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Neighborhood bully: no difference in territorial response towards neighbors or strangers in marmots

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Short title: No response to scents according to different intruders' characteristics

Abstract

Territorial animals are expected to adjust their response to intruders according to the perceived threat-level. One of the factors that drives threat-level is the identity of the intruder. The dear enemy phenomenon theory postulates that individuals should respond with lower intensity to neighbors, already possessing a territory, than to strangers that may fight to evict them. In social species, the hierarchical status of the intruder might also mediate this response. Such behavioral adjustments presuppose a capacity to discriminate between individuals posing different threat levels. Here, we tested the behavioral response of Alpine marmots to territorial intrusions in a wild population. We compared both dominant females and males responses to scents from neighbor and stranger dominant males (dear enemy phenomenon) and to dominant and subordinate stranger males (social status-specific response). In addition, we tested for any covariance between male scents and social status. We showed that female and male dominant marmots do not adjust the intensity of their behavioral responses to whether the intruder's territory is bordering or not (neighbors or strangers) or to the intruder's social status, even though dominant and subordinate males are thought to pose different threats and social status is encoded in scents. Thus, we did not find support for the dear enemy phenomenon and conclude instead that, in dominant Alpine marmots, no intruder should enter a foreign territory. Research taking a more holistic approach of the evolution and maintenance of territoriality is required to understand the flexibility of responses to intruders in group-living species.

Keywords: chemical communication, cooperative breeder, dear enemy phenomenon, dominant–subordinate discrimination, odor cues, scent marking

INTRODUCTION

Territoriality is often defined as the defense of an area in order to secure access to crucial resources, including food, shelter and/or mates (Maher and Lott 1995). Territory owners typically use deterrent signals (*e.g.* acoustic, visual or olfactory signalization) to discourage potential intruders but, when these signals are not enough, physical exclusions (*e.g.* chases and fights) may take place. Such active defense of the territory can be very costly as it may lead to injuries or even death (Bradbury and Vehrencamp 2011). To decrease these costs, some individuals can adjust their response to the level of threat an intruder represents. The perceived threat can depend on whether the intruder's territory is bordering or not (*i.e.* neighbor or stranger), its individual characteristics (e.g. sex, social status), or the location and timing of the intrusion (Christensen and Radford 2018; McGregor and Bee 2018; Radford and Christensen 2018). In addition, the receiver's response towards the intruder can also be influenced by the receiver's characteristics (e.g. sex, social status; Ferkin 2015, Christensen and Radford 2018).

Neighbors are commonly considered as less likely to enter adjacent territories with take over prospects (Jaeger 1981; Gosling and McKay 1990; Temeles 1994; but see Müller and Manser 2007) and territory owners may reduce their active defense behaviors towards known neighbors, once common boundaries have been established (Jaeger 1981; Gosling and McKay 1990; Temeles 1994). On the contrary, strangers (*i.e.* unknown individuals) may be looking to usurp a territory, thus representing a potentially higher threat requiring a more aggressive response. This lower level of response towards neighbors than strangers is known as the dear enemy phenomenon (Fisher 1954; Temeles 1994).

Studies on the topic provide many examples of the dear enemy phenomenon in invertebrates (e.g. Heinze et al. 1996; Booksmythe et al. 2010), birds (e.g. Stoddard et al. 1990; Moser-Purdy and Mennill 2016) and mammals (e.g. Rosell and Bjørkøyli 2002; Palphramand and White 2007). However, depending on the context, neighbors may represent a greater threat than strangers and trigger an inverse behavioral response of higher aggressiveness towards neighbors than strangers, as predicted by the nasty neighbor effect (Müller and Manser 2007). Many studies provided examples of the nasty neighbor effect in invertebrates (e.g. Newey et al. 2010), birds (e.g. Yoon et al. 2012) and mammals (e.g. Müller and Manser 2007).

Additionally, in territorial social species, the existence of a hierarchy between individuals may also mediate the behavioral response of an individual according to the intruder's social status (Christensen and Radford 2018). Whereas subordinate individuals are likely waiting for an opportunity to usurp a territory and become dominant, dominant individuals devote much of their time to the defense of their own territory (Kaufmann 1983, Lardy et al. 2011). Subordinate individuals are therefore likely to represent a higher threat than dominant individuals to other dominant individuals. However, relatively few studies accounted for the social status of tested individuals when studying the dear enemy phenomenon (Table 1).

Any adjustment of the behavioral response to an intruder presupposes the ability to identify individuals presumably posing different levels of threat, *i.e.* neighbors *vs.* strangers and/or subordinate *vs.* dominant individuals (Höjesjö et al. 1998; Aragón et al. 2000). One way to discriminate neighbors from strangers is by learning to recognize neighbors identities and identifying unknown intruders by contrast (Gheusi et al. 1997; Johnston and Bullock 2001). This type of discrimination between neighbors and strangers may be facilitated in species with stable territories where encounters with neighbors are repeated in time (Stoddard et al. 1990; Rosell and Bjørkøyli 2002). This situation can lead to habituation, a form of non-associative perceptual learning that arises from passive and prolonged exposure to a stimulus, which could lead to such discrimination and could generate lower behavioral response to a stimulus encountered regularly than to a stimulus encountered for the first time. For example, in a study with golden hamsters (*Mesocricetus auratus*), individuals faced repeatedly with scents from the same donor decreased the amount of time smelling these scents, suggesting that receivers were habituated and perceived them as familiar (Johnston 1993). Associative learning is another potent mechanism that can facilitate discrimination between stimuli. In territorial species, aggressive encounters with strangers in search of a territory could easily reinforce eliciting increased smelling and marking of scent-marks from unknown compared to familiar individuals.

Whatever the mechanism, successful recognition requires the existence of reliable indicators of the potential threat an individual represents. In mammals, scent-marking provides information about territory occupancy and serves as a preventative measure for territory defense (Ralls 1971; Gosling 1982). In addition, odors can provide information on the sender's identity (Scordato et al. 2007; Linklater et al. 2013; Harris et al. 2014), social status (Hayes et al. 2001; Burgener et al. 2009; Tinnesand et al. 2013; Zidat et al. 2018), sex (Setchell et al. 2010; Rosell et al. 2011; Vaglio et al. 2016; Spence-Aizenberg et al. 2018) or body condition (Buesching et al. 2002). Scent deposition may therefore play an important role in the behavioral response to territorial intrusion, if it allows for individual recognition and/or social status discrimination. However, in mammals, very few studies on the behavioral adjustment to whether an individual shares a territory boundary or not (*i.e.* the dear enemy phenomenon) and to its characteristics (*i.e.* social status) tested whether the scents used displayed this information in their chemical composition (Table 1).

