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Marginal habitats provide unexpected survival benefits to the alpine marmot

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Abstract

Age-specific survival trajectories can vary significantly among wild populations. Identifying the environmental conditions associated with such variability is of primary importance to understand the dynamics of free-ranging populations. In this study, we investigated survival variations among alpine marmot (*Marmota marmota*) families living in areas with opposite environmental characteristics: the typical habitat of the species (alpine meadow) and a marginal area bordering the forest. We used data collected during an 11-year study in the Gran Paradiso National Park (Italy) and performed a Bayesian survival trajectory analysis on marked individuals. Furthermore, we investigated, at a territorial level, the relationships among demographic parameters and habitat variables by using a path analysis approach. Contrary to our expectations, for most of the marmot's lifespan, survival rate was higher in the marginal site closer to the forest and with lower visibility than in the alpine meadow site. Path analysis indicated that the number of families living close to each other negatively affected the stability of the dominant couple, which in turn affected both juvenile survival and reproduction. Given the lower number of neighbouring families which inhabited the marginal site and the potentially different predation pressure by the most effective predator in the area (*Aquila chrysaetos*), our results suggest that species adapted to live in open habitats may benefit from living in a marginal habitat. This study highlights the importance of habitats bordering the forest in the conservation of alpine marmots.

Keywords: Marginal habitat, *Marmota marmota*, reproduction, stability, survival probabilities

Introduction

Under natural conditions, vertebrate population dynamics are influenced by several biotic and abiotic factors, which affect the ability of individuals to cope with external stimuli (Batzli 1992, Ecke et al. 2002, Zarnetske et al. 2017). In species distributed over a wide altitudinal range, habitat suitability may vary considerably. This may affect several life-history traits, such as individual survival (Maguire 2006), reproductive success (Pärt 2001, Sergio and Newton 2003), cooperative breeding (Komdeur 1992), and parasite load (Zanet et al., 2017). In a number of alpine avian species, life history strategies may vary according to the elevation of the site inhabited: individuals living at high elevations show higher survival rates but lower reproduction rates compared to those living at lower elevations (Bears et al. 2009, Camfield et al. 2010). Environmental suitability may also vary throughout the season. For example, Gillis et al. (2015) found higher summer mortality rates in females of Arctic ground squirrel (*Urocitellus parryii pleisus*) living in the boreal forest with respect to those living in the alpine environment, mainly on account of differences in the predation pressure. On the contrary, winter mortality rate was higher in the boreal environment compared to the alpine habitat, likely owing to the differences in elevation and vegetation cover (Gillis et al. 2015). Hormonal status may also vary according to the season and the area inhabited (Sheriff et al. 2012). Individuals which inhabit poor habitats were found to be more stressed than those which inhabit richer habitats, a condition which may lead to a reduction in fecundity (Lea et al. 2018). Populations which inhabit marginal and sink habitats (Dias 1996) are generally expected to be at lower density (Gonzales-Megìas et al. 2005), in poorer body conditions (Werner et al. 2015), and less fecund (Lea et al. 2018) in respect to populations which inhabit more suitable habitats. Marginal habitats usually indicate areas which are characterised by vegetation transition and located at the border of a species' typical habitat (Hester and Harrison 2007). Such marginal territories are generally expected to host smaller populations, which are composed of single individuals and small colonies of conspecifics following dispersal dynamics. In these sites, survival, reproduction, and population density tend to be lower than those in native areas, at least during the first stages of colonisation (Kawecki 2008).

In free-living rodents, factors such as slope, presence of rocks, and vegetation can influence the suitability of a certain territory since they affect the chances to escape from predators, foraging time, and the overall space use (Getz et al. 2001, Ferrari et al. 2009, Klein et al. 2012), thus modifying population density (Ecke et al. 2002) and survival (Gillis et al. 2015). For example, in vole species (*Microtus ochrogaster* and *M. pennsylvanicus*), survival is affected by the amount of vegetation cover and the frequency of predator attacks (Getz et al. 2005). Habitat factors were also found to influence the sociality of species, with an indirect effect on their group stability, survival, and reproduction (Bowyer et al. 2020). In the southern hairy-nosed wombat (*Lasiorhinus latifrons*), individuals which burrow in hard soils were found to live in larger groups and more clumped burrows than populations which inhabit friable soils (Walker et al. 2007). In a family living lizard (*Liopholis whitii*), sociality and mating tactics vary according to the distribution and localisation of crevices: when refuges are clumped together, social polygyny is favoured (Halliwell et al. 2017).

The alpine marmot (*Marmota marmota*) is a ground-dwelling rodent which preferably inhabits high elevation meadows. This habitat is currently facing conservation problems caused by the decrease in livestock grazing and climate changes, which led to an increase in shrubby and wooden areas (Filippa et al. 2019, Laiolo et al. 2004). Open alpine meadows offer a wider variety of vegetation and higher visibility to marmots compared to marginal areas bordering the forest. This favours longer foraging bouts with respect to vigilance and scanning for predators (Carey 1985a, Ferrari et al. 2009, Macchi et al. 1992), suggesting an overall lower environmental stress (Edwards and Edwards 2011).

Alpine marmots are mostly monogamous, with no sexual dimorphism (Allainé et al. 1998). Individuals live in families, in which the dominant pair monopolises reproduction, establishes and maintains the hierarchy, and maintains it by means of affiliative and agonistic social interactions (Arnold 1990). Dominants may be subjected to takeovers from subordinate individuals, an event which often leads to reproductive failure in the family for that year (Lardy et al. 2015).

In the present study, we investigated whether two contrasting habitats may trigger different dynamics in the population hosted and explored how environmental factors influence social parameters in such territories. To this aim, we collected data in an alpine meadow area with almost no cover and a marginal habitat bordering the forest with a high percentage of shrub and rocky cover. We used Bayesian age-specific survival trajectory models (Colchero et al. 2012) to analyse survival variations based on the sex of the individuals and the site they inhabited. We predicted no effect of sex on marmot survival, in accordance with previous findings on this species (Berger et al. 2016; Farand et al. 2002). Conversely, we predicted survival variations among the families which inhabited the two sites: in particular, we expected higher survival rates in the alpine meadow area as it provided marmots with better visibility of predators compared to the marginal area, which is closer to the forest boundary.

