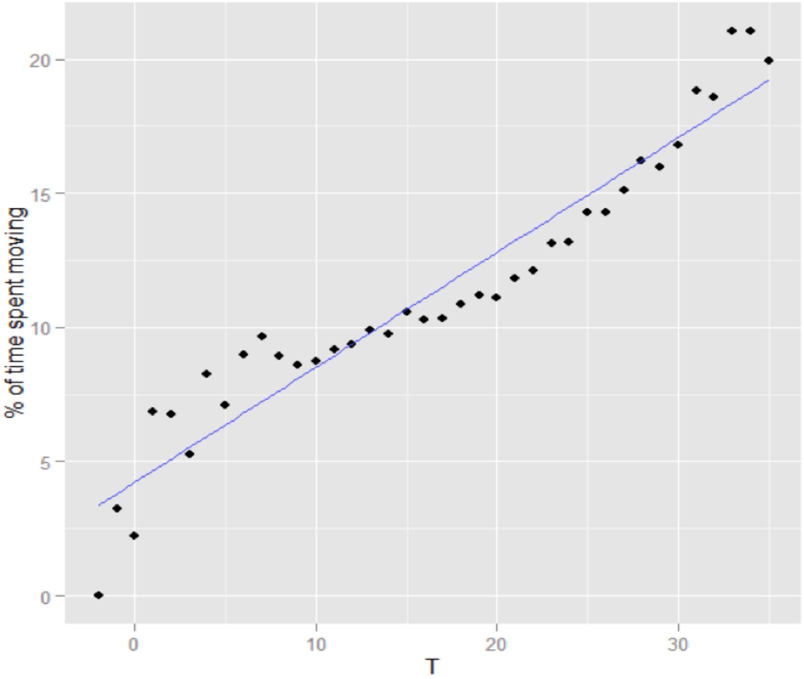


Figure 3. Percentage of time spent resting in relation to the temperature in adult female alpine chamois, at the Swiss national park in 2012. For the presentation, data is for all the females observed during the study. Blue regression line represents a linear fit of these data point.

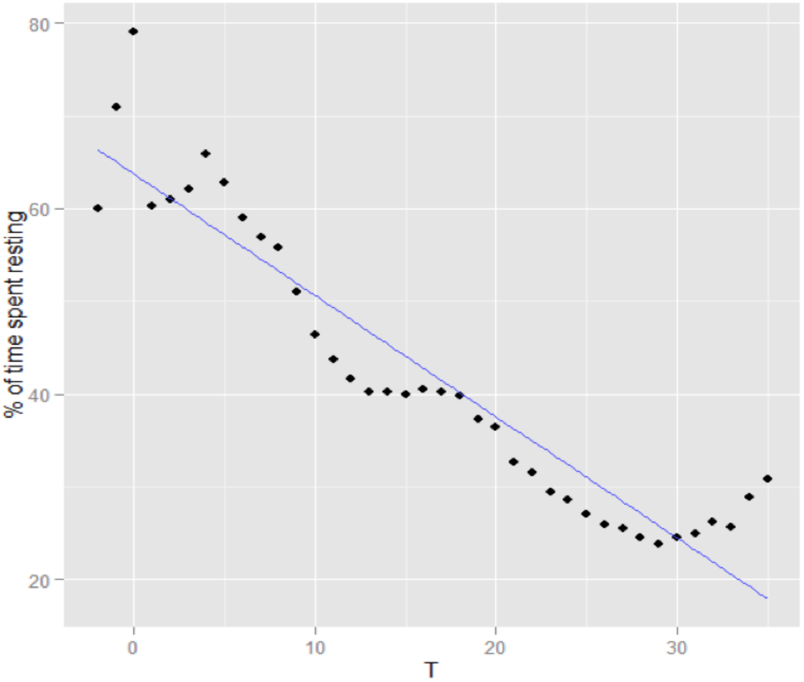


Figure 4. Percentage of time spent moving in relation to the age in adult female alpine chamois, at the Swiss national park in 2012. For the presentation, data is for all the females observed during the study. Blue regression line represents a linear fit of these data point.