Here, we studied the behavioral response of Alpine marmots (*Marmota marmota*) to territorial intrusion by different intruders (strangers *vs.* neighbors and subordinates *vs.* dominant individuals) in a wild population. The Alpine marmot is a perfectly suited species to investigate this question. It is a highly social, cooperatively breeding and territorial species. Alpine marmots live in family groups of two to 20 individuals composed of a couple of dominants monopolizing reproduction, subordinates of both sexes (related to at least one of the two dominant individuals), and pups (Allainé 2000; Allainé et al. 2000). Social interactions within families are frequent and typically cohesive whereas face-to-face interactions between marmots from different family groups are rare and agonistic (Perrin et al. 1993a). Territories, found adjacent to one another, are organized around a main burrow and are consistently used over the years. The establishment of the dominant status for several years as well as the existence of adjacent and stable territory boundaries, delimited by scent-marks deposited by dominant individuals of both sexes, lead to stable relationships between territory owners and create the necessary preconditions for a recognition of neighbors (Temeles 1994). Territories are mainly defended by dominant individuals (Allainé 2000) and scent-marking by orbital glands is the main passive mode of territory defense (Bel et al. 1995; Bel et al. 1999). Dominant individuals but also suborinate individuals in search of a territory mark the territory boundaries and around the main burrows, and they over-mark and counter-mark conspecific intruder scent-marks (Bel et al. 1995; Lenti Boero 1995). Orbital gland scent-marks are thus highly relevant signals potentially involved in the dear-enemy phenomenon in this species. Marmots, as many other rodent species, should be able to discriminate among odors of different conspecifics since chemical signatures are common in mammals' odorant secretions (Tinnesand et al. 2013, Zidat et al. 2018). Sexually mature subordinates (2 years and older) try to reach dominance (*i.e.* a territory and access to reproduction) by dispersing and displacing a dominant individual, which is then at high risk of mortality (Stephens et al. 2002; Lardy et al. 2011). Evicted dominant individuals are generally dramatically injured and their probability to survive is extremely low (Walter 1990; Lardy et al. 2011). Due to familiarity, neighboring individuals being frequently encountered and territories being stable, neighbors should be perceived as less threatening to a territory owner than strangers. Moreover, given the high cost of being displaced, a territory owner is expected to react more aggressively to same-sex sexually mature subordinates than to other dominant individuals.

We proceeded in three steps. First, we performed a behavioral experiment called "dear enemy", to test for the existence of the dear-enemy phenomenon, by conducting a two-way choice experiment between orbital gland scents of neighbor and stranger dominant males presented to dominant males and females. According to the dear-enemy hypothesis, we expected dominant marmots to spend more time smelling and/or marking scents from strangers than neighbors. Then, we performed a second behavioral experiment called "subordinate *vs.* dominant" to test for the existence of a social status-specific behavioral response by conducting a two-way choice experiment between orbital gland scents of sexually mature subordinate and dominant male strangers presented to dominant males and females. Following the hypothesis that subordinate individuals represent a higher threat than dominant individuals, we expected dominant individuals to spend more time smelling and/or marking scent-marks from subordinates than from dominant individuals. According to Ferkin (2015), dominant individuals of different sexes may have different motivations when faced with a single sex scent (e.g. dominant males might be threaten by male scents whereas dominant females might also see potential mating opportunities, see also Christensen and Radford 2018). Thus, we expected that dominant males and females might behave differently in our behavioral experiments. Finally, we searched for a signature of social status in the chemical composition of orbital gland secretions in male Alpine marmots, using a gas chromatography-mass spectrometry (GC-MS) analysis to check that discrimination of individuals' social status is possible.

METHODS

Field methods

This study was conducted from 2012 to 2017 taking advantage of a long-term individual-based study of a wild population of Alpine marmots initiated in 1990 in the Nature Reserve of La Grande Sassière (at 2,340 m a.s.l., French Alps, 45º29'N, 65º90'E, see Cohas et al. 2006 for details on protocol). Marmots from up to 27 territories consistently used over the years were monitored. Territories are spread at roughly the same altitude along a typical Alpine valley, in an area of approximately 1.5 km long and 0.5 km wide. These contiguous territories spanned between 0.9 ha and 2.8 ha (Perrin et al. 1993b). Marmots were followed from mid-April to mid-July each year, using both capture–mark–recapture and intensive behavioral observations. All individuals were individually marked with a metal numbered ear-tag (right side for females and left side for males). Dominant individuals were additionally identified with a colored plastic ear-tag on the opposite ear. Moreover, due to daily observations, the exact composition (sex, age and social status of individuals) of each family was known. Once captured, marmots were tranquilized with Zolétil 100 (0.1 mL.kg^{-1}) and the orbital gland area was shaved and cleaned with a sterile cotton swab saturated with ethanol 99% to remove any environmental contaminants. After full evaporation of ethanol, the orbital gland was pressed and its secretion was collected for both behavioral bioassays and chemical analyses.

Behavioral experiments

Experimental set-up

All behavioral experiments consisted of two-way choice trials where two vertical wooden sticks covered by glass tubes impregnated with scents were placed approximately 50 cm away from the main burrow entrance to maximize the chances to be encountered by marmots and 50 cm apart so that tested individuals could discriminate the scents on both tubes (Figure 1). Two clean tubes were placed on each territory at the beginning of the field season to avoid reactions to the introduction of a foreign object in the territory during each trial. We replaced these tubes by experimental tubes, *i.e.* tubes with scent-marks, at the beginning of each trial.

Orbital gland scent collection

We dragged the distal half of a clean glass tube (200 mm long x 25 mm outside Ø, vwr® reference number 212-1126) along the orbital gland of captured and anesthetized individuals of interest (dominant and subordinate males only) in order to mimic the natural marking behavior on a foreign object. Depending on the amount of secretion, we collected one to six glass tubes per individuals. We wrapped each tube in aluminum foil and stored them in the dark at ambient temperature (approximately 5ºC) until the beginning of the trials. Samples were used no more than three days after collection to avoid scent degradation and were always enclosed with aluminum foil to avoid contamination. Experimental tubes were collected from 40 dominant males (13, 22, 12, 14 and 17 in 2012, 2013, 2014, 2015 and 2017 respectively) and from 6 sexually mature subordinate males in 2017 (5 two-years old individuals and one older than two-years, all of them being the sons of a dominant male for which a tube was collected in 2017).