Subsequently, by using a confirmatory path analysis (Shipley 2000), we evaluated at a territorial scale how habitat (territorial index of vegetation quality, distance from the forest edge, and exposure) and demographic factors (stability of the dominant couple, juvenile survival, reproduction, and number of neighbouring families) interacted. We predicted that a lower number of neighbouring families might favour a reduced turnover frequency among dominants, thus increasing the stability of the dominant pair. We then predicted that the higher stability of the dominant couple may act as a direct survival and reproduction driver in alpine marmots. As for the biotic factors, we predicted that the quality of food resources (*i.e.*, vegetation) may positively influence juvenile survival and reproductive success of alpine marmots, with no direct effect on the stability of the dominant couple. Considering the hibernation period of the alpine marmot, we expected the southward exposure of the territory to positively influence the survival of both juveniles and adults by anticipating the time of snowmelt at the end of the winter season.

Methods

Model species

Alpine marmots are semi-fossorial rodents that hibernate during winter, from October to April. During the active season (April-September), they spend most of their time foraging and resting (Ferrari et al. 2021 *submitted*). Alpine marmots live in families, which permanently inhabit a territory throughout the year and, generally, across generations, though slight variations along the borders were observed (Pasquaretta et al. 2015). A family's territory always includes one or two main burrows, with several entrances and tunnels used by marmots to reach the rooms where they spend time when underground. Other secondary and emergency entrances are distributed throughout the territory and mainly serve as ways to escape in case of danger and disturbance during foraging and other activities above the ground. Alpine marmots are characterised by high sociality. Sociality is reinforced by social hibernation, a cooperative reproductive system, and cohesion among family members, which is established and maintained by social interactions carried out during the active season (Allainé and Theuriau 2004, Arnold 1990).

Marmots have a cooperative breeding system, in which only the dominant couple generally reproduces, while other members have to either postpone their reproduction or disperse elsewhere. Takeovers of the dominant individual may occur either at the beginning of the active season or, less frequently, in the following months (King and Allainé, 2002). The evicted dominant is forced to leave the family and, generally, the new one either kills or chases away the young and subordinates of that group (Hackländer et al. 2003). A female may reproduce during 2-3 consecutive years and yield a 2-4 pup litter at a time. Births occur underground at the end of May and, after a month, pups first leave the burrow and rapidly learn to move within their territory. One-year-old individuals (*i.e.*, yearlings) remain in the territory and can frequently be observed in affiliative social interactions. Sexual maturity is reached at 2 years of age (though reproduction generally begins at 3 years of age) and adults usually disperse at 3-4 years of age (although dispersal at 2 years of age can occasionally be observed; CF pers. obs.).

The alpine marmot is a key prey species for two characteristic predators of the Alps, the red fox (*Vulpes vulpes)* and the golden eagle (*Aquila chrysaetos*), which were both present in high density in the study area (Fasce et al. 2017). The main anti-predator tactic used by marmots consists of regular environment scanning while individuals are occupied with above-ground activities. Scanning frequency is higher in sites with limited visibility (Ferrari et al. 2009). Marmot anti-predator strategy also partly relies on the burrow system: their territory is composed of burrows which are dug into the ground and inter-connected by tunnels and blind bottom emergency burrows. Whenever they perceive a danger, marmots flee to the closest burrow to hide. Burrows can be dug into the ground, though big boulders and rocky debris are also commonly used by this species.

Study area

Data presented in this study were collected from 2007 to 2018 as part of a long-term project on alpine marmot in the Gran Paradiso National Park. Captures and observations of alpine marmot families were performed in 2 main areas of Valsavarenche (45°34’ N; 7°11’ E, AO, Italy), each characterised by different habitats. The first area (Low site) is located at 2,100 m. a.s.l. and marmot territories have a mean (± SD) distance of 100 ± 90 meters from the forest boundaries. It is a marginal habitat, composed of an ecotonal vegetation, with a forest along the border, isolated trees (*Larix decidua*), areas of plain meadows alternating with alpenrose (*Rhododendron ferrugineum*) bushes , and scattered big boulders. Such habitat composition results in discontinuous visibility for marmots. In the Low site, we monitored and included in this study 6 families living in the area.

The second area (High site) is located between 2,200 and 2,400 meters a.s.l.. The mean distance between the centre of the marmot territories and the closest forest boundaries is 320 ± 160 meters. This site is a typical alpine meadow, where mostly gramineae and a few dicotylendons grow. The absence of arboreal vegetation and other visual obstacles ensure a high visibility for marmots. Even in the High site, we monitored and collected data on 6 families.

Data collection

Fieldwork began every year in mid-April according to snow conditions and the accessibility of the area. Even though the team immediately began focal observations to recognise marked individuals, the first period was mainly devoted to trapping and marking new marmots belonging to the different families in the study area. Captures were carried out by using Tomahawk traps (150 x 30 x 30 cm, Tomahawk Live Traps, Hazelhurst, WI, U.S.A.), following the protocol described in Ferrari et al. (2013). Animal trapping ended around mid-July, when newborns emerged from the burrows. During captures, marmots were sexed and aged as pups, juveniles, and adults. Adult and juvenile individuals were marked with plastic coloured ear -tags (Minirotag, 5 cm length, Ghislandi and Ghislandi, Bergamo, Italy) and microchip transponders (Bayer Animal Coder, Bayer S.p.A., Milan, Italy). Pups were marked with microchip transponders. No ear-tag was used on account of the small size of their ears and, as a replacement, we used non-toxic fur bleach for visual recognition. The fur-marking lasted until mid-August of each study year, when pups shed their fur.