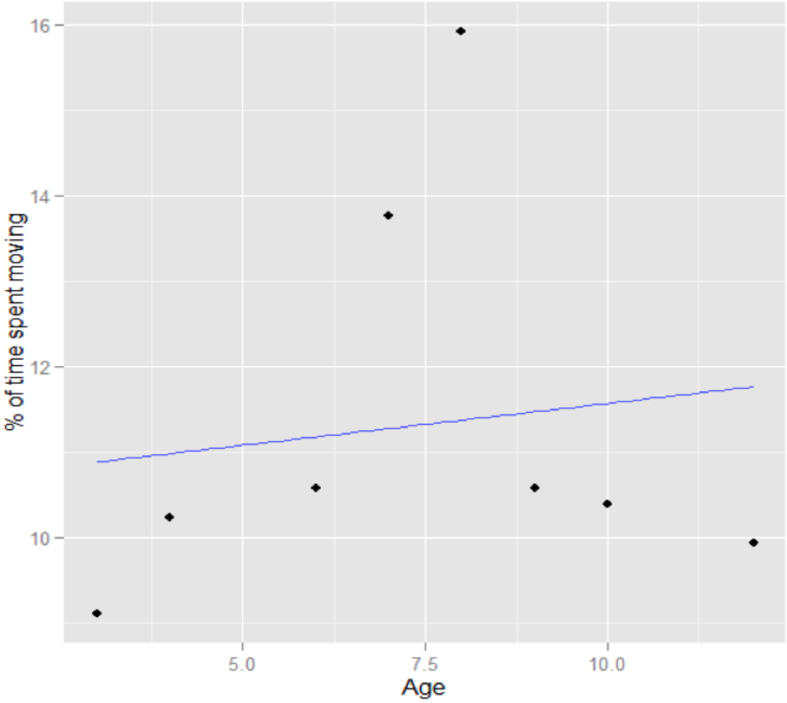


Figure 5. Percentage of time spent resting in relation to the age in adult female alpine chamois, at the Swiss national park in 2012. For the presentation, data is for all the females observed during the study. Blue regression line represents a linear fit of these data point.

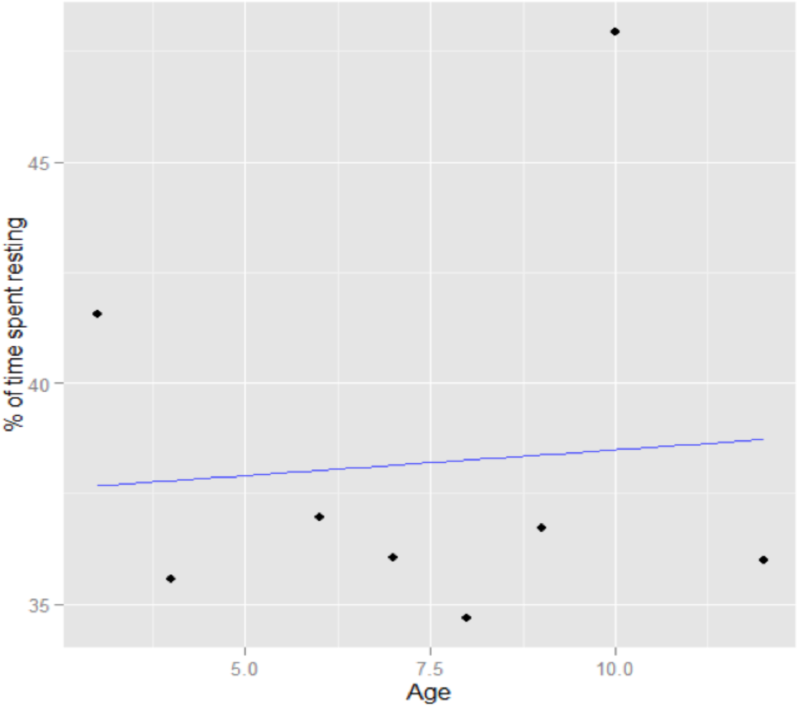


Figure 6. Percentage of time spent in each behavior (±SE) in relation to the month of observation in alpine chamois. Female activity budgets were collected in 2012 in the Swiss national park. The figure illustrates 89273 observations in the month of May, 93639 observations in the month of June and 87243 observations in the month of July for 10 different females.