General procedure

All trials were carried out between May 18th and June 27th from 2012 to 2017, *i.e.* after pups birth but before their emergence, and between 8:00 a.m. and 6:00 p.m, *i.e.* during the main activity period of the marmots. For each trial, we randomly designated scent-marked tubes to the wooden sticks to avoid any bias due to individual preference for one side or the other. We tried to avoid pseudo-replication coming from the same individuals being presented with the same experimental setting several times whenever possible. However, 56% of the individuals were tested more than once a year (median number of trials = 2, range = 2-4). Due to the limited number of scents we could collect (only from caught dominants) and also the short time scents can be stored before use, some scents had to be presented to different individuals in different trials (median number of the same scent combination in a given year = 1, sd = 1.04, range = 1-6). However, we tried to avoid pseudo-replication coming from the use of the same scents in the same year and individual whenever possible. Thus, some combinations of scents were used in several trials but no individual was ever presented with the same combination of two scents. Although we typically observed marmots retreating into their burrows during the installation, they re-emerged within minutes. Once the tubes installed, between one and three observers continuously monitored the experimental set-up with 10x42 binoculars and/or 20x60 telescopes in order to identify individuals interacting with the tubes. As soon as a dominant female or male was in close proximity to the experimental set-up (approximately 50 cm), its identity and sex were registered and one observer recorded its behavior with a digital video camera (Sony® Handycam model DCR-DVD650 or JVC® digital video model GZ-E 209) until it moved away from the set-up (more than 5 m or complete disappearance in the burrow). A given trial was considered a success when a dominant individual interacted (*i.e.* smelled and/or marked) with at least one tube and was considered a failure when no dominant individual approached the experimental set-up within four hours of the installation (Cross et al.

2013), or if a subordinate interacted with at least one of the tubes before a dominant individual. In case of failure, the trial was aborted and repeated later with new scent samples.

Dear enemy behavioral experiment

This behavioral experiment was conducted from 2012 to 2015 and in 2017 and consisted of three different experimental settings: 'stranger *vs.* control' (SC, N = 53), 'neighbor *vs.* control' (NC, N = 33) and 'stranger *vs.* neighbor' (SN, N = 41). The first two experimental settings (SC and NC) were meant to test for a difference in behavioral response of dominant individuals between scent-marked tubes and tubes without marmot scent (*i.e.* 'control' tubes). This was meant to check that responses towards scent-marked tubes were due to a scent recognition and not due to the presence of a new object in the territory. The third experimental setting (SN) was meant to test for a difference in intensity of the behavioral response of dominant individuals between ‘strangers’ (*i.e.* tubes scent-marked by a dominant male residing within a territory that has no common boundary with the focal individual) and ‘neighbors’ (*i.e.* tubes scent-marked by a dominant male residing within a territory that has a common boundary with the focal individual).

Subordinate vs. dominant behavioral experiment

This behavioral experiment was conducted in 2017 and consisted in one experimental setting ('subordinate *vs.* dominant' (SD)) to test for a difference in the behavioral response of dominant individuals to subordinate and dominant stranger male scent-marks. We performed 16 trials to test whether unknown sexually mature male subordinates that do not yet have a territory (hypothesized as highly threatening) elicit a stronger response than unknown dominant individuals which already have one. For each trial, we used two tubes: one scent-marked by a dominant male and the other by a sexually mature subordinate male, both strangers to the focal individual. In all trials, we used subordinate and dominant individuals of the same family to limit the differences between the two individuals other than their social status (*e.g.* group scent signature).

Measures of response

Video recordings were displayed in Microsoft Windows Media Player (Microsoft®) in slow motion (x 0.5) to ensure an accurate identification of behaviors as well as to score their duration with an accuracy of 0.5 s. Both the time the focal dominant marmot spent smelling and marking each tube were recorded as well as the number of marks. In rodents, these measures are widely recognized as proxies for interest (smelling) and aggressiveness (marking) once an odor stimulus has been discriminated (e.g. in the closely related yellow-bellied marmots (*Marmota flaviventris*; Johns and Armitage 1979; Brady and Armitage 1999; Cross et al. 2013)). In Alpine marmots, while smelling is not typically associated with aggressiveness, over-marking is recognized as an aggressive behavior (Bel et al. 1995).

Statistical analyses

According to our predictions (see Introduction), we calculated the differences in time spent smelling or marking between the tube that we hypothesized marmots would show more interest towards and the other tube:

$$\Delta\,\mathrm{time}_{SC} = \mathrm{time}_{\mathrm{stranger}} - \mathrm{time}_{\mathrm{control}}$$

$$\Delta\,\mathrm{time}_{NC} = \mathrm{time}_{\mathrm{neighbor}} - \mathrm{time}_{\mathrm{control}}$$

$$\Delta\,\mathrm{time}_{SN} = \mathrm{time}_{\mathrm{stranger}} - \mathrm{time}_{\mathrm{neighbor}}$$

$$\Delta\,\mathrm{time}_{SD} = \mathrm{time}_{\mathrm{subordinate}} - \mathrm{time}_{\mathrm{dominant}}$$

For the number of marks, we calculated this difference as :

$$\Delta\,\mathrm{marks}_{SC} = \mathrm{marks}_{\mathrm{stranger}} - \mathrm{marks}_{\mathrm{control}} - \min(\mathrm{marks}_{\mathrm{stranger}} - \mathrm{marks}_{\mathrm{control}})$$

$$\Delta\,\mathrm{marks}_{NC} = \mathrm{marks}_{\mathrm{neighbor}} - \mathrm{marks}_{\mathrm{control}} - \min(\mathrm{marks}_{\mathrm{stranger}} - \mathrm{marks}_{\mathrm{control}})$$

$$\Delta\,\mathrm{marks}_{SN} = \mathrm{marks}_{\mathrm{stranger}} - \mathrm{marks}_{\mathrm{neighbor}} - \min(\mathrm{marks}_{\mathrm{stranger}} - \mathrm{marks}_{\mathrm{neighbor}})$$

$$\Delta\,\mathrm{marks}_{SD} = \mathrm{marks}_{\mathrm{subordinate}} - \mathrm{marks}_{\mathrm{dominant}} - \min(\mathrm{marks}_{\mathrm{subordinate}} - \mathrm{marks}_{\mathrm{control}})$$

to keep all values strictly positive so that we could use a Poisson linear model (see the model scripts in Supplementary Material).