During the whole fieldwork season (from May to September), scan sampling and ad-libitum observations were conducted daily by using scopes (Swaroski 30x75 and Nikon ED82 25-56X82) to collect data on family composition, reproductive events, individual survival, use of the familiar territory, and behaviours (see Pasquaretta et al. 2012 for details).

Each individual was assigned to the family inhabiting the territory in which it was captured and observed in its daily activity. Family group territories measured 0.71 ± .44 hectares and remained almost stable throughout the years, with slight variations only in the peripheral edges (Pasquaretta et al. 2012). We mapped each territory with its main and secondary burrows in a GIS environment by using QGis 2.10 and checked for the consistency of territory use throughout the years. This type of data collection enabled us to particularise the demographic events that occurred in each of the territories included in the study.

To get a territorial index of vegetation quality, we sampled four 1-m^2 plots randomly distributed in each territory. Sampling was performed monthly from June to September for 2 consecutive years (in 2018:223 vegetation samples; in 2019: 216 vegetation samples) in 17 different territories (10 in the High site, 7 in the Low site; only 6 territories for each site were subsequently used in the analysis, as explained below). Samples were kept in paper bags and taken to the laboratory within

12 hours. Then, one by one, all samples were chopped and analysed with NIRS (Near Infrared Reflectance Spectroscopy) (Haughey et al. 2015). We obtained an instant quantification of pasture nutritional quality by analysing the characteristic reflection and absorption spectra of fresh forage in the near-Infrared (NIR) region (780–2500 nm) and comparing it to calibrated reference parameters. Finally, we performed a statistical analysis by using the ratio of the amount of proteins to the amount of fibres in the sample as an index of territorial vegetation quality (see Supporting Information 1 for further details).

Survival analysis

To estimate survival trajectory, we used the BaSTA package version 1.9.4 (Bayesian Survival Trajectory Analysis; Colchero et al. 2012) in the R statistical environment (R Development Core Team 2019). BaSTA draws inferences on age-specific survival from capture-recapture data in case of missing information about the birth and/or death of either a part or most of the individuals included in the analysis (Colchero and Clark 2012) (Table 1). This was also the case of our study as we were able to determine with certainty the age of a marmot only when its first capture was performed during either its first (as a pup) or second (as yearling) summer. In all other cases, a trapped marmot was considered adult, though its exact age could not be established. Furthermore, most of the times, we had no certainty about the age of death of marmots since we could not distinguish between death and dispersal and both events may have accounted for a missing individual in the area. Occasionally during the seasons, we observed the areas neighbouring the study sites to check for potentially dispersed marked individuals. However, we experienced a low percentage of positive observations (4 out of 330 captured individuals).

To compare the survival likelihood of the marmots which inhabited the two different sites, we used data collected by means of both captures and re-sighting. Since most of the individuals in the study area were individually marked and recognisable from distance, direct sighting can be considered a visual recapture of the individual (Minta and Mangel 1989). Data were analysed on a yearly basis. According to the package requirements, we built a dataset using 1 in case of either a capture or a re-sighting of an individual in a certain year and 0 when an individual was not observed throughout the year. The date of birth and/or death of each marmot was reported when known and indicated with 0 when missing.

BaSTA enables users to consider different structures of survival models:

- Gompertz model, in which the mortality hazard increases exponentially with age and is described by two parameters: $b_0$represents the basal mortality rate and b_1 its exponential increase;
- Weibull model, in which the mortality hazard either increases or decreases as a power function of age and is described by two parameters: b_0 represents the shape and b_1 the scale;
- Logistic model, in which the mortality hazard achieves a stable level at old ages and is described by three parameters: b_0 and b_1 correspond to the Gompertz model and b_2 represents the deceleration rate in mortality increase.

To better incorporate complex forms of the survival curve, BaSTA enables to use different shapes to extend the basic functions: simple (model shaped by using only the basic function described above), Makeham (age-independent mortality model, shaped by adding a positive constant c), and bathtub (U-shaped model, which includes decline in early mortality by adding two constants) (Colchero et al. 2012, Ronget et al. 2020).

BaSTA also includes the Exponential model, which was not used in our analysis as it assumes that mortality is constant at all ages (Cox and Oakes 1984). We run a model with no covariate to select the more appropriate shape and form of the survival functions by using the function MultiBaSTA included in the package. MultiBaSTA directly runs all the possible combinations of models altogether and calculates the Deviance Information Criterion (DIC), which is a measure of predictive power used as a criterion to select among different models (Spiegelhalter et al. 2014). We run 3 simulations for MCMC (Markov chain Monte Carlo) by setting 20,000 iterations with a 1,001 burn-in and a thinning interval every 50 iterations. We visually evaluated convergence, which was assured for all the models.

Once we found the best structure and shape for the data, we run a model with sex and one with site. For each model, we obtained a measure of the influence of the categorical variables on survival by using the Kullback-Liebler discrepancy (KLc) (Kullback and Lieblet 1951). This method measures the overlap between posterior distributions: a KLc value around 0.5 indicates an almost complete overlap between parameter estimates, while KLc=1 indicates no overlap; as a rule of thumb, KLc > 0.65 indicates a difference in the distribution (Larson et al. 2016).

BaSTA calculates and plots both survival likelihood and predicted mortality rate of the population analysed.

Path analysis of demographic parameters

We used confirmatory path analysis (Shipley 2000) to test and compare 10 theoretical models about the relationships among the demographic parameters of the families and the structural and biotic habitat factors of their territories. Path analysis tests whether the conditional independencies implied by the causal model proposed are consistent with the data (Bollen 1989). For this analysis, we used the *lavaan* 06-5 package (Rosseel 2012) in R.3.6.

In the analysis, we included the 12 territories for which we had a complete dataset from 2007 to 2018. For each territory, we selected and calculated 7 variables, which may affect marmot ecology. Among them, the following 3 are habitat characteristic variables:

- Exposure of the main burrow, calculated as a continuous variable, from North to South, by using the Horn function in QGIS 3.4.
- Distance between the edge of the forest and the main burrow in meters; whenever a territory had 2 main burrows, we calculated their mean distance from the edge of the forest in QGIS 3.4.
- Territorial index of vegetation quality, calculated by using NIRS.