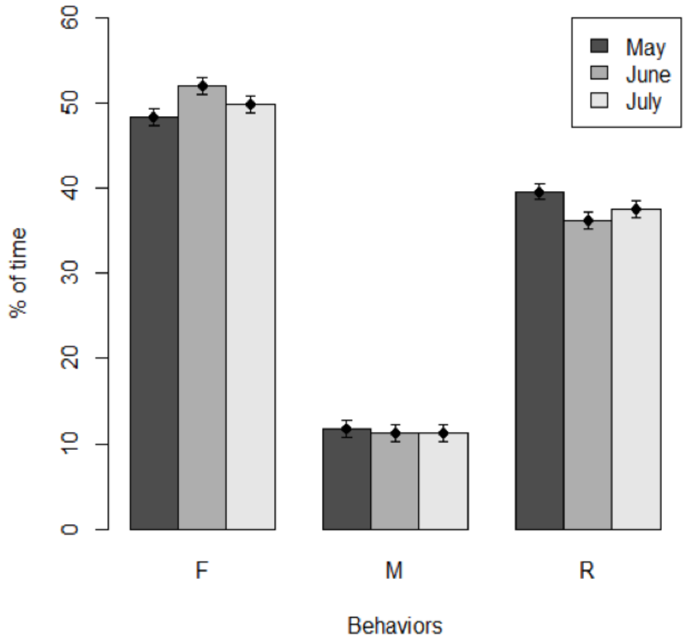


Figure 7. Percentage of time spent in each behavior (±SE) in relation to the valley of observation in alpine chamois. Female activity budgets were collected in 2012 in the Swiss national park. The figure illustrates 145674 observations in Val dal Botsch and 124481observations in Val Trupchun for a total of 10 different females.

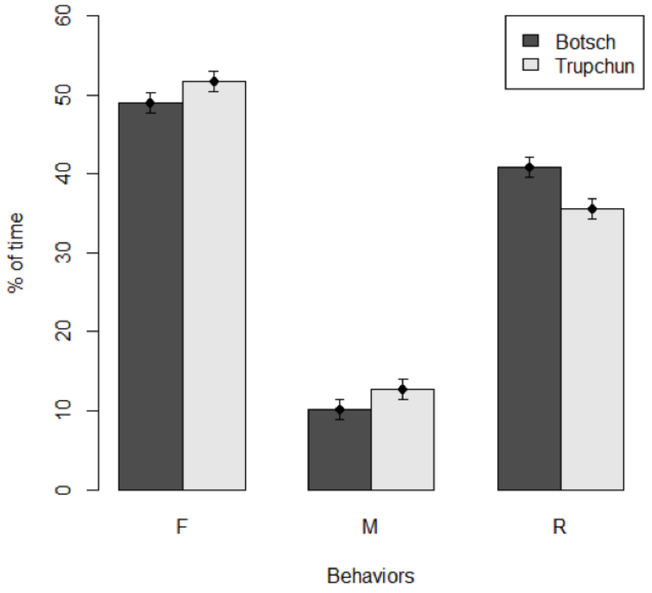
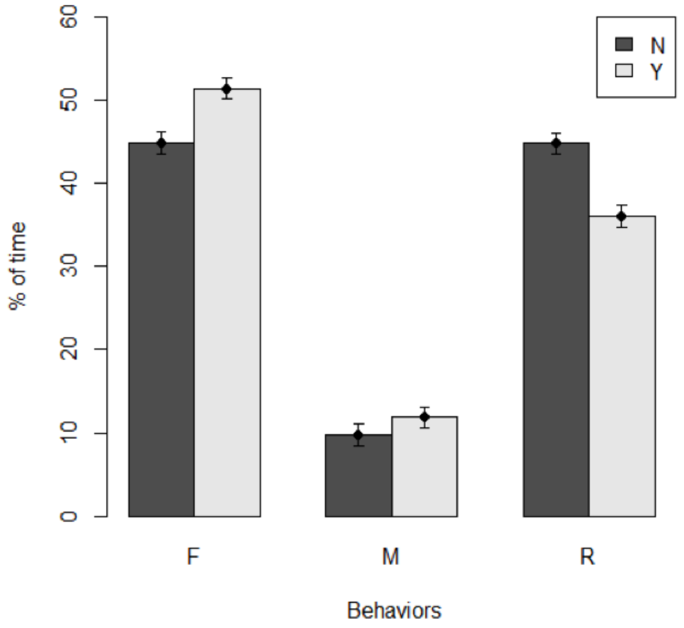


Figure 8. Percentage of time spent in each behavior (±SE) in relation to the female reproductive status in alpine chamois. Female activity budget were collected in 2012 in the Swiss national park. The figure illustrates 53447 observations of 2 non-lactating females and 218185 observations of 8 lactating females.



## Discussion

Individuals face every day behavioral compromise in order to meet their daily energetic requirements. We found here that some intrinsic and extrinsic factors play a role as they shape their everyday activity. As expected, while we advance in months, individuals will tend to spend more time resting at the expense of time spend foraging, and simultaneously they will move a lot less, in order to allocate more time to the eating behavior. This can be explained by the environment in which they have offspring as they tend to go in rocky areas at night in the first weeks after the birth (Grignolio & al. 2007), a comportment that protects the offspring from predation but involves a lot of movements. Furthermore, in early months they tend to eat more in order to increase the milk production as lactation consumes a lot of energy (Landete- Castillejos et al. 2000). Individuals without offspring tend to move less because of the availability of the food. As the spring months come around the vegetation is more luxurious and food patch are easier to find.