To test whether female and male dominant Alpine marmots responded differently to scents from different geographical origins, we built three Bayesian generalized linear mixed models where we modeled Δ smelling time, Δ marking time and Δ marks as functions of the experimental settings (SC, NC and SN experimental settings), the sex of the focal individual and their interaction as fixed factors and with the identity of the focal individual as a random factor. Similarly, to test whether female and male dominant Alpine marmots showed more interest towards scents from subordinate stranger males than from dominant stranger males (SD experimental setting), we built three other Bayesian generalized linear mixed models with the same response variables but with the sex of the focal individual as the sole fixed factor and the identity of the focal individual as random factor. We used Gaussian linear models for Δ smelling time and Δ marking time and Poisson linear models for Δ marks (see model scripts in Supplementary Material). We fitted all models by running three MCMC chains for 20,000 iterations and discarded the first 10,000 as burn-in. We used non-informative priors as we had no prior expectations or knowledge on the different parameters. Model convergence was assessed using the Gelman and Rubin convergence diagnostic ($R<1.01$, Gelman and Rubin (1992)). We considered that a difference in time and in number of marks between tubes was evidenced when the 95% credible interval did not include zero (*i.e.* the difference was different from 0, indicating a choice). Similarly, a difference in behavior between sexes was evidenced when the 95% credible of the difference between sex-specific parameters did not include zero. All Rhats obtained were < 1.001.

Chemical characterization of orbital gland secretion

Orbital gland scent collection

To analyze the chemical composition of Alpine marmot orbital gland scents, we collected orbital gland secretions from 43 male Alpine marmots of two years and older (up to 11 years old; 18 dominant individuals and 25 subordinate individuals), living in 24 different territories between 12th May and 9th July 2016. In addition, we re-sampled six of the 25 subordinate individuals in 2017 after they reached dominance. We collected orbital gland secretions with a 5 µL glass capillary wearing clean nitrile gloves to avoid contamination. Once collected, the secretion was then placed into a 1.5 mL opaque chromatographic glass vial filled in advance with 200 µL of dichloromethane solvent (HiPerSolv CHROMANORM for HPLC; VWR, Center Valley, PA, USA). In each 200 µL we added an internal standard, biphenyl (molecular weight, 154.21 g.mol^{-1}, 99.5%; Sigma Aldrich, St Louis, MO, USA) at a concentration of 0.2 g.L^{-1}. Several "field control samples" (*i.e.* vials without marmot secretions and only with solvent) were collected using the same protocol, to control for possible contamination related to the collection protocol. Finally, all samples were sealed with a Teflon-lined cap and stored at -20°C in the field and at -80°C in the laboratory until GC-MS analysis.

GC-MS analysis

We transferred all scent samples in 0.3 mL inserts in new, clean vials to enable their injection in an interfaced Hewlett-Packard 6890 GC system equipped with a non-polar DB-5 MS column (30 m long x 0.25 mm ID x 0.25 µm film thickness, Agilent technologies) coupled with an HP 5973 MSD (Mass Selective Detector) mass spectrometer (Agilent technologies, Palo Alto, CA, USA). Helium was used as a carrier gas at a flow rate of 1 mL.min^{-1} and an electron impact ionisation of 70 eV was applied. After having vortexed all vials to homogenize scent samples, 2 µL of sample was injected automatically in splitless mode. The temperature of injection was set to 300 °C and the oven temperature program started with 4 min at 90 °C, then increased by 12 °C.min^{-1} up to 210 °C, and then increased again at 5 °C.min^{-1} up to 310 °C and finally was held at 310 °C for 5 min. We also ran blank samples containing dichloromethane only every 7 samples. These controls allow an estimation of the potential noise related to the potential accumulation of some compounds along the column or of the instrument drift over time, for example.

Chromatographic data processing

Scent secretions of individuals were characterized by several peaks (*i.e.* a scent profile) and each of them represents one compound (defined by a specific retention time and mass spectrum). For each sample, we acquired the area of each peak by automatic integration with Agilent MassHunter Qualitative Analysis software (B.07.01 version) and manual check. Furthermore, the internal standard (biphenyl) was used to control instrument drift over time. Three compounds were found in field control samples that were considered as contaminants and were removed from analysis. We further removed all compounds present in less than 5% of the individuals of the two groups (*i.e.* subordinate and dominant individuals) because their rarity meant they were unlikely to make any contribution to the discrimination of the social status in subsequent analysis. Then, we converted each single peak area into a percentage of the sum of all compounds' area to obtain the relative abundance of each compound. Finally, we removed peaks with a relative low abundance (< 0.05%) to exclude background noise (Drea et al. 2013), and took the square-root of the final data set to reduce the impact of the most abundant compounds upon our analyses (Clarke and Warwick 2001).

Statistical analyses

We first tested whether orbital gland secretion provides information on social status and differs between dominant and sexually mature subordinate male marmots, using the 43 scent samples of 2016. For that, we calculated Euclidean distances between every pair of samples to obtain a resemblance matrix, from which we conducted a permutational multivariate analysis of variance (PERMANOVA; Anderson 2001; Anderson 2017) using 9999 permutations, to test whether chemical composition differed according to social status. Then, we carried out a principal components analysis (PCA) on the correlation matrix to reduce the number of compounds and to highlight only those that explain most of the variance (Drea et al. 2013). We retained compounds with a cumulative contribution on the first three axes > 60% of the total contribution. We conducted a second PERMANOVA on this chemical data subset to check that this compound selection did not change the results obtained with the first PERMANOVA. Then, we performed a Linear Discriminant Analysis (LDA) on all orbital gland scent samples (N=43 in 2016 and N=6 in 2017) to investigate whether variation in the chemical composition of orbital gland scents can be used to separate individuals according to their social status and, for the six dominant individuals in 2017 which were subordinates in 2016, to visualize the variation in chemical composition according to their change of social status. Although Bayesian analysis were used for Behavioral experiments, frequentist analyses were already useful to answer the chemical characterization of orbital gland secretions.

All statistical analyses were conducted in R v. 3.4.3 (R Core Team 2017) with “nimble” (de Valpine et al. 2017) for Bayesian models, “ade4” (Dray and Dufour 2007) and ‘adegraphics’ packages (Siberchicot et al. 2017) for PCA, “vegan” package (adonis function, Oksanen et al. 2018) for PERMANOVAs, and “MASS” package (lda function, Venables and Ripley 2002) for the LDA.