For each territory, we then calculated the following 4 variables corresponding to the demographic and social parameters of a family:

- Reproduction index: mean number of pups born in summer from 2007 to 2018 for each territory.
- Juvenile survival: ratio between the number of juveniles observed in a territory and the pups produced in the same territory the previous summer. Since pups do not disperse, a missing pup was classified as not survived. For each territory, we then computed the mean survival rate for the period 2007-2018. Juvenile survival referred to individuals from 0 to 1 years old. Conversely, it was almost impossible to distinguish between survival and dispersal in other age classes, since individuals may have moved to territories which were not included in the study area.
- Stability of the dominant couple: ratio between the numbers of years with the same dominant couple in the territory and the total number of observation years; this variable was considered a proxy of the stability of the whole family (see Model species).
- Number of neighbouring families: number of families sharing the territory boundaries with the focal family.

We then compared 10 models (Fig.1) in which the relationship among juvenile survival, reproduction index, stability of the dominant couple, and number of neighbouring families remained constant, while we changed the variables related to the habitat factors. We selected the model which best fitted the data, following the overall multiple criterion: comparative fit index (CFI) and Tucker-Lewis Index (TLI) higher than 0.9, standardised root mean square residuals (RMSEA) lower than 0.1, and chi-square higher than 0.05 (Hu and Bentler 1999). Akaike Information Criterion (AIC) values of the models were indicated as further criteria of model selection (Burnham and Anderson 2002).

All data are available at: https://data.mendeley.com/datasets/62xkwzvrzm/draft?a=74d07f6e-1543-4672-b519-ec63b7a92679

Results

Survival analysis

Since the model following a logistic function and a *bathtub* shape had the lowest DIC (Table 2), we maintained this combination of structure and shape for all the subsequent analyses. The predicted age-specific survival trajectory indicated that survival likelihood sharply decreased until 5 years of age and then became constant (Fig.2 a).

Predicted mortality rate (or death rate) increased in pups and juveniles and then remained almost constant after 2 years of age (Fig. 2 b).

When sex was included as a covariate in the model, the discrepancy between the parameter estimates describing the shape of the survival curve indicated no difference in survival likelihood among sexes, with all the estimated KLc values ≤0.5 (Table 3, Figure S1).

In the model including site as a covariate, age-specific survival trajectory split according to the site inhabited, with no overlap of the credibility intervals in most of the curves, thus suggesting differences in survival likelihood according to the site (Fig. 3). Survival was similar at the very early stages of life and then rapidly started to differ from 4 years of age until the end of the curve, with the Low site showing a higher survival likelihood.

Predicted mortality was similar at the very early stage of life and then started to split after 1 year of age: mortality rate curves did not overlap in the interval from 1 to 4 years of age, indicating a higher mortality rate in the High site compared to the Low site (all estimated KLc values > 0.68) (Table 3, Fig. 3).

Path analysis

Model 3 and Model 9 showed the overall best indicators and an equivalent AIC (Δ AIC <2) (Table 4). For the principle of parsimony, we decided to use Model 9, which included one relation less as the distance from the edge of the forest was considered to be an independent variable. Model 9 included the effect of exposure and stability of the dominant couple on juvenile survival; reproduction had a high value, whereas the quality of vegetation had a low positive relation with juvenile survival (Fig. 4). The number of neighbouring families directly and negatively affected stability. Stability and quality of vegetation showed a positive relationship with the reproduction index.

Discussion

The survival trajectory which best represented our data on alpine marmot indicated that survival rate initially decreased and then reached a plateau at advanced ages (6 years old, Fig. 2). Our results seem to confirm those of Farand et al. (2002), which found that, in the same species, the mean survival rate was lower in young individuals than in adults. In a study focusing only on dominant individuals of *Marmota marmota*, Berger et al. (2016) showed a constant survival rate of dominants until 6 years of age, followed by a sharp decrease after 8 years of age and then a further slow but constant decrease, thus demonstrating the occurrence of actuarial senescence.

Contrary to these findings, in our curve, we detected no sharp decrease after 8 years of age. However, this may be related to the relatively small size of our sample of old marmots since, in most cases, we could not cover the entire life span of this species.

As we expected and in accordance with previous literature (Berger et al. 2016, Farand et al. 2002), we found no effect of sex on the survival likelihood of an individual. Since alpine marmot is a monogamous species, male and female life-history strategies are similar, thus suggesting limited or absent survival variations based on sex, as found in other mammal species (Larson et al. 2016).

Unexpectedly, we found a higher survival likelihood in the marmots which inhabited the Low site compared to those living in the High Site. Most of the previous studies indicated lower survival and recruitment rates in marginal and sink habitats mainly on account of differential predation pressure, resource scarcity, and poor body conditions of individuals (Gillis et al. 2015; Sheriff et al. 2012). Consequently, we based our expectations on the fact that colonies located closer to the forest may be affected by a lower vegetation quality, given the heterogeneity of the marginal habitats. In addition, the chances to spot predators are likely to decrease, thus increasing potential fox attacks on pups and, occasionally, yearlings, though not on healthy adults. However, it is important to highlight that the main foraging habitat for eagles, which are able to predate upon all marmot age classes, are open meadows. Conversely, eagles tend to attack less frequently in areas bordering the forests (Pedrini and Sergio 2001). Although marmots are one of the main prey for this raptor (Pedrini and Sergio 2001), studies on fox feeding habits in the Alps indicated that this rodents represent only a small part of the fox diet, which is mostly based on small mammals, carrions, and fruits (Cagnacci et al. 2003, Lucherini and Crema 1994). Unfortunately, we cannot provide a reliable predation index for the two sites to include in our analysis. However, we know that the territory of the Gran Paradiso National Park hosts 27 breeding pairs of golden eagle and shows the highest density of this species in the Alps (Fasce et al. 2017). Therefore, based on our results, we suggest that marmots living in marginal habitats may benefit from a reduced eagle predation pressure and this may account for the long-term survival of the colonies we observed.