Another very interesting finding is that having a baby modifies greatly the behavior of adult females as they rest 34% less; so they spend more time foraging when they have an offspring but also tend to move about 6% more. Even if this species is of the follower type where mothers defends their offspring against predators (Lent 1974), it can happen that the mother and her child are separated. He will usually be in the company of a "baby-sitter" or grouped with other young individuals in a "kindergarten" (Rückstuhl & Ingold 1998). During that time the mother will have more time to search for good quality forage increasing the movement behavior. The maternal care is another reason for both these findings. As Toïgo (1999) showed, mothers are more vigilant than females without offspring in order to increases the chances of detecting a predator. The vigilance behavior might have an impact on the survival of children (Lima & Dill 1990).

The valley in which they live has also a great impact on their behavior. Individuals in Val Trupchun move and rest less than individuals from Val dal Botsch (about 30% and 4% respectively). As said earlier, Val Trupchun has a higher tourist density per year and individuals have to avoid human groups more often and must also be more vigilant to their environment. Some studies already showed that human activities could have a major impact on the species distribution and the accessibility of resources (Breitenmoser 1998, Laliberte and Ripple 2004). However, both valleys do not have the same surface, data that we don't have. Val dal Botsch might be bigger so the effect of tourists is probably overrated. Another point is that both valleys might have different forage quality. The altitude is not the same in both valleys therefore we expect different temperature. Pettorelli (2007) showed that warm 54 temperatures coupled with high moisture favor rapid plant growth thus shortens the period of high forage quality. The latter have been shown to modify ungulate behaviors (Clutton-Brock & al. 1982). In summary, while the results are significant for the two female populations separately, we lack too much information about the differences between the two valleys to conclude that tourism is the only cause.

The age, impacts the behavior as expected. Older individuals tend to rest more and younger individuals tend to move more at the expense of the eating behavior. While the first part can be explained by the fact that growing individuals have more energetic needs (Pelletier & Festa-Bianchet 2004), the second part however can be explained by the social rank. It has been shown in another ungulate study that the age is positively correlated with leadership (Festa-Bianchet 2003). This implies that younger individuals will have to move more to get to food patch as dominant often have priority access to forage (Hamel & Côté 2008). These findings are consistent with Hamel & Côté (2008) results, as they say that individuals dominant for their age may have more experience with finding high-quality or more abundant forage than females subordinate for their age allowing dominant females to meet their energetic requirements faster.

The temperature had unexpected effects. Indeed, the higher the temperature is, the lower is the chance an individual will rest and the higher is he will move. While the time spent foraging indeed shortens at high temperatures, the fact that they move more when it is hotter is hard to explain. On the other hand, we observe more resting when the temperature is lower. This might be explained by the fact that individuals tend to have reduced activity at night, when temperature is lower. A study about the Himalayan Thar (Hemitragus jemlahicus) shows that it is unlikely that active foraging occurs during the night (Tustin & Parkes 1988). Similarly, individuals will move more during the day, when the temperatures are hotter. Most of the studies tackling with activity in relation to the temperature stop recording data at sunset which might explain why the present findings differ. Also, Berger (1986) and Duncan (1992) showed that the activity can be influenced by daily patterns of temperature.

In the present study, we estimated the effects of individual characteristics coupled with extrinsic factors on the activity budget of adult female Alpine chamois. Our results underline the compromises in activity that an individual must face depending on its location, its age, whether it is lactating, but also on the time of the year and the temperature. Our findings allow a better understanding of how these trade-offs are interconnected and how they can vary through time.

Future studies should be designed to look at individual variations on more parameters.

Previous findings showed that factors such as the chewing rate and the time spend ruminating (Hamel & Côté 2008, Hamel et Côté 2009), forage quality (Clutton-Brock & al. 1982), social rank (Hamel & Côté 2008), group density of the herd (Conradt 1998; Ruckstuhl & Neuhaus 2001) and the child sex (Hamel & Côté 2008) all have an effect on the activity budget of ungulates. We therefore need to combine the present study with data on plants abundance and quality to evaluate compromise between foraging and ruminating behaviors according to environment quality, plant phenology, and group characteristics.

## Acknowledgements

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