Ethical Note

All work adheres to the ASAB/ABS Guidelines for the Use of Animals in Research. The laboratory “Biométrie et Biologie Evolutive” is authorized to use animals in research (arrêté préfectoral n° DDPP69-2013-008), the protocol was approved by the University of Lyon 1 Ethical Committee (CEEA-55, protocol BH2012-92-V1) and the authorization to capture Alpine marmots was issued by the Préfecture de Savoie (arrêté préfectoral n° 2013/02) after approval by the advisory committee of the Nature Reserve of La Grande Sassière. All the handling and sampling were done by four co-authors who are authorized for experimentation with animals by the French Ministry of Agriculture and Fisheries (diploma numbers R45GRETAF110, R69UCBL-ENVL-F1-03, R-13CNRS-F1-10 and 0ETRY20090520).

Once captured, marmots were rapidly transferred in a dark burlap bag to limit stress and were transported to a nearby cabin to be handled in a calm and cool room. Once tranquilized, handling lasted a maximum of 10 min. The recovery did not require the use of an antidote. To recover, marmots were placed again in a calm and cool room for 15 min until they were able to walk. All tranquilized marmots recovered well and no adverse effects have been noticed: all individuals were observed alive the day after their capture. Tranquilizing pregnant or lactating females did not have any obvious impact on offspring as all the females successfully raised offspring to weaning. Overall, individuals were absent from their territory for a maximum of 40 min. We never observed exclusion from the territory for any individual of any age following capture.

Although behavioral bioassays required continuous observation of the focal individual, care was taken to avoid disturbance. To do so, animals were observed from a distance with 10x42 binoculars and/or 20x60 telescopes and filmed with cameras with powerful optical zoom. This allowed observers to sit on the path that crosses the study site and to avoid entering the focal marmot territory or the neighboring territories.

RESULTS

Behavioral experiment

Dear enemy behavioral experiment

As expected, when facing scent and non-scent tubes (SC and NC experimental settings), dominant males spend more time smelling stranger and neighbor scents of dominant males than control tubes (*i.e.* without scents) (posterior mean Δ smelling time of dominant males in SC = 10.56s [95%credible interval: 5.44;15.60]; and in NC = 8.00s [1.17;14.79]) while dominant females only displayed a tendency to do it (posterior mean Δ smelling time of dominant females in SC = 6.33s [-0.48 ; 13.13]; and in NC = 2.08s [-4.42 ; 9.66]; Table 2, Figure 2a). However, dominant females and males behavior did not differ, although males smelled more dominant male scents compared to females (posterior mean sex difference in Δ smelling time for SC = -4.23s [-12.68;4.22] and for NC = -5.96s [-16.11;4.21], Figure 2a). Neither dominant females nor males spent different time smelling stranger dominant male scents than neighbor scents but dominant males tended to spend more time smelling neighbor scents (Table 2, Figure 2a). Again, no sex difference in smelling behavior was evidenced (posterior mean sex difference in Δ smelling time for SN = 2.35s [-6.84;11.52], Figure 2a).

According to our hypothesis, dominant females spent more time marking and did a higher number of marks on stranger dominant male scents than control (posterior mean Δmarking time = 1.53s and posterior mean Δ number of marks = 1.26 for dominant females in SC) while males did not (Table 2, Figure 2b,c). Moreover, a sex difference in marking behavior was evidenced (posterior mean sex difference in Δmarking time for SC = 1.42s [0.03;2.85]) and a tendency was observed for the difference in number of marks (posterior mean sex difference in Δ number of marks for SC = 1.08 [-0.20;2.43]; Figure 2b,c). Neither females nor males spent more time marking or did a higher number of marks on neighbor dominant male scents than on control tubes nor on stranger scents than on neighbor scents (Table 2, Figure 2b,c), and no sex difference were evidenced (posterior mean sex difference in Δmarking time = 0.65s [-1.03 ; 2.33] for NC and = 0.62s [-0.89 ; 2.15] for SN, Figure 2b; posterior mean sex difference in Δ number of marks = -0.01 [-1.55 ; 1.55] for NC and = 0.23 [-1.05 ; 1.53] for SN, Figure 2c).

Subordinate vs. dominant behavioral experiment

Contrary to our expectations, neither females nor males spend different time smelling subordinate and dominant male scents (posterior mean Δ smelling time = 4.55s [-3.19 ; 11.92] (N = 6) and -3.61s [-9.83 ; 2.82] (N = 10), for females and males, respectively, Figure 3a). However, dominant females and males behaviors tended to be opposite: females spent more time smelling scents of subordinate strangers than dominant stranger scents compared to males that spent more time smelling the scents of dominant strangers than subordinates strangers (posterior mean sex difference in Δ smelling time = -8.16s [-17.44 ; 1.53], Figure 3a).

Neither females nor males spend different time marking (posterior mean Δ marking time = -1,79s [-5,45 ; 2.07] (N = 6) and -2.64s [-5.87 ; 0.57] (N = 10) or did different number of marks on subordinate and dominant male scents (posterior mean Δ number of marks = -0.61 [-3.03 ; 2.17] (N = 6) and -1.76 [-3.55 ; 0.16] (N = 10), for females and males respectively; Figure 3b,c). No sex difference in marking behaviors were evidenced (posterior mean sex difference in Δ marking time = -0.85s [-5.50 ; 2.36], posterior mean sex difference in Δ number of marks = -0.19 [-0.71 ; 0.32]; Figure 3b, c).

Social status impacts on scent profiles

A total of 28 chemical compounds were detected in the 43 individual's orbital secretions sampled in 2016 (mean ± SD = 12.54 ± 3.26 compounds per individual). Orbital gland secretions from dominant (N=18) and subordinate (N=25) males contained the same number of chemical compounds (dominant: mean ± SD = 13.17 ± 3.76, subordinate: mean ± SD = 12.08 ± 2.84, $t_{1,41}$ = 1.08, p-value = 0.29). However, scent secretions from dominant and subordinate individuals strongly differed in their composition (PERMANOVA: pseudo-F $F_{1,41}$ = 2.51, p-value = 0.004). The PERMANOVA performed on the 11 compounds with a global contribution to the first three axes of the PCA > 60% gave similar results than the one performed on all compounds (pseudo-$F_{1,41}$ = 2.52, p-value = 0.03). The linear discriminant analysis performed on the orbital gland secretions collected in 2016 and 2017 revealed that dominant individuals were easily discriminated from sexually mature subordinates on the basis of these 11 compounds: 75% (18 over 25; N=18 in 2016 and N=6 in 2017) of dominant individuals and 80% (20 over 25) of sexually mature subordinates were correctly assigned (Figure 4). In addition, the orbital gland secretions of the six individuals that became dominant in 2017 changed in agreement with their social status (Figure 4). Even if two misclassified individuals had one of their secretions assigned to the wrong social status they still presented a drastic change in the characteristics of their secretion associated with their change of social status (Figure 4).