While survival rates differed considerably between the two sites after 1 year of age until the end of the curve, the difference in mortality rates was noticeable between 1 and 4 years of age. Such year span follows the period of higher mortality for the young (Farand et al. 2002), which is similar in the two sites, and generally precedes the first reproduction (reproduction at 3 years of age was seldom observed, CF *pers. obs.*). According to these results, we maintain that the overall mortality rate linked to the physiological cycle of the marmot reproductive system is similar in the two sites, though other variables, which are investigated below, may exert a different influence as marmots grow.

We used path analysis to disentangle the differential effects of territorial vegetation quality, distance from the edge of the forest, exposure, and social aspects of the families (number of neighbouring families and stability of the dominant couple) on juvenile survival and reproduction in each site. The results of our analysis indicated that the stability of a family increases in a territory with fewer neighbours. Even though in the final model distance from the forest was independent of other factors, we have evidence that families living close to the forest border (or at the foot of an extremely steep mountain wall) are surrounded by fewer families. The decrease in the mean level of stability of the dominant couple in a ‘crowded’ area is likely due to the higher pressure exerted by the larger number of individuals; a higher frequency of attacks from individuals of neighbouring families may reduce the chances for a dominant couple to remain together.

The stability of the dominant couple in a territory directly increases its reproduction index, as expected in the social and reproductive system of the alpine marmot. Once an intruder takes over the territory of a dominant marmot, it may kill the pups and chase away the subordinates (Hackländer and Arnold 1999). Although direct observations of infanticide are rare (see Coulon et al. 1995), evidence of a reduction in female reproduction after the takeover of a territory was highlighted (Hackländer and Arnold 1999). Our results confirmed those obtained by King and Allainé (2002) on the same species and showed that the effect of social variables on alpine marmot reproduction is stronger than that of environmental factors. However, we have no evidence of differences in reproductive success between long-lasting and short-lasting couples.

The stability of the dominant couple proved to be of utmost importance for marmot families as it had a strong effect on juvenile survival: in a reproductive system in which dominant pairs are the ones that mainly reproduce and, in case of takeover, subordinates of all ages are either killed or chased away, high juvenile survival is expected in more stable territories where dominant couples last over time.

The reproduction index of a territory had a negative relation to juvenile survival and was just below the threshold of significance: a higher reproduction rate may lead to a lower survival of young individuals. This may be a density-dependent effect, which entails a higher mortality rate with the increase of density and, consequently, social stress and competition for resources.

Thermoregulation is a key factor in determining the habitat preferences of the alpine marmot. In our study, juvenile survival was positively affected by the southern solar exposure of a territory. Previous literature reported that marmots tend to select habitats with either south- or east-facing steep slopes (Allainé et al. 1994) since exposure may facilitate a faster snowmelt at the end of winter and favour the growth of new vegetation. Accordingly, marmots which inhabit well-exposed slopes may have to leave less frequently the burrow to search for food, thus decreasing both energy expenditure and predation risk at the beginning of the active season.

In hibernating mammals, qualitatively higher nutritional resources potentially influence both reproduction (Hackländer and Arnold 1999) and survival (Siutz et al. 2017). According to our results, the quality of vegetation within a territory had a positive effect on marmot reproduction, though its relationship with juvenile survival was not significant. Yellow-bellied marmots were found to consume only a minimum part of the total net production of pasture (1-2%; Svendsen 1974). Diet composition is subjected to seasonal alterations owing to changes in nutritional requirements (Carey 1985b), phenology, and the relative abundance of food plants (Frase and Armitage 1989). Forb species are preferred over graminoids, especially during spring and early summer (Carey 1985b) and alpine marmot feeding behaviour is characterised by high selectivity on specific parts of each plant species (*i.e.*, flowers vs. leaves of *Aquilegia cerulea*, Frase and Armitage 1989). Since our qualitative value of vegetation resources was obtained by NIRS on bulk vegetation from sample quadrants, it did not account for seasonal variations of plant phenology and marmot nutritional preferences. In fact, this measure (see Supporting Information 1) may have underestimated the variation among vegetation samples and thus among territories.

The present study aimed to investigate the variation of demographic parameters in alpine marmots which inhabit different territories. Habitat structural characteristics were frequently reported to influence species behaviours and demography, just as social factors influence group-living species.

The main finding of our study is that a marginal habitat may show a higher survival rate, thus highlighting the lack of knowledge about small-scale mechanisms favouring stable populations in marginal areas. We indicated two non-exclusive mechanisms which likely account for this result. Firstly, as suggested in previous literature on rodents, we maintain that differential predation pressure in habitats with different characteristics may play a crucial role. Habitats with high and dense vegetation are often linked to lower survival rates and population growth with respect to open habitats. Conversely, our findings suggested an unexpected benefit of marginal and more closed habitat. We presume that predation pressure may change according to age classes, with major pressure exerted on the long-term in an open habitat with respect to a marginal one. However, further data are needed to confirm this hypothesis. Secondly, as expected from a cooperative breeding species, the stability of the dominant couple is a major reproduction and juvenile survival driver. In addition, we found that the number of colonies living close to each other also influences the demographic dynamics of the alpine marmot. Following our results, which confirm that marginal habitats tend to host fewer families (Kawecki 2008), we argue that, when analysing population dynamics, social context as well as environmental characteristics should always be taken into account. Moreover, species characterised by high sociality, such as the alpine marmot, are an interesting case-study to investigate the influence of environmental characteristics on family group features and individual interactions within and among families. Kin structure of marmot families can also be informative: in low-quality marginal habitats, kin bonds among individuals are expected to be lower compared to those in native habitats (Peery et al. 2008). However, in a number of cases, empirical studies did not support this theory, rather suggesting that reproduction rates may benefit from the scarcity of mates and, when resources are scarce, kin sharing is favoured (Banks et al. 2005; Walker et al. 2007).

In conclusion, we stress the need for further research on mountain environments, where habitats bordering the forest are in rapid evolution, with bushes and trees quickly colonising open areas and thus producing marginal, fragmented habitats. This phenomenon was already described for the protected area of the Gran Paradiso National Park and the neighbouring areas (Filippa et al. 2019, Laiolo et al. 2004), where several wild species of considerable conservation and ecological interest live. As noted in a recent review, studies on the demography of mammals living in regions that are sensitive to climate change are needed in order to investigate how several species managed (or failed) to adapt (Paniw et al. 2021). For example, survival and reproduction dynamics of populations living in marginal areas may rapidly rise over time, thus resulting in stable populations, and this suggests how relevant these areas may be from an evolutionary point of view.

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Ethical note: All applicable institutional and national guidelines for the care and use of animals were followed.

Table 1 Total number of Alpine marmots included in the age predicted survival rate analysis run with the Bayesian Survival Trajectory Analysis (BaSTA) approach and based on the comparison between sexes and two sites with different ecological conditions.

	Nb individuals in survival analysis	**Birth and death date unknown**	**Birth and death known**	**Birth only known**	**Death only known**
High Site	195	60	60	73	2
Low Site	133	41	13	75	3

Table 2 Model selection of survival models run with Bayesian Survival Trajectory Analysis (BaSTA). Selection of the best mortality model structure (“Gompertz”, ” Weibull” and “Logistic”) and shape (“simple”, “makeham”, “bathtub”) was done by using MultiBaSTA, which uses DIC (Deviance Information Criterion) to select the more suitable model. No covariates were included in this selection and the selected model was then used in further analysis. Survival data refers to Alpine marmot individuals living in the Gran Paradiso National Park (Italy).

Model	**k**	**DIC**	**ΔDIC**
LO bathtub	7	3215	0.0
WE bathtub	6	3241	26.7
LO Makeham	5	3254	38.7
LO simple	4	3257	41.8
WE simple	3	3269	54.4
WE Makeham	4	3276	61.3
GO bathtub	6	3308	93.9
GO simple	3	3319	104.2
GO Makeham	4	3341	125.8

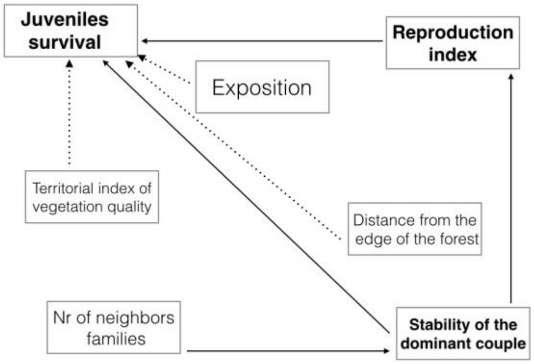
Table 3 Coefficients estimates of model parameters with standard error and mean Kullback-Lieber discrepancy values calculated for the models with sex and site as covariates. KL metric is a measure of the overlap between the posterior distributions of the categorical variables included in the analysis. A value of KLc ≤ 0.5 indicate overlap (no difference among the distribution). A KLc > 0.6 indicate a difference, and KLc > 1 indicate no overlap at all, so a complete difference. Mean KLc values higher than 0.6 are in bold in the table.

	DIC	**Parameter**	**Estimate ± standard error**		**Mean KLc**
Model_sex	3274.45		**Male**	**Female**	
		a0	-3.20 ± .71	-3.19 ± .70	0.50
		a1	0.71 ±.64	0.72 ± .63	0.50
		c	0.08±.07	0.09 ±.06	0.50
		b0	-2.74 ±.66	-2.92 ± .70	0.51
		b1	0.63 ± .34	0.57 ± .27	0.54
		b2	1.82 ± .87	1.51 ± .84	0.56
	DIC	**Parameter**	**Estimate ± standard error**		**Mean KLc**
Model_site	3238.23		**Low Site**	**High Site**	
		a0	-3.13 ± .69	-3.41 ± .68	0.53
		a1	0.82 ±.68	0.84 ± .64	0.50
		c	0.07 ±.05	0.03 ±.04	**0.68**
		b0	-3.20 ±.65	-2.64 ± .45	**0.74**
		b1	0.48 ± .20	1.42 ± .46	**0.97**
		b2	1.31 ± .75	3.12 ± .87	**0.95**
		pi	0.75 ± . 01		

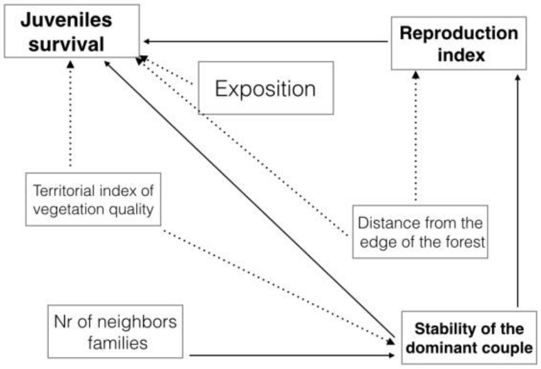
Table 4. Table of the theoritical models included in the path analysis. All of these included the same variables, but different relationships among variables were tested. Multiple indicators were calculated, and the final model was selected based on the overall best values. In bold the selected models.

model	**P-value** $\vert^{2}$	**AIC**	**CFI**	**TLI**	**RMSEA**
Model1	0.24	18.4	0.92	0.86	0.17
Model2	0.25	20.0	0.94	0.85	0.17
Model3	**0.47**	**16.7**	**1.00**	**1.00**	**0.00**
Model4	0.31	18.0	0.95	0.91	0.13
Model5	0.16	21.2	0.89	0.74	0.22
Model6	0.41	18.2	0.99	0.99	0.03
Model7	0.35	17.9	0.97	0.94	0.10
Model8	0.35	17.1	0.97	0.94	0.10
Model9	**0.46**	**15.7**	**1**	**1**	**0.00**
Model10	0.29	16.8	0.94	0.91	0.13