DISCUSSION

Contrary to our predictions, we did not find any evidence of the dear enemy phenomenon in female and male dominant Alpine marmots. The dominant individuals' response indeed was not more intense towards stranger than neighbor dominant scents. Furthermore, dominant individuals did not respond more strongly towards orbital gland secretions of subordinate than dominant males, although the social status was encoded in these secretions. However, some sex differences were detected in the behavioral response of dominant individuals. Overall, our results suggest that dominant individuals are equally threatened by any type of intruder from outside their family group.

No evidence of the dear enemy phenomenon in the Alpine marmot: neighbors, strangers, same fight

Dominant individuals of both sexes did not respond more strongly towards orbital gland scents from dominant strangers than neighbors emphasizing an absence of dear enemy phenomenon in our population. This result was observed even though the chosen stimulus was involved in territory defense and defensive behaviors. Indeed, Alpine marmots defend their territory by scent-marking their territorial boundaries with their orbital glands and by over-marking and counter-marking conspecific intruder orbital scent-marks (Bel et al. 1995; Lenti Boero 1995; Lenti Boero 1995). This absence of dear enemy phenomenon in Alpine marmots contrasts with both theoretical predictions (Temeles 1994) and empirical findings in other mammals (Table 1). For example, in beavers (*Castor canadensis* and *C. fiber*), anal gland scents of stranger males elicit stronger responses (*i.e.* smelling and marking) from both sexes than anal gland scents of neighbor males (Schulte 1998; Rosell and Bjørkøyli 2002, Table 1). However, recent literature supports the idea that defensive behavior towards neighbors and strangers is not as dichotomous as it was previously thought, especially in social species (Christensen and Radford 2018; Kranstauber and Manser 2018; McGregor and Bee 2018; Radford and Christensen 2018; Ridley and Mirville 2018; Stamps 2018; Thompson and Cant 2018, see Table 1 for examples in mammals). Indeed, different neighbor-stranger behavioral responses could be displayed such as the dear enemy phenomenon (the most studied hypothesis), the nasty neighbor effect, but also the apparent absence of differential neighbor-stranger responses (Fisher 1954; Müller and Manser 2007; Christensen and Radford 2018). In the yellow-bellied marmot, a social species closely-related to the Alpine marmot, no difference was found between the time dominant females spent marking anal gland scents from stranger and neighbor females, indicating the absence of the dear enemy phenomenon also in this species (Cross et al. 2013, Table 1).

Social status as a confounding factor?

The absence of dear enemy phenomenon in our population could be explained by the fact that in Alpine marmots, only subordinates, which potentially are in search of a territory, could be threatening while dominant individuals never change territory and thus represent no threat, and this independently of being neighbors or strangers. Even though subordinate and dominant individuals pose different levels of threat, we did not observe any difference of behaviors in response to male subordinates' and dominants' scents. Although the analysis comparing behaviors towards the scents of subordinate and dominant individuals has a limited statistical power, the direction of the effect seems contrary to that expected in dominant males, as the majority of males tend to react more strongly to the scents of dominants than those of subordinate individuals. Previous studies on other species did evidence a difference in behavior towards individuals with different social status with comparable sample size (Table 1). In group-living species, the level of threat posed by an intruder is likely to depend on other characteristics of the intruders and the social status of an intruder should highly drive owners interests and motivations (Rosell et al. 2008). For instance, in Eurasian beavers, Tinnesand et al. (2013) found that dominant residents spend more time smelling anal gland scents from subordinate than dominant strangers. In Alpine marmots, dispersing subordinates play an all-or-nothing tactic. Indeed, sexually mature subordinates (two years and older) either reach dominance or die by dispersing during the active season, but never become subordinates in a new family group. Subordinate and dominant strangers thus clearly represent different levels of threat to a dominant individual's tenure in marmots although no difference in behavioral responses was evidenced.

Discrimination of intruders

Previous studies in social species (including Alpine marmots, Zidat et al. 2018) confirm that discrimination of neighbors *vs.* strangers is likely to occur. In social species, discrimination between own-group members (no threat) and other individuals (potential threat) through scent has been largely reported (Radford 2005; Christensen et al. 2016). If individuals learn how to discriminate their own-group members from out-group members based on their scents, it is conceivable that neighbor and stranger scents could also be discriminated. Individuals are repeatedly exposed to neighbor scents and may therefore remember neighbors identities and then discriminate unknown (stranger) individuals by contrast (Gheusi et al. 1997; Johnston and Bullock 2001). Such discrimination has even been hypothesized to be enhanced in species with stable territories and repeated encounters with neighbors (Stoddard et al. 1990; Rosell and Bjørkøyli 2002) such as in Alpine marmots.

Chemical composition of orbital gland secretions of both dominant and subordinate males differed, suggesting the orbital gland secretions can potentially inform Alpine marmots about the males' social status. Therefore, the absence of behavioral differences in response to subordinate and dominant orbital gland scents is not caused by a lack of chemical composition difference between subordinate and dominant individuals scents. Such chemical signature of social status is common in mammals' odorant secretions (e.g. Burgener et al. 2009; Setchell et al. 2010; Tinnesand et al. 2013). Although in our data social status may be confounded with age (because the majority of subordinate individuals were two-years old, whereas all dominant individuals were 3 years or older), Zidat et al. (2018) found that differences in chemical composition according to the social status persist within a given age class (three-years old) in Alpine marmots. Furthermore, regardless of whether the observed variation in chemical composition reflects the social status or an age effect, the same behavioral response is to be expected since two-years old individuals are the most likely to be in search of a territory.