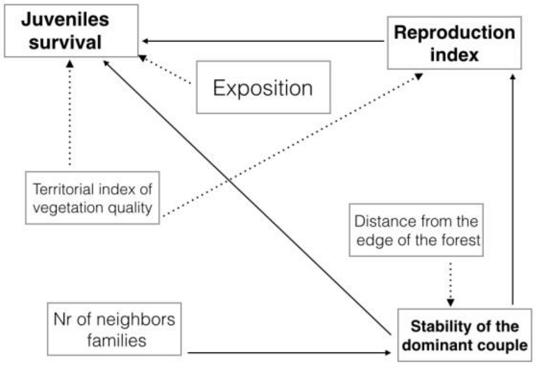
Model 1



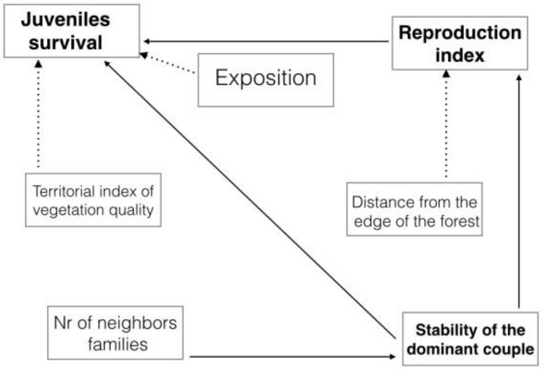
Model 2



Model 3



Model 4



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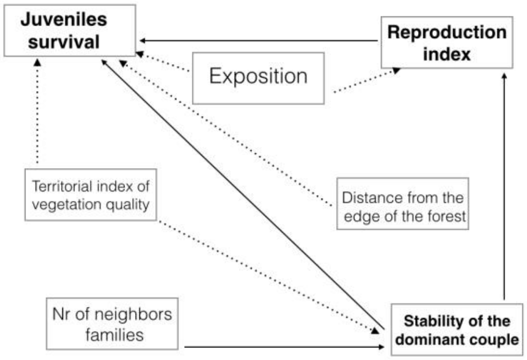
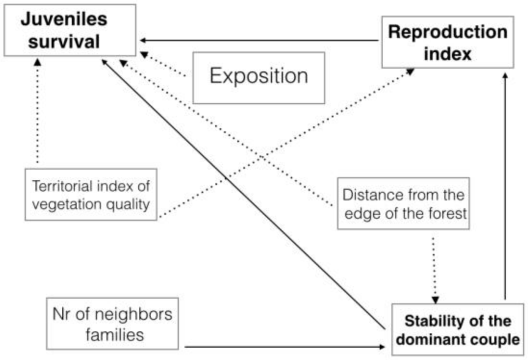


Model 6



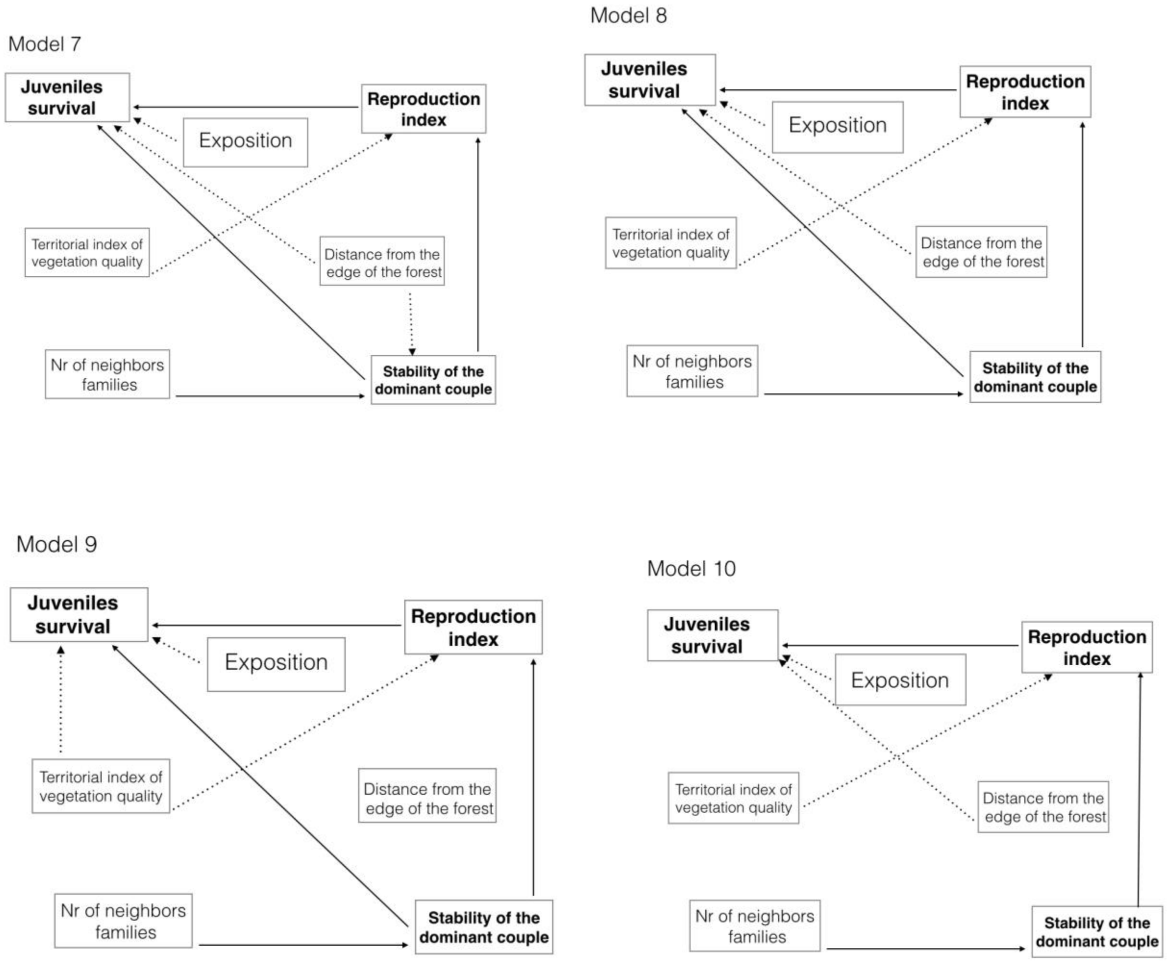


Fig. 1 Diagrams of the theoretical models tested with the path analysis. Relations among demographic parameters were kept fix, while others were tested differentially.

Fig. 2 Predicted age specific survival probabilities (a) and predicted mortality rate (b) in Alpine marmot population using logistic bathtub model. The structure of the model was selected with Multi BaSTA function in the package Basta and ran 3 simulations for MCMC with 20000 iterations. This structure was used in the further analyses. The colours around the main curve are the 95% credibility intervals of age survival rate.

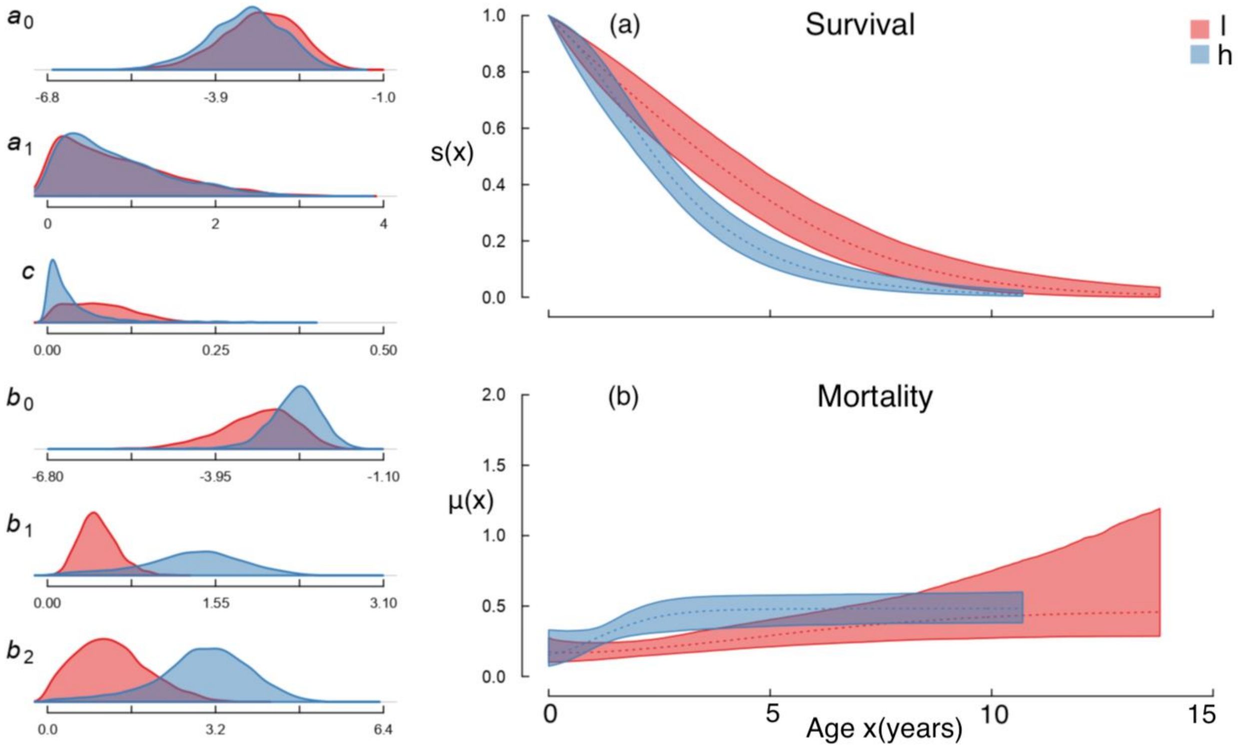


Fig. 3 Predicted age specific survival probabilities (a) and predicted mortality rate (b) of Alpine marmots inhabiting two Sites characterized by different characteristics: Low site is closest to the edge of the forest in a marginal habitat and High site is an open Alpine prairie. The colours around the main curve are the 95% credibility intervals of age specific survival rate.

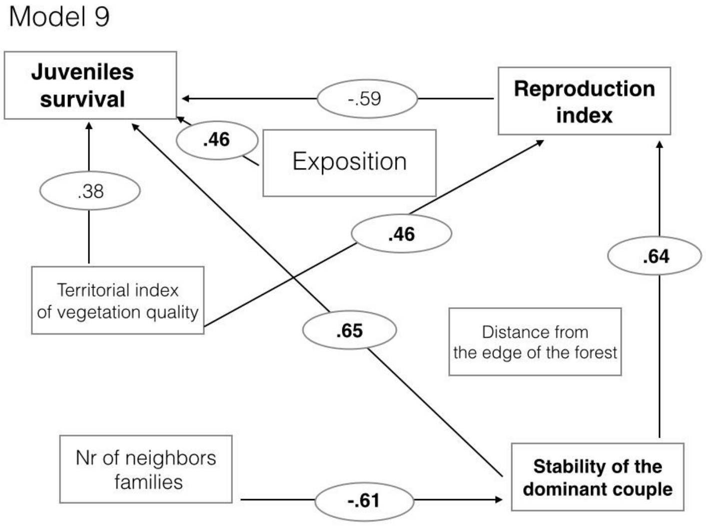


Fig. 4 Path analysis diagram of the selected model with the standardized coefficient and standard error in circles. Survival is referred to juvenile survival. In bold are relationships with a p-value <0.05.