Dominant males and females behave differently

Interestingly, although we did not evidence the dear enemy phenomenon, sex differences were detected. In agreement with this result, a review of rodents showed that receiver's responses differ when they encounter scent marks from different conspecifics and thus, receiver's responses are not fixed, but are flexible and context-dependent (Ferkin 2015). While establishing and reassuring their dominance could be the primary motivation of scent behavior in male Alpine marmots, mate choice could also be at stake for females. Although Alpine marmots are socially monogamous, extra-pair paternity occurs in this species, a behavior only displayed by dominant females (Cohas et al. 2006, Ferrandiz-Rovira et al. 2016). By counter-marking dominant stranger scents, dominant females could signal their presence to unfamiliar individuals and increase their mating opportunities according to the mate attraction hypothesis (Ferkin and Pierce 2007).

Such context-dependence linked to scent behaviour could also explain that, despite no difference in the response depending on the social status of the scent donor, opposite tendences between sexes were detected: females showed more interest towards the scents of subordinate stranger individuals than dominant stranger individuals while males showed the opposite behavior. To our knowledge, the only study that has investigated the responses towards subordinate and dominant male scents in mammals showed no sex differences in Eurasian beavers (Tinnesand et al. 2013).

The whole social group is threatened by any intrusion

The absence of behavioral adjustment by dominant males and females to the fact that an intruder shares a territory boundary or not or to the social status of the intruders - despite a social status signature in orbital gland secretions, suggests that intruders may all represent similar perceived threats in Alpine marmots. In this species, no conspecific intruders seem admitted to enter in foreign territories. This is in agreement with the observation that interactions between dominant marmots and marmots from different family groups are rare and always agonistic, regardless of the intruder’s status (Perrin et al. 1993b). In group-living species, the threat posed by an intruder (any individual from outside the social group, regardless of being neighbor, stranger, dominant or subordinate) should be understood not only as a threat to the dominant pair, but also as a risk for all the members of the group (e.g. group dynamics, reproductive success, fitness). An intrusion by a male, as simulated in our behavioral experiments, often results in the eviction and the death of the dominant resident male (Lardy et al. 2011). But, a take-over by a male can also involve the infanticide of the pups and of yearling males (Lardy et al. 2011; Lardy et al. 2015) and force dispersal of male subordinates (Dupont 2017) and thus strongly decreases the dominant female's reproductive success. Therefore, any intruder, whatever its identity, might represent an important threat in Alpine marmots, and not only to dominant individuals' tenure. Moreover, although rare, dominant individuals have been observed killing their neighbors' pups. Such threats could explain why dominant female Alpine marmots show similar response to any dominant or subordinate male intruder scent in our experiments, despite their own tenure not being at stake.

These threats could have been further strengthened by the location of the presented scent. Indeed, we placed the trial at the center of the territory and not at the border in order to maximize the chances to get a successful trial (*i.e.* individuals spend more time around the main burrow situated at the center of the territory). The placement of the stimulus outside, at the border or in the center of the territory may modify the territory owners' behaviors (McGregor and Bee 2018; Radford and Christensen 2018; Stamps 2018, but see Tinnesand et al. 2015). For example, in the green woodhoopoe (*Phoeniculus purpureus*), individuals responded faster when encountered their neighbors in unexpected areas of the territory (Radford 2005). Although dominant Alpine marmots mark their main burrows in addition to the territory boundaries (Bel et al. 1995; Lenti Boero 1995), the central position of the experiment may have strengthened the level of the perceived threat. Indeed, if an intruder reaches the center of the territory not only a risk of territory lost is present but there is a high risk of serious attack (*e.g.* infanticide). The location of the experimental set-up at the center of territories may thus have caused or reinforced the idea that no conspecific intruders are admitted. Another possible confounding factor that we avoided taking into account for lack of sample size is that we performed all our behavioral experiments before the emergence of the pups. Thus, we suggest the necessity to perform further behavioral experiments in our study system at different distances from the main burrow (including at territory boundaries) and both in periods with and without emerged pups to better understand how these factors can influence territorial behavior in Alpine marmots.

CONCLUSION

Territorial behaviors in group living species are far from being stereotyped. Although a higher intensity of the responses towards strangers and subordinates than towards neighbors and dominant individuals respectively has been repeatedly predicted, species responses show a high variation (Table 1). Our results suggest that, in Alpine marmots, no outsider should enter into a given territory regardless of whether it shares a territory boundary or not (*i.e.* neighbor or stranger) or its social status.

The present study follows the Christensen and Radford (2018)'s call for empirical research considering a more holistic approach of the evolution and maintenance of territoriality. Our study emphasizes the necessity to step away from the simplistic dichotomy between neighbors and strangers to move towards a more comprehensive, multifactorial, nature of territory defense through the consideration of various characteristics of territory owners (e.g. sex, body condition) and social groups (e.g. size, sex and age composition), the characteristics of an intruder (e.g. sex, social status, familiarity), the characteristics of the intrusion (e.g. location, timing) and of the impact of these different characteristics on the perceived threat.

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FIGURE LEGENDS

Figure 1. The two-way choice experimental set-up (a) and a dominant male with a light green plastic tag on the right ear (indicating its social status and sex) involved in a trial (b)

Figure 2. Violin plots of (a) the difference in smelling time (Δ smelling time), (b) the difference in marking time (Δ marking time), and (c) the difference in the number of marks (Δ marks) by female (red) and male (yellow) dominant Alpine marmots for the three dear enemy experimental settings ('stranger *vs.* control' (SC), 'neighbor *vs.* control' (NC) and 'stranger *vs.* neighbor' (SN)). The Δ was calculated between the tube that we hypothesized marmots would show more interest towards and the other tube (stranger, control and stranger for each of the three experimental settings respectiveley). The black dots represent the observed data and the white dots represent the estimated parameters.

Figure 3. Violin plots of (a) the difference in smelling time (Δ smelling time), (b) the difference in marking time (Δ marking time), and (c) the difference in the number of marks (Δ marks) by female (red) and male (yellow) dominant Alpine marmots in the 'subordinate *vs.* dominant' (SD) experimental setting. The Δ was calculated between the tube that we hypothesized marmots would show more interest (S) towards and the other tube (D). The black dots represent the observed data and the white dots represent the estimated parameters.

Figure 4. Violin plots of the score on the 1st axis of the linear discriminant analysis based on the 11 chemical compounds contributing the most to secretions discrimination (see Materials and Methods for details on identification of these compounds) for dominant and subordinate individuals. Black symbols indicate observed values classified according to their social status, red symbols indicate observed values misclassified. Triangle, square and cross symbols represent observed values for the six individuals sampled as subordinate in 2016 and as dominant in 2017. From these six individuals, the square represents the individual misclassified as a subordinate when it was dominant and the cross represents the individual misclassified as dominant when it was subordinate.

TABLES AND TABLE LEGENDS

Table 1. Empirical studies investigating the dear enemy phenomenon using scents in mammals with different sociality levels and testing for additional discrimination and chemical signature of the scents.

a References for the sociality levels: **1.** Allainé, 2000; **2.** Blumstein, Im, Nicodemus, and Zugmeyer, 2004; **3.** Lukas and Clutton-Brock, 2012; **4.** Zenuto, 2010**; 5.** King, 1989; **6.** Isler and van Schaik, 2012.

b Number of trials with an actual response involving signs of interests (e.g. sniffing) and of response intensity (e.g. overmarking) respectively, or total number of trials with an actual response when the distinction is not specified.

c Test of the "dear enemy phenomenon" (stranger *vs.* neighbor). **YES** = higher interest towards the stranger's scent, **NO** = no significant difference in the interest towards the stranger's and neighbor's scents (no differences), or higher interest towards the neighbor's scent ("nasty neighbor phenomenon"). The measured signs of interest most generally involve scent sniffing.

d Test of the "dear enemy phenomenon" (stranger *vs.* neighbor). **YES** = higher response intensity towards the stranger's scent, **NO** = no significant difference in response intensity towards the stranger's and neighbor's scents (no differences), or higher response intensity towards the neighbor's scent ("nasty neighbor phenomenon"). The measured signs of response intensity most generally involve scent overmarking, but could also involve scraping, vocalization, etc. in some cases.

e Test of additional discrimination of the scents. **YES** = differences in interest and/or response intensity response towards the scents, **NO** = no significant difference in interest and/ or response intensity towards the scents.

Scientific name	Sociality[a]	Scent source	Dear enemy phenomenon			Additional discrimination			Chemical signature	References
			N[b]	Interest[c]	Aggressivness[d]	N[b]	Test	Response[e]		
Rodentia										
Marmota marmota	Cooperative breeder[1]	Orbital gland	127 / 86	NO (no differences)	NO (no differences)	16 / 11	Dominant *vs.* subordinate	NO / NO	YES	*This study*
Marmota monax	Solitary[1]	Buccal gland	32	YES	NO	-	-	-	-	Meier 1991
		Buccal gland	-	-	-	19	Future social status	YES	-	Hébert and Barrette 1989
Marmota flaviventris	Matrilines[2]	Anal gland	15 / 1	NO (no differences)	NA	-	-	-	-	Cross et al. 2013
Castor canadensis	Cooperative breeder[3]	Castoreum	97 / 49	YES	YES	-	-	-	-	Schulte 1998
		Castoreum	-	-	-	13	Adult *vs.* subadult	NO	-	Herr et al. 2006
Castor fiber	Cooperative breeder[3]	Castoreum and anal gland	38 / 35	YES	YES	-	-	-	-	Rosell and Bjørkøyli 2002
		Anal gland	-	-	-	22 / 19	Dominant *vs.* subordinate	YES	YES	Tinnesand et al. 2013
Ctenomys talarum	Solitary[4]	Urine and faeces	90 / 45	YES	YES	-	-	-	-	Zenuto 2010
Urocitellus columbianus	Matrilines[5]	Oral gland	88 / 53	YES	YES	-	-	-	-	Harris and Murie 1982
		Oral gland	48	YES	NO (no differences)	26	Kin *vs.* non-kin	YES	-	Raynaud and Dobson 2011
Carnivora										
Meles meles	Communal breeder[3]	Faeces	93 / 8	YES	NA	-	-	-	-	Palphramand and White 2007
		Anal gland	197 / 141	YES	YES	351	Sex and age	YES	-	Tinnesand et al. 2015
		Anal gland	-	-	-	-	-	-	YES	Buesching and Jordan 2018
Mungos mungo	Communal breeder[3]	Urine and faeces	142 / 70	NO (nasty neighbor)	NO (nasty neighbor)	-	-	-	-	Müller and Manser 2007
Helogale parvula	Cooperative breeder[3]	Faeces	13	NO (no differences)	NO (no differences)	-	-	-	-	Christensen et al. 2016
Lagomorpha										

Oryctolagus cuniculus	Plural breeder[6]	Faeces	152	-	YES	-	-	-	-	Monclús et al. 2014

Table 2. Estimates of the model testing the interaction between the experimental settings and the sex of the focal individual (a) on the difference in smelling time in s (Δ smelling time), (b) on the difference in marking time in s (Δ marking time) and (c) on the difference in the number of marks (Δ marks) for the dear enemy experimental setting. N: number of trials; Mean: estimate of the posterior mean; SD: estimate of the posterior Standard Deviation; CI: Credible Interval; SC: 'stranger vs. control' experimental setting; NC: 'neighbor vs. control' experimental setting; SN: 'stranger vs. neighbor' experimental setting. Evidenced differences in parameters are indicated in bold. The Δ was calculated between the tube that we hypothesized marmots would show more interest towards and the other tube.

Model	Experimental setting	Parameter	N	Mean(Δ)	SD(Δ)	95% CI
(a) Δ smelling time	SC	Female	18	6.33	3.46	-0.48 ; 13.13
		Male	35	**10.56**	**2.58**	**5.44 ; 15.60**
	NC	Female	15	2.08	3.83	-4.42 ; 9.66
		Male	18	**8.00**	**3.47**	**1.17 ; 14.79**
	SN	Female	18	-0.18	3.46	-6.97 ; 6.63
		Male	23	-2.56	3.09	-8.63 ; 3.51
(b) Δ marking time	SC	Female	18	**1.53**	**0.57**	**0.41 ; 2.64**
		Male	35	0.12	0.44	-0.76 ; 0.98
	NC	Female	15	0.77	0.63	-0.47 ; 2.02
		Male	18	0.12	0.56	-0.98 ; 1.23
	SN	Female	18	0.44	0.58	-0.69 ; 1.59
		Male	23	-0.16	0.51	-1.17 ; 0.84
(c) Δ marks	SC	Female	18	**1.26**	**0.56**	**0.24 ; 2.41**
		Male	35	0.18	0.36	-0.50 ; 0.92
	NC	Female	15	0.65	0.58	-0.40 ; 1.84
		Male	18	0.66	0.52	-0.31 ; 1.74
	SN	Female	18	0.14	0.49	-0.77 ; 1.17

	Male	23	-0.09	0.43	-0.88 ; 0.78